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Influences du climat sur la démographie des passereaux communs

Mesure à grande échelle spatiale, variabilité interspécifique et prise en compte dans les prédictions biogéographiques sous scénario climatique

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Résumé

Les conséquences du changement climatique actuel sur les populations d'oiseaux ont fait l'objet de nombreux travaux au cours des deux dernières décennies. Ces études ont mis en évidence les principaux mécanismes de l'influence climatique sur les étapes du cycle de vie aviaire. Au cours de la thèse, nous avons tenté de proposer une vision intégrée de ces mécanismes et d'en explorer la variabilité interspécifique. Pour cela, nous avons utilisé les données du Suivi Temporel des Oiseaux Communs (STOC). Nous avons développé des outils d'analyse de la phénologie et de la survie à l'échelle des populations françaises. Nous avons ensuite exploré les liens qui relient l'ajustement phénologique aux conditions climatiques printanières et le taux de croissance à long terme des populations de passereaux communs et étudié la variabilité interspécifique de cet ajustement en examinant les corrélations avec les traits d'histoire de vie et les caractéristiques de la niche écologique des espèces. Nous trouvons que les espèces qui ajustent le mieux leur phénologie de reproduction à la température printanière possèdent les taux de croissance à long terme les plus élevés. La capacité d'ajustement phénologique est négativement corrélée à la distance migration et au degré de spécialisation écologique des espèces alors qu'elle est positivement corrélée à la taille de leur cerveau. Nous nous sommes enfin intéressés à la sensibilité des populations au climat le long de l'aire de distribution afin de mieux comprendre les changements observés et attendus des aires de distributions chez les oiseaux et d'améliorer la qualité des prédictions de distributions futures sous scénario climatique.

Title : Climatic influences on common passerine demography. Large spatial scale analysis, interspecific variability and improvements of biogeographical predictions under climatic scenarios.

Abstract

The consequences of the ongoing climatic change on bird populations have been intensively studied during the past two decades. The most important mechanisms underlying climate influence on the different stages of bird's lifecycle have been highlighted. During the PhD, we tried to integrate all these mechanisms at the scale of the lifecycle and explore the interspecific variability of the responses. To achieve this, we used the data of the Common Bird Temporal Monitoring Scheme (STOC). We first developed statistical tools to estimate phenological variations and survival rates for the French breeding populations. We then investigated the relation between the adjustment of the breeding phenology to spring climatic conditions and species long term population growth rates before attempting to relate the interspecific variability of the phenological adjustment capacities to species life history traits and ecological niche features. We found that species with the highest phenological adjustment capacities had higher long term population growth rates. The phenological adjustment capacity was negatively correlated to species migration distance and degree of ecological specialization, while it was positively correlated to their brain size. Eventually, we studied the variations of the sensitivity of demography to climate along the distribution in order to better understand the current observed and future expected distribution range shifts and improve the quality of species distribution models output predictions under climatic scenarios.

Mots-clés : changement climatique, phénologie, oiseau, démographie, survie, niche écologique, spécialisation, biodiversité, migration.

Keywords: climate change, phenology, bird, demography, survival, ecological niche, specialization, biodiversity, migration.

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Introduction générale

Nous allons, pour commencer, décrire le contexte scientifique dans lequel j'ai effectué les travaux de ma thèse. Nous établirons dans un premier temps le rôle fondamental du climat sur l'évolution de la biosphère, avant de caractériser la perturbation climatique actuelle, ce qui permettra d'en distinguer les propriétés hors norme. Ceci nous conduira à nous interroger sur les réponses écosystémiques observées et attendues à ce changement inédit et débouchera sur la mise en place du cadre de travail et des objectifs de cette thèse.

1. La biosphère sous influence climatique : retour sur le passé.

Le climat regroupe un ensemble de paramètres physicochimiques dont le rôle sur l'apparition, la composition et l'évolution de la biosphère est fondamental. Un regard par-dessus notre épaule, en direction du passé, nous fournit de nombreux exemples du rôle prépondérant de l'un de ces paramètres, la température, dans l'histoire de la Vie (Clarke 1996). Ainsi l'importante radiation évolutive à laquelle on assiste à l'étage du cambrien, c'est-à-dire il y a 550 millions d'années, donc au tout début de l'ère primaire, se déroule pendant un épisode marqué par l'augmentation de la température moyenne à la surface du globe, dans un contexte géologique propice, faisant intervenir une tectonique extensive et un apport d'éléments minéraux lié à l'érosion des chaînes montagneuses protérozoïques (Marshall 2006). Les principaux phylums qui dessinent l'arbre du vivant que nous connaissons actuellement sont nés ou ont probablement proliféré à partir de ces conditions climatiques et géologiques favorables. Depuis cet évènement fondateur pour notre biosphère, plusieurs « accidents » ou crises biologiques ont jalonné le parcours de la Vie (Hubbard & Gilinsky 1992). Pour chacun d'entre eux, le climat est supposé avoir joué un rôle direct ou indirect dans les extinctions massives qui marquent de façon caractéristique ces épisodes de l'histoire de notre planète (Donovan 1989; Carey 2009). Pour ne citer que la plus médiatisée de ces paléocrises biologiques, la crise qui se produisit à la limite entre le Crétacé et le Paléocène, il y a environ 65 millions d'années, et qui aboutit entre autres à la disparition des dinosaures, serait liée aux actions conjointes de deux phénomènes. Le premier serait un impact météoritique de grande ampleur, au niveau du Mexique actuel, et le second, un épisode de volcanisme intense, dans le Deccan de l'Inde actuelle (Keller 2005, 2008). Ces deux phénomènes se seraient traduits par d'importantes variations de température et de luminosité qui auraient à leur tour modifié considérablement la productivité primaire des écosystèmes conduisant à des cascades d'extinctions en chaînes. Plus proche de nous, il y a quelques « années géologiques », la succession d'évènements glaciaires et interglaciaires durant l'ère quaternaire a considérablement remodelé les communautés biologiques et les écosystèmes (Comes & Kadereit 1998). Le changement climatique périodique qui marque cette période est lié aux paramètres de rotation de la Terre décrits par les cycles de Milankovitch. Ces variations climatiques se sont traduites par un enchaînement d'épisodes froids, dits glaciaires, pendant lesquels la température globale moyenne se situe quelques degrés en dessous de son niveau moyen sur quelques centaines de milliers d'années, et d'épisodes chauds, dits interglaciaires, pendant lesquels la température moyenne se situe quelques degrés au dessus de son niveau moyen (IPCC 2007). Nous disposons, pour étudier ces variations climatiques et leurs conséquences, de véritables thermomètres dans les carottes glaciaires extraites des calottes de glace des deux pôles. Les températures déduites de ces enregistrements par des méthodes indirectes faisant intervenir les rapports isotopiques des petites bulles d'air atmosphériques piégées lors de la formation de la glace, nous permettent de dater précisément ces épisodes anormalement chaud et froids. Les réponses de la biosphère à cet ensemble de conditions climatiques ont-elles aussi été conservées dans les archives sédimentaires. Ainsi les études palynologiques, c'est-à-dire l'analyse des pollens fossilisés dans les sédiments, nous montrent que la distribution géographique des espèces d'arbres de nos régions tempérées a considérablement varié en fonction de la période (glaciaire ou interglaciaire) considérée (Bennett et al. 1991). Il en a été de même pour les animaux, comme le prouvent les fossiles de ces différentes époques. On constate par conséquent que la variation climatique est une règle plutôt qu'une exception au cours des temps géologiques et que chaque variation a inévitablement conduit à des restructurations de la biosphère. Ce constat conduit donc à se demander en quoi les variations climatiques très récentes se distinguent de ce que la biosphère a connu et subi par le passé.

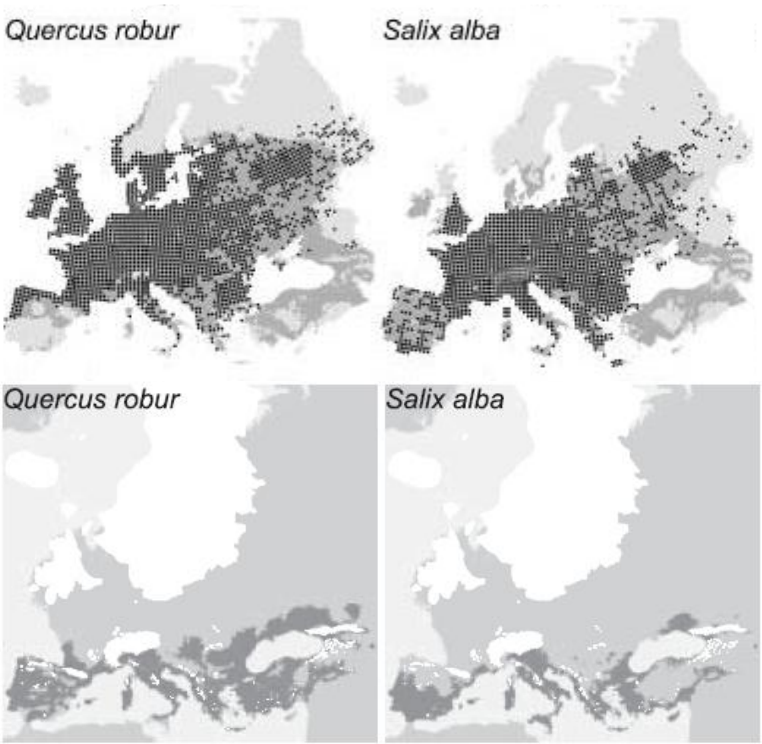


Figure 1. Modélisation de l'aire de distribution actuelle (en haut) et à l'époque du dernier maximum glaciaire (il y a 21000 ans, en bas) de deux espèces d'arbres, le Chêne pédonculé (*Quercus robur*) et le Saule blanc (*Salix alba*). Le figuré blanc, sur les cartes correspondant au dernier maximum glaciaire, représente l'extension des calottes glaciaires. Ces résultats de modélisation concordent avec les données palynologiques. Figure extraite de Svenning et al. (2008).

2. Le changement climatique actuel : un épisode hors norme à l'échelle des temps géologiques récents.

Le climat connaît actuellement d'importants changements. Avant de m'intéresser aux conséquences biologiques que peuvent occasionner ces bouleversements, il convient en premier lieu de bien caractériser ces variations afin tout d'abord, de montrer leur caractère exceptionnel dans l'histoire géologique récente. Cela permettra de comprendre tout l'intérêt de l'étude de ses conséquences potentielles sur la biodiversité. Par ailleurs, faire un état des lieux du changement et des prédictions concernant ces changements permet de quantifier l'intensité de la perturbation imposée aux systèmes biologiques.

C'est une fois de plus grâce aux archives géologiques que le changement climatique actuel prend tout son sens. Le Groupe Intergouvernemental d'Etude sur le Climat (GIEC) dans son dernier rapport (2007) compare le changement climatique actuel à plusieurs évènements de réchauffement passés. Le pliocène (3 Ma) a connu des températures globales moyennes de 2 à 3 degrés Celsius (°C) supérieures aux températures pré-industrielles (Jiang et al. 2005) et dans une configuration continentale très similaire à la disposition actuelle. Les analyses isotopiques montrent que le réchauffement fut plus important aux hautes latitudes qu'au niveau des tropiques (Chandler et al. 1994; Haywood et al. 2000). Il semble donc que les milieux tempérés soient relativement plus sensibles aux modifications climatiques que les milieux se trouvant en zone intertropicale. Cet évènement est également marqué par une concentration atmosphérique en dioxyde de carbone (CO_2) élevée (Raymo et al. 1996). On retrouve ce couplage entre concentration atmosphérique de CO_2 et températures moyennes globales au cours des 650 000 dernières années comme en témoignent les enregistrements isotopiques des carottes glaciaires (Monnin et al. 2001). Au cours de cette période récente, les évènements de glaciations et de déglaciations se sont succédé. A chaque maximum glaciaire, la concentration en CO_2 atmosphérique a augmenté et un réchauffement s'est opéré donnant lieu à un épisode interglaciaire (Monnin *et al.* 2001; Caillon *et al.* 2003). Cependant, l'augmentation actuelle de la concentration de CO_2 et le réchauffement auquel on assiste depuis la seconde moitié du $20^{ème}$ siècle ne se produisent pas en contexte glaciaire mais en contexte interglaciaire, ce qui est inédit dans les archives climatiques depuis les 650 derniers milliers d'années (IPCC 2007). Il ne fait maintenant plus aucun doute que les activités humaines et notamment le rejet dans l'atmosphère de gaz à effet de serre sont les responsables du changement climatique que nous connaissons (IPCC 2007). En premier lieu, la raison majeure d'essayer de comprendre les conséquences possibles de ce brusque changement climatique est qu'il rompt complètement avec la cyclicité naturelle connue jusqu'à maintenant. Par conséquent les réponses biologiques à ce réchauffement pourraient elles aussi être tout à fait inédites.

En second lieu, le caractère hors norme de la tendance climatique actuelle ne se trouve pas seulement dans le fait que l'augmentation de températures se produit pendant une période déjà relativement chaude, mais également dans la vitesse à laquelle cette augmentation se produit. Ainsi, au cours des successions d'épisodes glaciaires et interglaciaires du dernier million d'années, la température moyenne globale a varié de 4°C à 7°C en relation avec des variations de la concentration en CO_2 atmosphérique de 180 à 300 parties par million (ppm). Les données montrent que ces changements se sont déroulés sur des périodes d'environ 5000 ans (IPCC 2007). Au cours du siècle passé, la température a augmenté d'environ 0.7°C en moyenne globale (Smith & Reynolds 2005; Brohan *et al.* 2006). Par conséquent la vitesse de variation de la température est de l'ordre de 5 fois supérieure à ce qui était connu (**figure 2**).

Enfin, la dernière particularité des bouleversements climatiques est qu'il est maintenant quasi certain que l'homme, par ses activités, en est la cause principale. Cette cause identifiée lui permet d'une part d'avoir une influence sur cette tendance au travers de mesures prises pour la limiter, mais aussi de mieux prédire l'avenir de cette variation en tenant compte des scénarios de son propre développement.

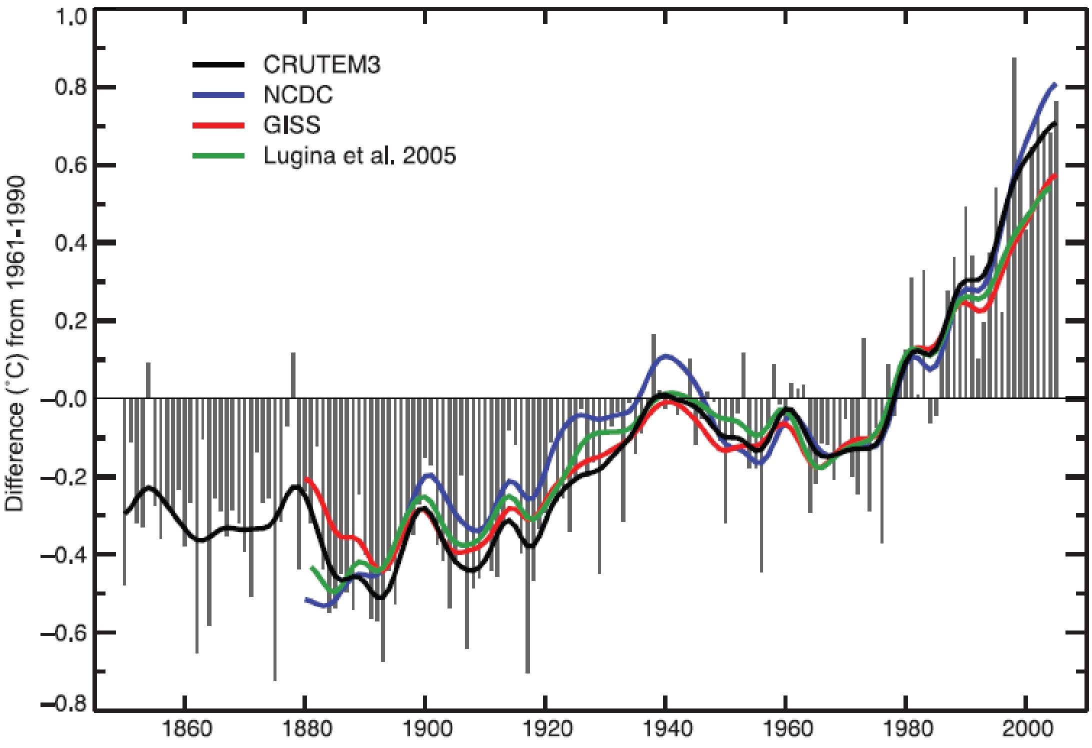


Figure 2. Anomalies de températures par rapport à la moyenne de la période 1961-1990 entre 1850 et 2006 (barres verticales grises). Les courbes représentent les moyennes lissées sur des périodes de 10 ans et selon différents jeux de données. On peut noter l'accélération marquée du réchauffement au cours de la période 1980-actuel. Figure extraite du 4$^{\text{ème}}$ rapport du GIEC (IPCC 2007).

Les prédictions concernant l'évolution de la température moyenne globale ou régionale entrevoient une augmentation de 2.3 à 5.3 °C d'ici 2080, ce qui constitue une accélération du réchauffement par rapport au siècle dernier (IPCC 2007). En Europe, le GIEC distingue deux évolutions régionales distinctes pour l'Europe du Nord et le Bassin Méditerranéen (**figure 3**). En Europe du Nord, ce sont essentiellement les températures hivernales qui seront en augmentation alors que le pourtour méditerranéen devrait connaître des étés plus chauds. La variabilité associée à ces changements climatiques devrait aussi augmenter mais de façon hétérogène (Schar *et al.* 2004; Giorgi & Bi 2005). Ainsi, la variance du climat sur le sud de l'Europe devrait être plus élevée que dans le nord. On voit donc l'ampleur des changements à venir au regard de évènements passés, ce qui pose bien entendu la question des conséquences de ces changements sur le fonctionnement des écosystèmes résultant notamment des multiples interactions entre les espèces qui constituent ces systèmes extraordinairement complexes.

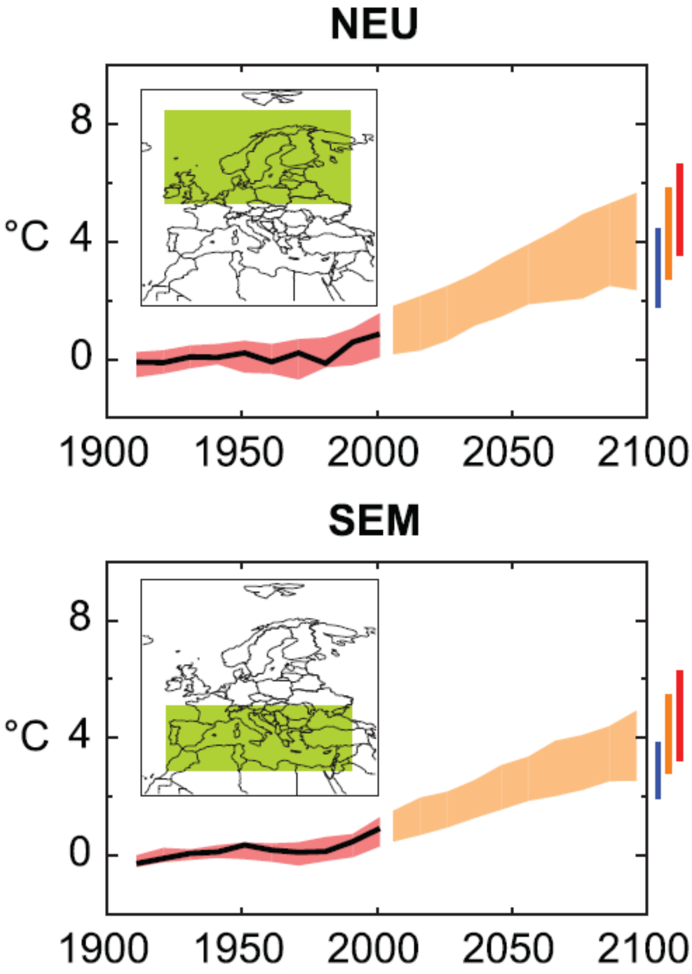


Figure 3. Prévisions concernant la hausse des températures au cours du 21ème siècle pour le nord de l'Europe (NEU) et le bassin Méditerranéen (SEM). La courbe noire représente les anomalies de température par rapport à la moyenne 1901-1950 pour la période 1906-2005. L'enveloppe rouge représente les anomalies calculées par simulations. L'enveloppe orange représente les anomalies de température estimées selon un scénario A1B (Population mondiale décroissante à partir de 2050, croissance économique rapide avec réduction des inégalités régionales et sources d'énergies équilibrées entre énergies fossiles et non fossiles). Les barres bleue, orange et rouge représentent l'enveloppe des anomalies de température pour 2100 respectivement selon les scénarios B1 (Population mondiale croissante jusqu'en 2050, croissance économique rapide et utilisation de technologies écologiquement propres, recherche de solutions globales aux problèmes d'inégalités régionales), A1B et A2 (population mondiale continument croissante, persistance d'inégalités régionales et recherche systématique de solutions locales). Figure extraite du 4ème rapport du GIEC (IPCC 2007).

3. Les conséquences biologiques du réchauffement climatique : des prédictions aux faits.

Cette dépendance étroite entre conditions environnementales (climatiques entre autres) et possibilité pour une espèce ou un assemblage d'espèces de se maintenir en un endroit donné est théorisé par le concept de niche écologique tel qu'il est défini par Hutchinson (Hutchinson 1957). L'hypervolume à N dimensions, dont chacune des dimensions correspond aux différentes valeurs prises par une variable environnementale, regroupe l'ensemble des combinaisons physico-chimiques autorisant la persistance d'une espèce en un endroit donné. La température, la quantité de précipitations et d'autres variables caractérisant le climat, font partie des dimensions élémentaires de la niche écologique ainsi définie. Ce cadre théorique élargi depuis pour tenir compte des interactions interspécifiques (Case & Gilpin 1974; Bruno *et al.* 2003) rend donc bien compte des observations actuelles et passées concernant la distribution et l'abondance des espèces comme fonction du contexte climatique. En effet les conditions climatiques ne cessent de changer au cours de l'histoire de la vie, ce qui fait varier la projection de la niche écologique (climatique en l'occurrence) de chaque espèce à la surface du globe. Par conséquent, chercher à comprendre les mécanismes régissant le forçage climatique sur la distribution et l'évolution des espèces, donc le devenir de la biodiversité, passe nécessairement par l'observation et la quantification des processus élémentaires de réponse à court terme à petite ou moyenne échelle. En d'autres termes, si l'on impose une quantité définie de variation d'un paramètre comme la température à un écosystème ou à une population, de combien varie le comportement de ce système ou de cette population, quelle est sa quantité de réponse ?

Les premières mises en évidences des conséquences biologiques du réchauffement climatique datent du milieu des années 1990 (Jarvinen 1994; Crick *et al.* 1997; Parmesan *et al.* 1999; Parmesan *et al.* 2000; Walther *et al.* 2002; Parmesan & Yohe 2003). En 2000 Hughes dresse un état des lieux des conséquences prédictibles du réchauffement climatique d'origine anthropique sur les systèmes biologiques (Hughes 2000). Dans son article, il propose un classement des conséquences possibles en quatre catégories principales.

- Tout d'abord, des conséquences directes de la hausse des températures et de l'augmentation de la concentration de CO_2 atmosphérique au travers la physiologie des organismes. Cette action directe est à mettre en relation avec la dépendance directe de certains processus métaboliques comme la photosynthèse, la respiration et la croissance vis-à-vis de la température. Ainsi, il prédit que certaines espèces pourraient disparaître du fait de stress physiologiques directement induits par les variations de température ou de composition atmosphérique.
- La deuxième catégorie de conséquences proposée par Hughes comprend les changements de distributions géographiques. Du fait de l'importance de la

température dans la définition de la niche écologique des espèces, on s'attend à observer une contraction vers le nord des aires de distribution des espèces plutôt septentrionales et une extension vers le nord des aires de distributions des espèces d'affinités méridionales. Cette prédiction s'applique à l'identique pour la distribution altitudinale des espèces.

- Troisième type de changement biologique prédit par l'augmentation des températures : des modifications d'ordre phénologique. La phénologie est la science qui s'intéresse au positionnement dans le temps des différentes étapes des cycles de vie (Morisette et al. 2009). La dépendance climatique de la chronologie des cycles de vie étant forte (Carey 2009), on peut donc attendre que des variations climatiques soient à l'origine d'importantes modifications dans les rythmes annuels des êtres vivants.
- Le dernier type de changement prédit est lié à l'adaptation des espèces à leurs nouvelles conditions environnementales due à des processus microévolutifs se déroulant sous de nouvelles contraintes imposées par ces conditions.

Les prédictions faites par Hughes sur la base de quelques frémissements des écosystèmes perceptibles à l'époque se sont avérées exactes pour toutes les catégories de changements. En effet, un très grand nombre d'exemples sont venus étayer les différentes catégories de conséquences envisageables du réchauffement climatique. Ainsi, les récifs coralliens qui subissent un blanchiment très certainement lié à l'augmentation des températures à la surface de la mer qui modifient les équilibres de dissolution des carbonates et se traduisent par une acidification des océans, témoignent de stress physiologiques induits par la hausse des températures (Hoegh-Guldberg et al. 2007). La remontée vers le Nord des aires de distributions de nombreuses espèces de rhopalocères sur les îles britanniques (Parmesan et al. 1999; Warren et al. 2001) ainsi que celles de nombreuses espèces d'oiseaux sur les continents américain (Hitch & Leberg 2007) et européen (Devictor et al. 2008) témoignent de modifications biogéographiques importantes également liées au réchauffement climatique. De nombreuses études ont par ailleurs mis en évidence des modifications de la phénologie des plantes (Badeck et al. 2004; Cleland et al. 2007) et des animaux (Wuethrich 2000; Walther *et al.* 2002). Parmi les phénomènes les plus étudiés figurent le débourrement des bourgeons au printemps (Wielgolaski 1999; Korner & Basler 2010), les dates de floraison (Menzel et al. 2006), mais aussi les dates d'émergence des insectes (van Asch & Visser 2007), de retour migratoire chez les oiseaux (Cotton 2003; Sparks *et al.* 2005; Gordo 2007) et leur dates de reproduction (Both et al. 2004; Visser et al. 2009a). Enfin depuis quelques années, des travaux commencent à apporter la preuve que le changement climatique exerce une pression environnementale qui se traduit par une sélection naturelle des organismes les plus adaptés à ces changements et ce à des échelles de temps relativement courtes de quelques décennies ou moins (Berthold *et al.* 1992; Pulido & Berthold 2004; Nussey *et al.* 2005; Rivalan *et al.* 2007; Charmantier *et al.* 2008).

4. Une vision intégrée des conséquences démographiques des changements climatiques : vers la définition des objectifs de la thèse.

Comme je l'évoque plus haut, les points d'action de l'anomalie climatique actuelle sur les organismes sont désormais bien identifiés à l'échelle de l'espèce. Cependant, si de nombreux exemples viennent renforcer les prédictions faites il y a une quinzaine d'années, une vision intégrée des mécanismes d'action du changement climatique à l'échelle d'un groupe taxonomique manque cruellement. Avant de proposer une explication à ce manque, qu'entends-je par vision intégrée de l'action du changement climatique sur un groupe ? La plupart des études sur les conséquences biologiques du changement climatique illustrent un mécanisme isolé sur un groupe taxonomique donné et concernent une partie du cycle de vie (Visser *et al.* 2003; Jonzen *et al.* 2006; Sparks *et al.* 2009; Visser *et al.* 2009a). Considérer l'ensemble des mécanismes d'influence du climat sur une espèce ou un groupe d'espèce n'a pas été envisagé jusqu'à présent. Si le développement de la modélisation intégrée des populations a permis de mettre en place les outils nécessaires à cette démarche, l'action de la phénologie sur la démographie n'a été associée qu'une fois à une étude intégrée des influences climatiques sur la démographie (Wright et al. 2009), et ce pour une espèce, l'Alouette lulu (*Lullula arborea*). Cette lacune ne permet pas de juger de la variabilité des influences climatiques entre différentes espèces, ce qui prive d'une vision à grande échelle de l'impact du réchauffement climatique. La revue de l'ensemble des mécanismes et des réponses trouvées sur des groupes différents permet de proposer une généralisation et un cadre théorique des mécanismes d'action du climat sur les communautés (Crick 2004; Moller *et al.* 2004; Jonzen *et al.* 2007). Néanmoins, il manque cruellement d'exemples où les mécanismes mis en évidence séparément chez différentes espèces sont considérés comme un ensemble d'hypothèses A PRIORI, que l'on teste sur un ensemble d'espèces d'un ou plusieurs groupes taxonomiques. Les raisons qui expliquent cette lacune scientifique sont bien entendu d'ordre pratique. Pour tester cet ensemble d'hypothèses, il faut disposer d'une part de données sur un grand nombre d'espèces représentatives du groupe taxonomique que l'on souhaite étudier. Il faut que la récolte de ces données ait débuté il y a assez longtemps pour que la variabilité climatique soit suffisante et permette de détecter les effets. Enfin, ces données, afin de permettre une généralisation des mécanismes, ne doivent pas uniquement concerner une ou quelques populations mais couvrir de larges échelles spatiales. Enfin, le dernier critère pour permettre la mise en œuvre d'une telle approche concerne le groupe taxonomique considéré.

4.1. *Les oiseaux : un groupe taxonomique d'intérêt majeur pour l'étude des conséquences du changement climatique sur la biodiversité.*

La grande complexité des systèmes biologiques ainsi que le grand nombre d'espèces concerné par les perturbations climatiques actuelles et à venir constituent un important problème dans l'étude des mécanismes d'impact du changement climatique. Face à l'impossibilité d'étudier le phénomène dans sa globalité, il faut se résoudre à choisir des modèles d'étude dont les réponses au climat puissent être représentatives de celles d'un grand nombre d'espèces que l'on ne peut considérer (Caro & O'Doherty 1999; Gregory *et al.* 2005; Gregory *et al.* 2008). Plusieurs auteurs ont tenté d'établir des critères qui permettent de juger de la qualité de ces espèces ou groupes taxonomiques indicateurs de l'impact des changements qui affectent les écosystèmes (Caro & O'Doherty 1999; Hilty & Merenlender 2000). Parmi ces critères figure la quantité d'informations disponibles sur les espèces choisies. A ce titre les oiseaux constituent l'un des groupes les mieux connus du point de vue biologique. Par ailleurs, ce groupe fait l'objet de suivis populationnels à grande échelle sur tous les continents, et ce depuis parfois plusieurs dizaines d'années (le « Common Birds Census » au Royaume Uni a été un protocole de suivi actif entre 1962 et 2000 et aux Etat Unis le « Breeding Bird Survey » est toujours en cours après avoir débuté en 1966). Quelques espèces ont par ailleurs fait l'objet de suivis intensifs dans des forêts expérimentales pourvues de centaines de nichoirs comme à Witham Wood près de l'université d'Oxford pour la Mésange charbonnière (*Parus major*) et à Harjavalta en Finlande pour le Gobemouche noir (*Ficedula hypoleuca*). Il s'agit également d'un groupe au sein duquel l'identification des espèces est relativement aisée et où le nombre d'espèces est plutôt faible comparé à d'autres groupes. Cette caractéristique facilite d'une part le développement de suivis participatifs et donc le développement de protocoles à large échelle spatiale, mais donne également aux résultats scientifiques issus de ces programmes une plus large portée dans la mesure où de nombreuses espèces communes sont connues de tous. Toutefois, les avantages de considérer les oiseaux comme indicateurs d'impact du réchauffement climatique ne se limitent pas à des questions d'ordre pratique. Au niveau des réseaux trophiques, la plupart des espèces communes se trouvent en position intermédiaire. En effet, de très nombreuses espèces d'oiseaux et notamment de passereaux (qui constituent la grande majorité des espèces qui seront étudiées dans la thèse) sont insectivores. En cela, elles intègrent les conséquences des perturbations de leur écosystème (climatique ou autres) sur les niveaux trophiques inférieurs (producteurs primaires et proies). Cette caractéristique les rend très utiles dans l'évaluation de la santé des écosystèmes. Par ailleurs, l'existence au sein de ce taxon d'espèces « spécialistes », c'est-à-dire à la niche écologique fondamentale réduite, mais très performantes dans l'exploitation de conditions environnementales à l'intérieure de cette niche fondamentale, est aussi un avantage majeur (Hilty & Merenlender 2000). En effet, dans un contexte de perturbation spatiale et temporelle des écosystèmes, la théorie de la niche écologique prédit un relatif succès des espèces dites « généralistes » c'est-à-dire possédant une niche écologique fondamentale plus large (Julliard *et al.* 2004a; Devictor *et al.* 2007; Clavel *et al.* in press). Ainsi, suivre le devenir des espèces spécialistes et généralistes au sein de ce groupe revient à mesurer l'intensité de l'impact du changement auquel il se trouve confronté. Le dernier point important concerne le temps de génération d'un grand nombre d'espèces d'oiseaux. Chez la plupart des espèces de passereaux, le temps de génération moyen est inférieur à 3 ans. Cette vitesse relative rend les populations plus sensibles aux changements (Hilty & Merenlender 2000). Ainsi, les oiseaux combinent l'avantage d'intégrer un certain nombre de réponses de niveau trophiques inférieurs tout en permettant à l'observateur de quantifier les effets des changements dans des délais intéressants. Toutefois, certaines de leurs caractéristiques les rendent plus résilients aux perturbations que d'autres groupes. En effet, ils sont attachés à un territoire, qui lie les individus à des sites donnés, dont ils ont une parfaite connaissance, et sur lesquels ils peuvent demeurer même si les conditions se dégradent (Samuels et al. 2005). D'autre part, le vol, qui permet l'exploitation de sites éloignés les uns des autres, est aussi un frein à la réactivité des oiseaux aux perturbations qui peuvent affecter leur environnement, notamment la fragmentation (Schmiegelow et al. 1997). L'utilisation des oiseaux comme modèle pour l'étude de l'impact des perturbations climatiques sur les écosystèmes, apparaît donc comme un compromis entre la sensibilité et l'intégration de nombreuses réponses, comme le suggèrent plusieurs travaux qui ont porté sur la résilience des communautés d'oiseaux à la destruction de leur habitat par le feu (Jacquet & Prodon 2009) ou par certaines pratiques agricoles (Raman et al. 1998).

4.2. Les observatoires de biodiversité : des outils exceptionnels pour tester l'ensemble des mécanismes démographiques d'influence du climat à grande échelle spatiale.

Les jeux de données que j'évoque plus haut existent bel et bien. En effet, dans de nombreux pays en Europe et aux Etats Unis, de véritables observatoires nationaux de la biodiversité se sont développés (le Royaume Uni est un précurseur en la matière). Depuis la prise de conscience par les hommes et femmes politiques de la nécessité de stopper à court terme l'érosion de la biodiversité, ces observatoires préexistants ont pris de l'ampleur et davantage de moyens y sont alloués. Dans le cadre de ces observatoires, des données de diverses natures, pour un groupe taxonomique donné, sont récoltées par des bénévoles (on parle alors de suivi participatif dans la mesure où ce sont des volontaires et non exclusivement des scientifiques qui participent à l'effort de terrain) selon des protocoles simples mais standardisés, définis à l'avance. La simplicité de mise en œuvre des protocoles favorise la participation d'un grand nombre de personnes (souvent plusieurs milliers à l'échelle d'un pays) et optimise donc la couverture spatiale du territoire. La standardisation permet quant à elle de faciliter le traitement statistique des données. Cette collaboration entre volontaires et scientifiques dans le but de suivre les populations d'oiseaux à large échelle a fait l'objet d'une importante synthèse par Jeremy Greenwood (Greenwood 2007).

En France, nous disposons pour les oiseaux du Suivi Temporel des Oiseaux Communs (STOC) qui se décline en deux volets (Julliard & Jiguet 2002). Le premier volet comprend un protocole de suivi d'abondance par points d'écoute (Echantillonnage Ponctuel Simple ou EPS). Les observateurs se rendent deux fois par an sur les mêmes points d'écoute, répartis de façon représentative des différents habitats, à l'intérieur d'un carré de 2km x 2km tiré aléatoirement dans un cercle de 10 km de rayon autour d'une commune qu'ils choisissent. Cet observatoire fournit donc des données datées d'abondance pour plus d'une centaine d'espèces d'oiseaux communs. Le second volet consiste en un programme de Capture-Marquage-Recapture (CMR) à l'échelle du territoire national. Dans environ 200 stations de baguage réparties sur toute la France, des ornithologues amateurs et professionnels, formés par le Muséum National d'Histoire Naturelle à la capture et au baguage des oiseaux, appliquent un protocole de CMR standardisé à effort constant (**figure 4**). Chaque année au moment de la reproduction, un nombre constant de séances de capture sont organisées, ce qui permet le suivi longitudinal d'un grand nombre d'individus pour environ 30 à 40 espèces d'oiseaux communs. Les premiers suivis STOC ont été réalisés en 1989. Ainsi ce sont maintenant plus de 20 ans de données standardisées pour un groupe taxonomique et un pays qui sont disponibles pour l'étude intégrée des mécanismes d'influence démographique des changements climatiques.

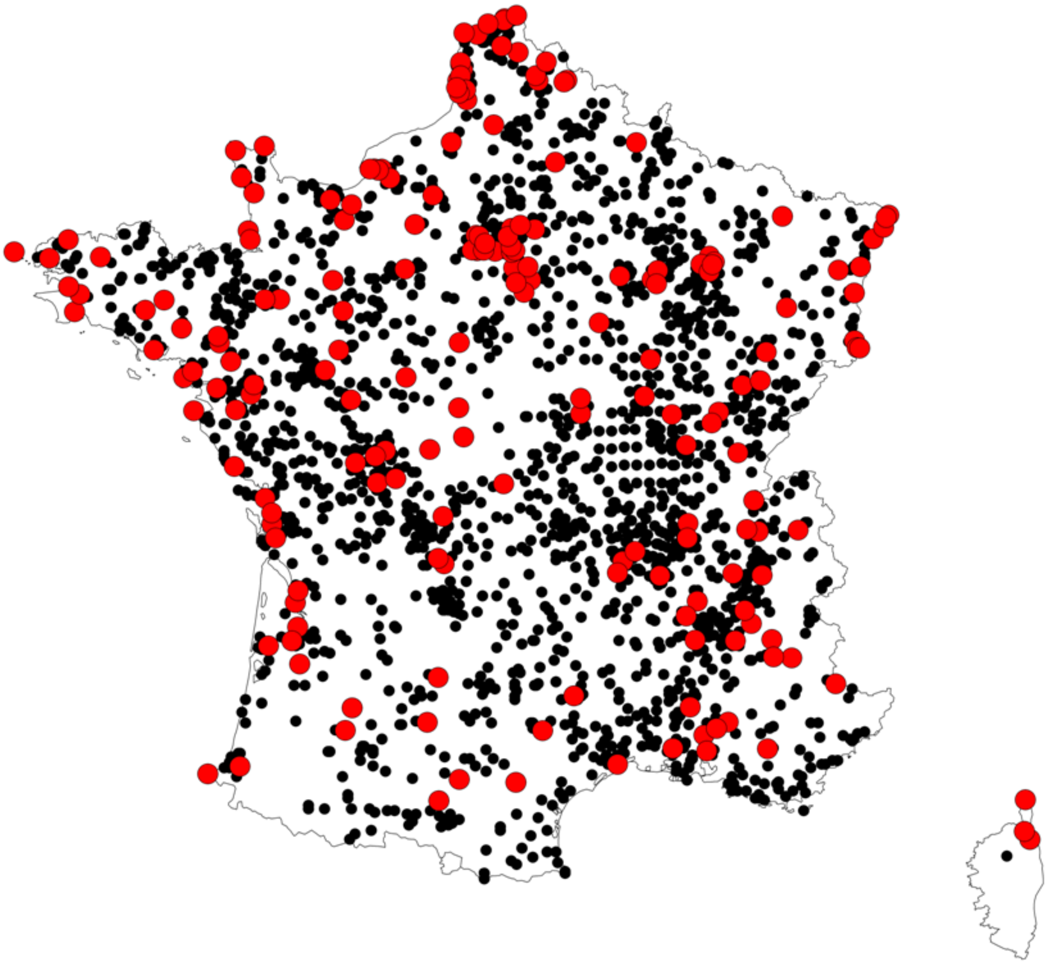


Figure 4. Ensemble des sites ayant contribué au moins 1 an à l'observatoire de Suivi Temporel des Oiseaux Communs (STOC) entre 1989 et 2009. Les points noirs représentent les sites appartenant au réseau STOC EPS. Les points rouges représentent les sites appartenant au réseau STOC capture, (site à effort de capture constant).

4.3. Modèle démographique des influences climatiques sur les populations d'oiseaux : hypothèses de la thèse.

J'ai donc pendant ma thèse utilisé les données issues de l'observatoire STOC pour tenter d'aboutir à une compréhension intégrée des mécanismes d'action du climat sur le cycle de vie des oiseaux et de mener une réflexion sur la prise en compte de ces mécanismes, afin d'améliorer les prédictions concernant le devenir des espèces communes c'est-à-dire celles qui représentent 99% des oiseaux de France en nombre d'individus. En pratique, j'entends par espèces communes, celles qui représentent la très grande majorité des données de l'observatoire et dont l'observation dans le cadre de STOC n'est pas simplement occasionnelle. Ce sont pour la grande majorité d'entre elles des passereaux. Avant d'arriver au modèle général que je me propose de tester, je vais parcourir chacune de ses composantes afin d'établir des hypothèses claires sur la base des résultats mis en évidence par des études récentes.

La variable d'intérêt concernant les populations mesure la variation temporelle d'abondance, le taux de croissance moyen de l'ensemble des populations suivies. Il est probable que les très nombreuses populations qui existent à l'échelle d'un pays ont toutes un comportement démographique et une sensibilité aux conditions environnementales différentes. Chacune de ces entités possède donc son taux de croissance propre. Toutefois de nombreux éléments suggèrent une part commune de variation de ces taux de croissance à commencer par l'utilisation de données agrégées pour la production d'indicateurs de biodiversité (Gregory et al. 2005; Gregory et al. 2007; Jiguet et al. 2009). C'est sur cette part commune de variation, forcément sous influence de facteurs environnementaux variant à grande échelle comme le climat, que mes travaux portent. Le taux de croissance d'une population ou d'un ensemble de populations reflète un bilan des gains et des pertes d'individus. Si l'on considère les phénomènes d'émigration et d'immigration comme essentiellement « internes » au système, ce qui paraît raisonnable lorsque l'on se place à l'échelle d'un pays et que la distance de dispersion natale des passereaux est de quelques kilomètres en moyenne (Paradis et al. 1998), le seul phénomène qui génère de nouveaux individus dans le système est la reproduction et le seul mécanisme qui soustrait des individus au système est la mort. Le succès de reproduction (qui comprend la survie des jeunes jusqu'à leur accès à la reproduction) et le taux de survie local des adultes (individus qui participent à la reproduction) moyens sont les deux variables qui vont donc contrôler les variations temporelles d'abondance d'une espèce. C'est donc au niveau de ces deux variables qu'il faut rechercher les influences climatiques.

La littérature nous fournit deux modes d'influence du climat sur le succès de reproduction (**figure 5**). Le point d'ancrage du climat sur le succès reproducteur est principalement lié à la ressource alimentaire. Tout d'abord, le climat peut influencer la quantité et ou la qualité de ressource disponible. Plusieurs études soutiennent ce mécanisme indépendant de la phénologie (Kitaysky & Golubova 2000; Crick 2004; Wright *et* *al.* 2009). Par ailleurs, les deux études menées suite à la canicule du printemps et de l'été 2003 en France suggèrent également un effet positif de la température sur le succès de reproduction en cette année particulièrement chaude, même si l'influence du climat au travers de réponses phénologiques ne peut être complètement exclue (Julliard *et al.* 2004b; Jiguet *et al.* 2006).

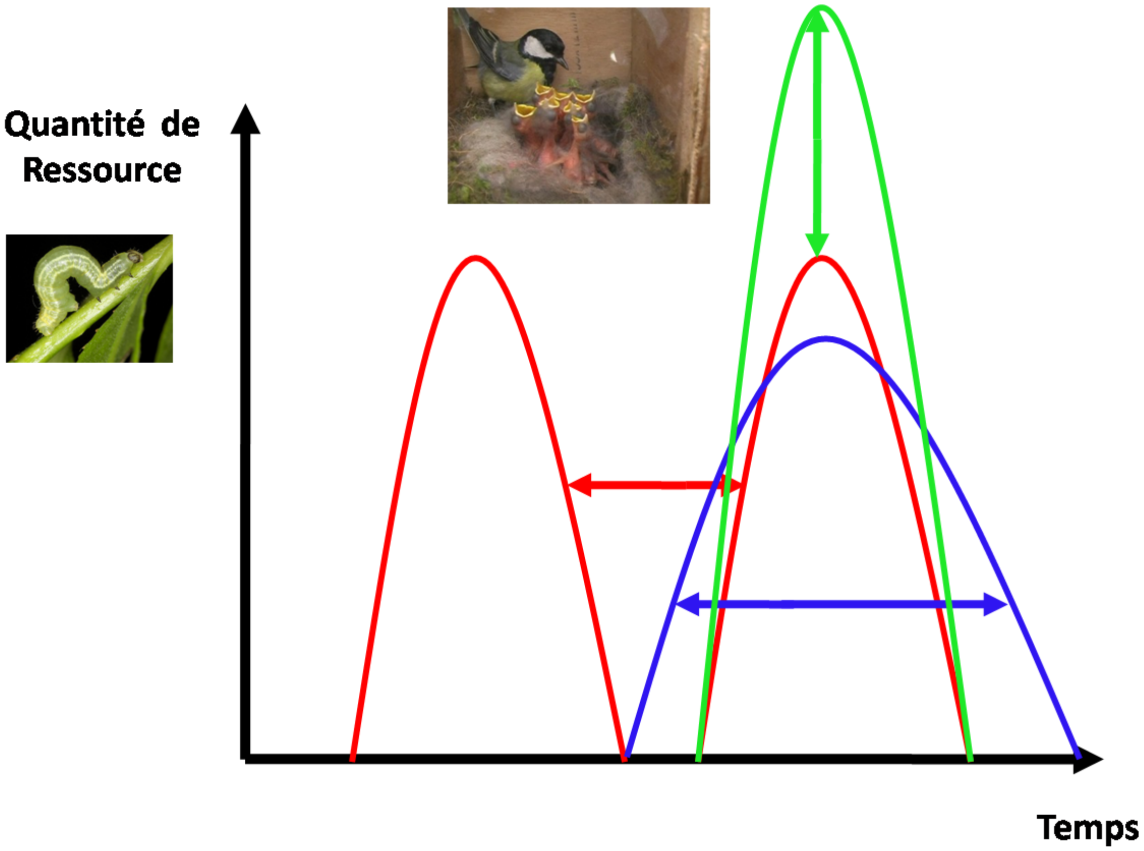


Figure 5. Mécanismes d’influence du climat sur le succès reproducteur via la ressource alimentaire. Si l’on admet que l’abondance de la ressource n’est pas uniformément distribuée au cours de la période de reproduction, le climat peut influencer le positionnement temporel du pic d’abondance de la ressource (en rouge), dans ce cas le climat agit par l’intermédiaire de la phénologie. Le climat peut aussi influencer la durée pendant laquelle la ressource est disponible (en bleu) ainsi que sur la quantité et ou la qualité de la ressource disponible (en vert). Ces dernières influences sont indépendantes de la phénologie.

Le second fait intervenir le climat au travers de la phénologie de la reproduction. Cette fois, ce n'est pas la quantité de ressource, ni sa qualité, mais la distribution temporelle de son abondance que le climat peut affecter. Les liens entre phénologie et climat ont fait l'objet de très nombreux travaux chez les oiseaux. Les deux évènements du cycle de vie aviaire qui ont le plus intéressé les auteurs sont incontestablement la migration (Huin & Sparks 2000; Sparks & Braslavska 2001; Cotton 2003; Jenni & Kery 2003; Lehikoinen *et al.* 2004; Saino *et al.* 2004; Sparks *et al.* 2005; Torti & Dunn 2005; Huppop & Winkel 2006; Jonzen *et al.* 2007; Miller-Rushing *et al.* 2008b; Tottrup *et al.* 2008) et la date de ponte (Crick *et al.* 1997; Crick & Sparks 1999; Cresswell & McCleery 2003; Sanz 2003; Both *et al.* 2004; Both & te Marvelde 2007; Visser *et al.* 2009a). Concernant la migration, et notamment le retour migratoire sur les quartiers de reproduction au printemps, on constate une tendance à des retours plus précoces (Sparks *et al.* 2005; Jonzen *et al.* 2006). De plus, les retours sont également d'autant plus précoces que la température est élevée (Cotton 2003). La variation phénologique est plus prononcée chez les migrateurs non transsahariens que chez les migrateurs transsahariens (Saino et al. 2009). Par ailleurs, il semble que malgré la distance qui les sépare de leur lieu de reproduction, la date de retour des migrateurs transsahariens est fonction de la température sur leur lieu de reproduction ou de grands indices climatiques comme l'Oscillation de l'Atlantique Nord (NAO) ce qui peut suggérer un couplage climatique permettant l'acquisition d'une information sur les quartiers d'hivernage (Saino & Ambrosini 2008) ou laisser penser que l'essentiel de l'ajustement s'effectue selon les conditions rencontrées pendant le retour (Ahola *et al.* 2004; Gordo & Sanz 2008; Tottrup *et al.* 2008). On attend par conséquent un ajustement phénologique significatif des migrateurs transsahariens à la température printanière, cet ajustement demeurant moins prononcé que chez les espèces sédentaires.

En ce qui concerne les dates de ponte, leur avancement en fonction des températures printanières a été montré pour un grand nombre d'espèces dès le milieu des années 90 grâce à un programme participatif de suivi des nids au Royaume Uni (Nest Record Scheme)(Crick *et al.* 1997; Crick & Sparks 1999). Par la suite, la date de ponte a fait l'objet d'études ciblées sur des populations occupant des nichoirs suivis régulièrement. Ces études ont principalement concerné quelques espèces cavernicoles, notamment les Mésanges charbonnières et bleues (respectivement *Parus major* et *Cyaniste caeruleus*) et le Gobemouche noir (*Ficedula hypoleuca*) (Visser *et al.* 2003; Both *et al.* 2005; Both *et al.* 2006b; Visser *et al.* 2006; Both & te Marvelde 2007; Visser *et al.* 2009a). Ces études confirment d'une part que la date de ponte est largement sous influence de la température printanière mais aussi qu'il s'agit d'un caractère possédant une héritabilité élevée et qui pourrait donc évoluer très rapidement sous la pression d'un climat qui se réchauffe (Nussey *et al.* 2005; Charmantier *et al.* 2008).

En revanche, le lien entre réponse phénologique au climat et taux de croissance d'une population reste plus difficile à mettre en évidence (Both et al. 2006a). Le cadre théorique incitant à rechercher ces liens est celui des chaînes et réseaux trophiques (Harrington *et al.* 1999; Durant *et al.* 2005; Durant *et al.* 2007; Tylianakis 2009). Il est peu probable en effet que toutes les espèces soient capables de répondre de façon uniforme à l'avancement du printemps causé par le réchauffement climatique (Visser & Both 2005). Cette affirmation repose sur les mécanismes biologiques du déclenchement des étapes de la reproduction à la sortie de l'hiver. Alors que les producteurs primaires et les arthropodes en diapause, et d'une façon plus générale les organismes occupant les niveaux trophiques les plus bas, sont souvent sensibles directement à la photopériode et à la température (Buse *et al.* 1999; Schaber & Badeck 2003; Korner & Basler 2010), les organismes qui dépendent de ces ressources ne le sont pas forcément (Durant et al. 2007). La prise d'information concernant la phénologie des ressources repose sur des indices peu connus actuellement malgré quelques pistes (Bourgault *et al.* 2006; Visser *et al.* 2009a; Visser & Sanz 2009). De plus, la phénologie du développement des plantes et des invertébrés se répercute sur les individus eux-mêmes, c'est-à-dire ceux chez qui la décision est prise. Dans le cas du prédateur, le positionnement de la phénologie de reproduction en relation avec la phénologie des proies est plus complexe (**figure 6**) puisqu'il s'agit de faire correspondre le pic d'abondance de la ressource avec celui des besoins de la progéniture alors que la ressource n'est pas encore disponible dans l'environnement (Durant et al. 2007). En d'autres termes, l'environnement dans lequel est prise la décision de débuter la reproduction est différent de celui où s'opère la sélection relative à cette décision (Both et al. 2009).

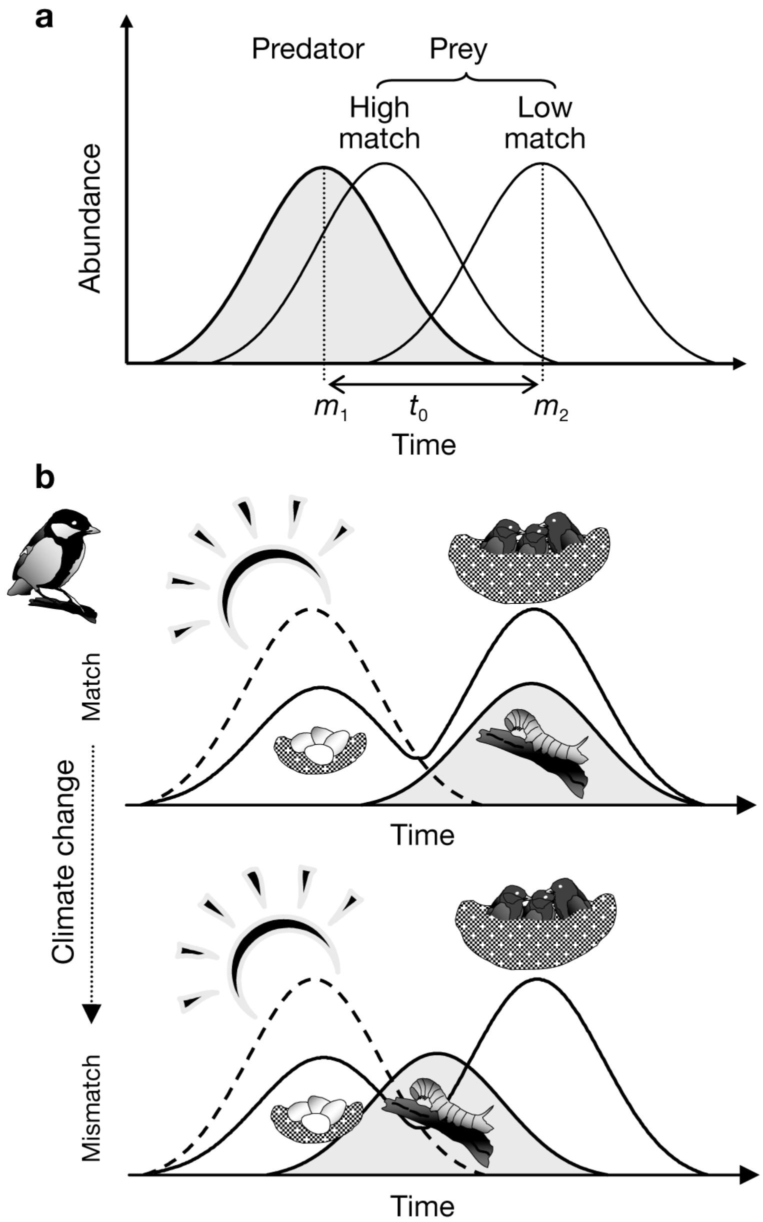


Figure 6. Illustration de la théorie de la désynchronisation d'une chaîne trophique sous influence climatique (Match-Mismatch hypothesis). En (a), on distingue deux cas de figure selon que les phénologies du prédateur et de la proie sont synchrones ou asynchrones d'un temps t_0. Cette synchronisation des phénologies du prédateur et de la proie dépend de l'information qu'ils utilisent pour entamer leur cycle de développement ou de reproduction : en (b), on voit que la Mésange charbonnière (prédateur) positionne sa date de ponte en réponse à des stimuli environnementaux tels que la température, alors même que la ressource dont aura besoin sa progéniture n'a pas encore fait son apparition. Si l'information utilisée par la Mésange est pertinente, c'est-à-dire bien corrélée avec l'apparition de la ressource, alors les phénologies de la ressource et des besoins alimentaires des juvéniles seront synchrones (cas en haut). Dans le cas contraire, les phénologies seront asynchrones et des conséquences sur le succès de reproduction sont prévisibles. Figure extraite de Durant et al. (2007).

Les travaux de Marcel Visser, Christiaan Both et leur collaborateurs, montrent pour deux espèces, la Mésange charbonnière (*Parus major*) et le Gobemouche noir (*Ficedula hypoleuca*), que le succès de reproduction et /ou le taux de croissance de populations suivies de façon intensive à l'aide de nichoirs, est lié à la capacité de ces oiseaux à ajuster leur date de ponte ou leur retour de migration à la température printanière moyenne (Both et al. 2006a; Visser et al. 2006). Dans une de leurs études, le lien avec la quantité de proies disponibles est même explicite puisqu'ils quantifient les variations d'abondance des chenilles au cours de la saison de reproduction et les mettent en relation avec le succès de reproduction de couples de mésanges ayant démarré leur reproduction plus ou moins tôt (Visser et al. 2006). Dans un autre travail, Both et ses collaborateurs étudient les différences de réponses phénologiques le long d'une chaîne trophique simple composée de 4 niveaux. Le premier correspond au végétal (en l'occurrence le chêne, *Quercus robur*), le second à un hétérocère, la Tordeuse du Chêne (*Tortrix viridana*) dont la chenille se nourrit sur le chêne et est consommé par trois espèces de Mésanges (bleues, charbonnières et noires) et le Gobemouche noir, qui constituent le troisième niveau. Enfin le quatrième niveau est occupé par l'Epervier d'Europe (*Accipiter nisus*) dont le succès de reproduction dépend de la présence de jeunes passereaux. L'étude montre que les réponses phénologiques à la température varient le long de cette chaîne trophique. Toutefois les auteurs ne sont pas en mesure d'établir un lien clair avec le succès de reproduction (Both et al. 2009). On voit donc que la variabilité interspécifique des réponses phénologiques aux variations climatiques peut provoquer une désynchronisation des chaînes et des réseaux trophiques (van Asch & Visser 2007), et qu'au moins certaines études montrent que cela peut affecter le taux de croissance d'une population donnée (Both *et al.* 2006a; Moller *et al.* 2008).

La question de la dépendance climatique de la survie a été traitée principalement grâce à deux approches. La première a consisté à mettre en relation les variations d'abondances printanières estimées par les données de Monitoring à large échelle (du type Suivi des Populations d'Oiseaux Nicheurs, Breeding Bird Survey) avec des paramètres climatiques comme la température ou les précipitations sur les zones d'hivernage ou les zones de reproduction (Newton 2004). Cette approche repose sur l'hypothèse que les variations d'abondances observées d'une année sur l'autre sont essentiellement le reflet de la survie. L'autre approche utilise les données de baguages et de contrôles qui permettent de modéliser explicitement un taux de survie locale grâce à un traitement statistique adapté (Lebreton et al. 1992; Peach et al. 1996; Robinson et al. 2007a). Deux grandes tendances ressortent de ces études. Pour les espèces sédentaires, il semble que la rigueur de l'hiver mesurée soit par la température moyenne soit par la durée d'épisodes particulièrement froids ou neigeux influence les taux de survie de nombreuses espèces communes (Robinson et al. 2007a). La variabilité de la survie chez les espèces migratrices semble quant à elle plus complexe et dépendre notamment de la localisation de leurs quartiers d'hivernage. Ainsi, plusieurs espèces voient leur survie diminuer quand la quantité de précipitations est faible dans la zone sahélienne soit à l'automne soit au printemps (Newton 2004; Mihoub *et al.*

2010). Nous n'avons pour l'instant que peu ou pas d'informations sur la mortalité associée aux conditions rencontrées par les oiseaux lors de leur trajet migratoire.

La présentation des différentes dépendances climatiques du cycle de vie des oiseaux permet désormais d'envisager un modèle intégrant l'ensemble de ces composantes pour estimer leur contribution au taux de croissance des populations à l'échelle d'un pays comme la France. Ce modèle est présenté en **figure 7**. On distingue les influences du climat sur les processus démographiques que sont le succès reproducteur et la survie par l'intermédiaire de la quantité et /ou de la qualité des ressources (flèches bleues) et l'influence du climat sur le succès reproducteur par le biais de l'ajustement phénologique des populations (flèche verte). On peut s'attendre pour chacune de ces influences climatiques à une importante variabilité interspécifique (Encarts). Néanmoins, on peut aussi penser que cette variabilité est corrélée aux caractéristiques propres à chaque espèce, à ses traits d'histoires de vie.

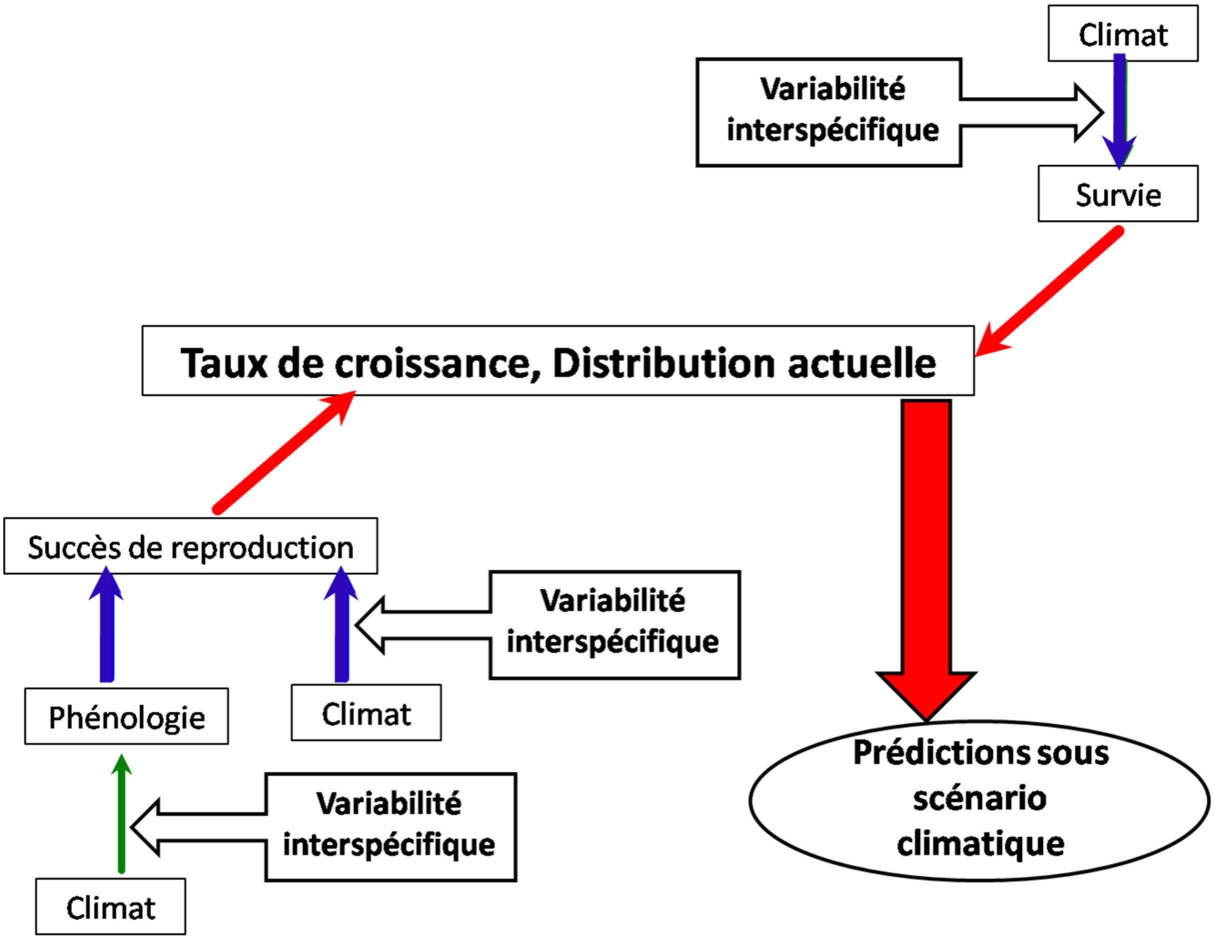


Figure 7. Modèle intégré des influences climatiques sur la démographie aviaire. Ce modèle rend compte des principales hypothèses à tester pendant la thèse. La quantification des différentes influences climatique et leur importance dans la détermination du taux de croissance des populations sera étudiée pour plusieurs dizaines d'espèces communes d'oiseaux à l'aide des données provenant de l'observatoire de Suivi Temporel des Oiseaux Communs (STOC).

Par conséquent, les objectifs de la thèse correspondent à l'étude de l'ensemble des mécanismes apparaissant dans ce modèle. Cette étude se décline donc selon les points suivants :

- La mise au point d'outils d'analyse permettant de mesurer à partir des données de l'observatoire STOC, les influences climatiques sur les différents paramètres du cycle de vie aviaire pour de nombreuses espèces communes. Ces méthodes doivent donc permettre d'une part de quantifier les réponses phénologiques de la plupart de ces espèces aux variations climatiques. Elles doivent également permettre l'estimation des taux de survie et du succès reproducteur afin que ces taux puissent être mis en relation avec les variations climatiques.
- La recherche de corrélations entre les influences climatiques sur la survie et la phénologie et les traits d'histoires de vie ou les caractéristiques de la niche écologique des espèces communes. Les données de l'observatoire STOC permettent en effet d'utiliser une approche de type méta-analytique, consistant en l'estimation de paramètres de réponse spécifiques, suivie d'une recherche de facteurs corrélés à la variabilité de ces réponses. Cette approche comparative a été plusieurs fois mise en œuvre au laboratoire (Julliard *et al.* 2004b; Jiguet *et al.* 2006; Bas *et al.* 2008) et constitue un intermédiaire analytique entre la méta-analyse au sens classique qui consiste en une synthèse de résultats publiés sur différentes espèces et différents sites d'études, et une étude sur une espèce formant une population en un site donné.
- La prise en compte de la dépendance de la démographie des espèces vis-à-vis du climat dans les méthodes de prédictions de distributions futures sous scénario climatique.

Je présenterai les avancées réalisées pendant la thèse en commençant tout d'abord par l'étude de l'influence du climat sur les taux de croissance des populations à travers la phénologie des espèces communes, puis j'exposerai les résultats obtenus sur la relation entre la survie et le climat. Cette dernière partie me permettra également de proposer une approche permettant la prise en compte des influences climatiques sur la démographie pour améliorer les prédictions quant aux distributions futures des espèces communes sensibles à la température.

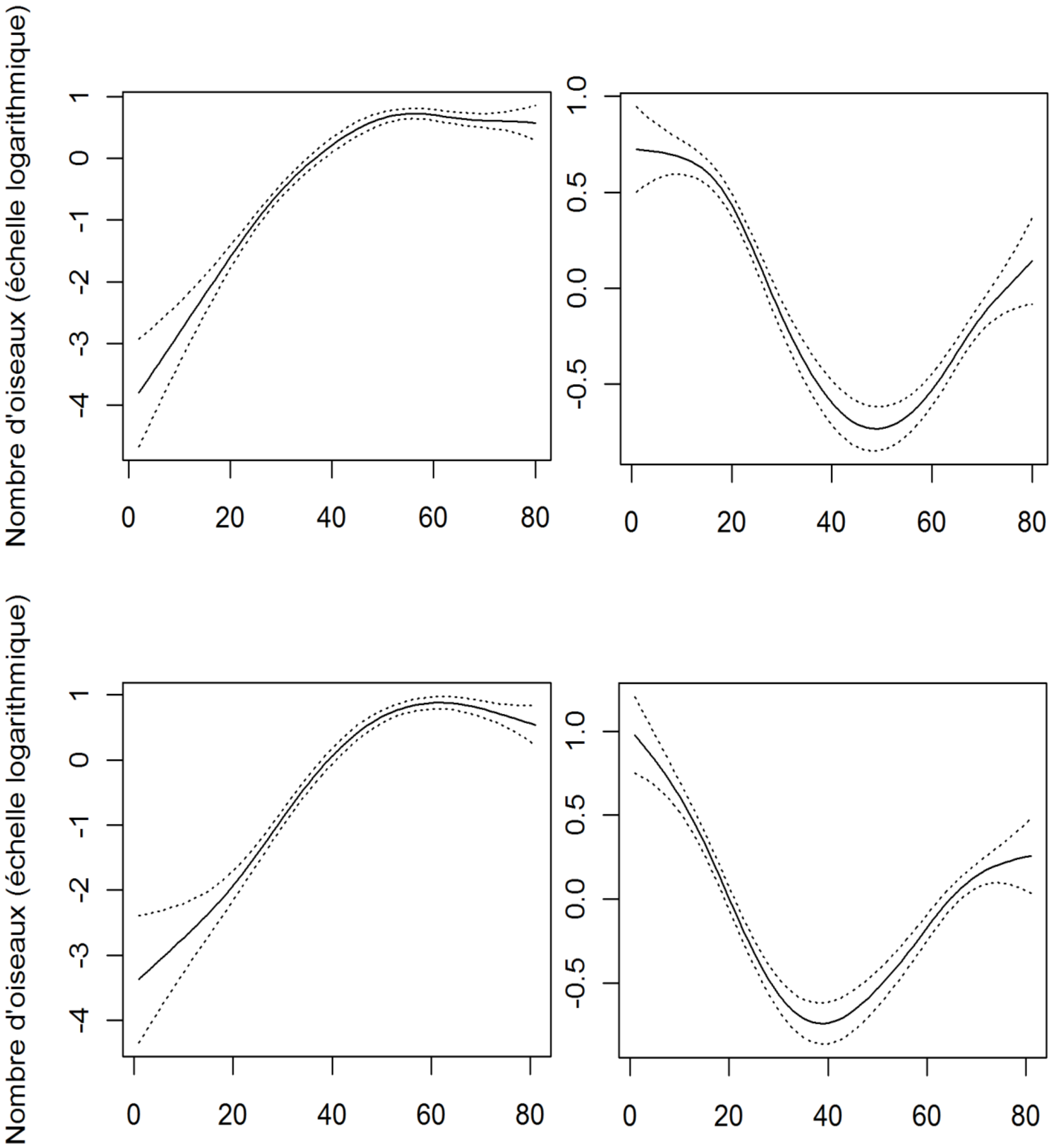
1. Phénologie printanière chez les oiseaux communs : mesure à large échelle, variabilité interspécifique des réponses et conséquences sur les populations.

1.1. Extraire le signal phénologique à partir de données d'observatoire.

1.1.1. Nature du message phénologique

Au sein d'une espèce à temps de génération relativement court, comme c'est le cas pour les espèces d'oiseaux considérées ici, les étapes du cycle de vie sont communes à l'ensemble des individus. Ainsi, au printemps tous les individus appartenant à des espèces migratrices transsahariennes font leur retour sur leurs zones de reproduction. Chez les espèces sédentaires, dès la fin de l'hiver, les mâles délimitent des territoires par une intense activité de chant (Hegelbach & Spaar 2000; Amrhein *et al.* 2008; Tremain *et al.* 2008). Toutefois, si la nature des étapes qui composent la phase reproductive est identique pour la plupart des individus, le moment auquel survient chacune de ces étapes est variable entre les différents individus (Lambrechts *et al.* 1997; Caro *et al.* 2009). Les études qui montrent par exemple la grande héritabilité de la date de ponte chez les Mésanges bleues (*Cyaniste caeruleus*) et charbonnières (*Parus major*) le suggèrent (Vannoordwijk *et al.* 1981; Lambrechts *et al.* 1997), puisque des individus possédant des génotypes différents au loci impliqués pondront en moyenne à des dates différentes. De plus la plasticité phénotypique des individus entraîne également des variations phénologiques. Par conséquent, le positionnement temporel d'un évènement du cycle de vie étudié à l'échelle d'une population ne sera pas ponctuel mais distribué sur une période de temps qui varie selon l'espèce et le phénomène biologique considéré. Chez les oiseaux, on observe des distributions gaussiennes plus ou moins étalées pour les passages migratoires tels qu'ils sont relevés sur les sites de suivis (Jonzen et al. 2006; Knudsen et al. 2007). Ces distributions peuvent parfois également comprendre plusieurs modes comme c'est le cas chez de nombreuses espèces de rapaces (Kjellen 1992). Ces modes correspondent aux passages d'individus de sexes, d'âges ou de populations différents (MacMynowski & Root 2007). De la même façon les dates de pontes étudiées grâce à des nichoirs dans des « forêts expérimentales » montrent des distributions gaussiennes chez les Mésanges charbonnières (*Parus major*) (Perrins 1970, 1991). Les jeux de données décrits précédemment offrent aux scientifiques désireux d'étudier les variations temporelles de la phénologie des outils très performants. En effet, lorsque les dates de ponte de centaines de couples de Mésanges sont relevées dans les nichoirs, la distribution réelle réalisée est *exactement* connue (en faisant l'hypothèse que la ponte en nichoir est représentative de la ponte en milieu naturelle) et ses variations temporelles peuvent être mesurées avec des estimateurs statistiques très simples comme des dates moyennes ou médianes. On peut faire un constat similaire pour les données issues du suivi intensif et standardisé des sites de migration. Le protocole « Transpyr » qui vise à suivre la migration postnuptiale au niveau des cols pyrénéens (Devisse & Urcun 1994) a en effet permis des comptages quotidiens sur une période définie depuis 1981. Toutefois, pour ces suivis, certaines variables peuvent déjà influencer les distributions et bruiter le signal phénologique. Ainsi, la direction des vents peut orienter les migrateurs vers d'autres zones de franchissement du massif. Par conséquent, il y a passage non détecté d'individus ce qui altère la qualité des distributions et donc du message phénologique. La probabilité de détection est en effet un paramètre fondamental dans tout suivi de biodiversité (Royle *et al.* 2005; Kery *et al.* 2009). Elle correspond à la probabilité d'observer un individu, un phénomène, conditionnée à sa présence ou à son existence. Dans le cas des suivis de date de ponte dans les nichoirs, cette probabilité de détection vaut 1. Si tous les nichoirs sont vérifiés régulièrement, la date de ponte est effectivement connue pour tous les couples et il est assez simple de modéliser la distribution probabiliste sous-jacente. Dans le cas des comptages migratoires, elle est inférieure à 1 puisque selon les conditions météorologiques, des individus vont passer sans être comptabilisés. Ces variations de la probabilité de détection constituent un problème majeur dans l'extraction du message phénologique (Moussus et al. 2010). Cependant, dans le cas de données de comptages ou de baguage sur les zones de reproduction, elles offrent une opportunité très intéressante.

Le protocole STOC EPS fournit des données d'abondance d'espèces deux fois par an sur chaque site suivi. En réalité, le terme abondance n'est pas absolument exact. Ce que le suivi fournit, ce sont des données de détections. L'évènement de détection peut être divisé en deux composantes (Moussus et al. 2009). La première est la présence vraie de l'espèce autour du point d'écoute. La détection est évidemment conditionnée à cette présence vraie. L'illustration la plus évidente de cette composante est donnée par les espèces migratrices qu'il est impossible de détecter sur les sites de comptage avant leur retour. La deuxième composante est la détectabilité de l'espèce. Cette probabilité de détecter les individus d'une espèce sachant leur présence autour du point d'écoute est fonction de caractéristiques propres à l'espèce comme les caractéristiques du chant (volume, fréquence sonore), la taille, la couleur, le comportement, l'observateur et la météo (Bas et al. 2008). Ces variables peuvent être considérées en première approximation comme des constantes à l'échelle de l'espèce et peu variables au cours de la saison de comptage. En revanche, la détectabilité est aussi fonction de variables liées à l'activité des individus. Ainsi l'activité de chant par les mâles est fonction de la saison comme cela a été montré chez plusieurs espèces (Hegelbach & Spaar 2000; Amrhein *et al.* 2002; Kunc *et al.* 2005; Amrhein *et al.* 2007; Amrhein *et al.* 2008; Bas *et al.* 2008 (**Article 1**)). Cette activité est très forte en fin d'hiver et en début de printemps chez les espèces sédentaires, et dès leur retour, pour les espèces migratrices. Par la suite l'activité de chant diminue (Amrhein et al. 2008). Par ailleurs, sitôt la ponte survenue, les femelles ne sont plus détectables dans la mesure où elles couvent les œufs. Si la distribution moyenne de ces phénomènes sur un grand nombre d'années peut aussi être considérée comme une constante propre à l'espèce (il existe des nicheurs précoces, des migrateurs au retour plus ou moins précoces), c'est la variation inter annuelle qui nous intéresse car elle devrait permettre d'estimer la réponse phénologique des espèces aux variations inter annuelles des conditions environnementales. Ainsi, prises dans leur globalité, les données de comptage issues du protocole STOC EPS ou STOC capture en considérant l'apparition des jeunes dans les captures, comportent un message phénologique pour des dizaines d'espèces d'oiseaux communs de par la relation qui lie les comptages à la probabilité de détection, elle-même fonction du comportement qui varie selon l'étape du cycle biologique (Moussus et al. 2009). Les variations saisonnières des comptages STOC EPS prennent deux formes différentes qui renvoient aux deux stratégies de migration différentes (**figure 8**). Pour les espèces sédentaires, on observe une phase de décroissance des comptages au cours du printemps et une stabilisation suivie pour certaines espèces d'une augmentation secondaire. Pour les espèces migratrices et notamment migratrices transsahariennes, on observe au contraire une très forte augmentation saisonnière du nombre des comptages qui finissent par se stabiliser, voir par décroître en fin de printemps. L'intérêt majeur de ces distributions est la relative constance de leur forme d'année en année à l'échelle de l'espèce. Par conséquent, la question de la mesure de la phénologie printanière des espèces communes suivies par le STOC se retrouve réduite à celle de l'extraction d'un message phénologique à partir de distributions répétées comme c'est le cas pour les comptages migratoires. Deux différences importantes subsistent quand même : la forme des distributions est variable selon l'espèce (en première approximation croissante ou décroissante), et les données ne proviennent pas d'un seul et même site mais de sites distribués à une vaste échelle spatiale. Par conséquent, le message phénologique contenu dans ces distributions correspond à la phénologie printanière moyenne d'une espèce à l'échelle de la France.


Nombre d'oiseaux (échelle logarithmique)
1
0
-1
-2
-3
-4
0
20
40
60
80
1.0
0.5
0.0
-0.5
0
20
40
60
80
Nombre d'oiseaux (échelle logarithmique)
1
0
-1
-2
-3
-4
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1.0
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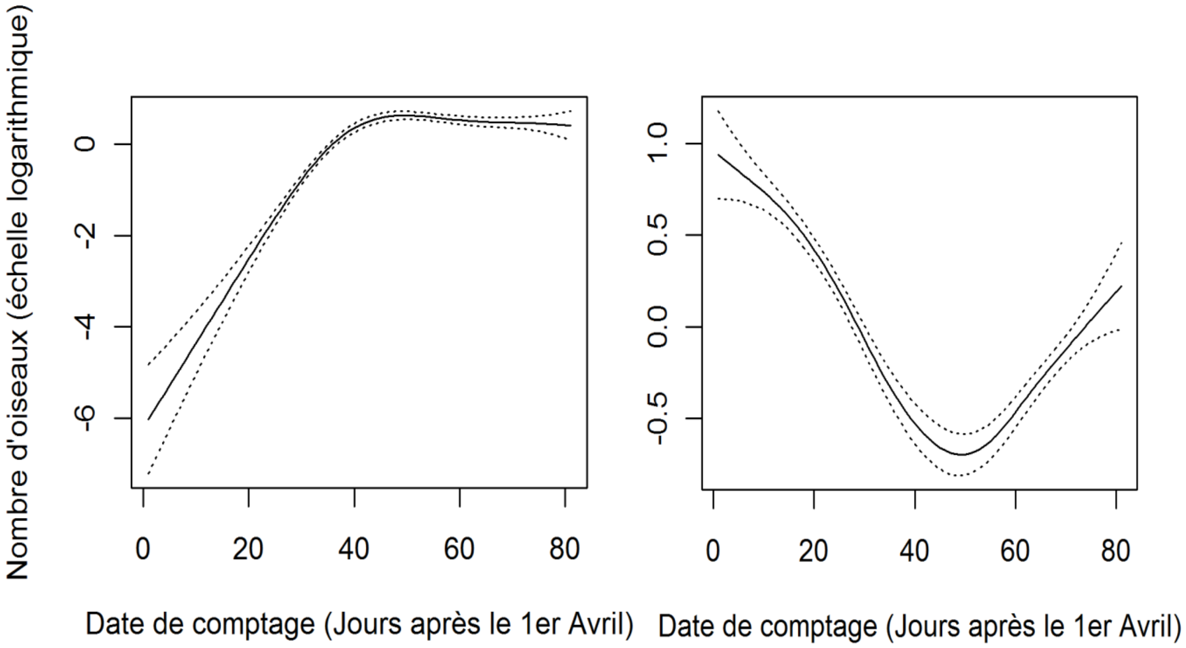


Figure 8. Exemples de distributions saisonnières des comptages STOC EPS pour l'Hypolaïs polyglotte (*Hippolais polyglotta*), colonne de gauche, et de la Sittelle torchepot (*Sitta europaea*), colonne de droite. De haut en bas les distributions correspondent aux comptages de 2006, 2007 et 2008. Noter d'une part le pattern inverse pour deux espèces à la stratégie migratoire différente (l'Hypolaïs polyglotte est une espèce migratrice transsaharienne alors que la Sitelle torchepot est sédentaire) et la très grande reproductibilité des patterns pour une même espèce d'une année sur l'autre.

1.1.2. Estimation des anomalies de phénologie printanière à partir des données STOC EPS.

Le signal phénologique contenu dans les données STOC EPS étant caractérisé, se pose alors la question de la méthode d'estimation des variations interannuelles de cette phénologie. L'utilisation d'estimateurs basés sur les dates de premières apparitions est exclue d'office. En effet les espèces sédentaires sont présentes toute l'année et cet estimateur n'aurait donc aucun sens pour elles. De plus, même appliqué aux espèces migratrices cet estimateur est très peu précis puisqu'il résume l'intégralité d'une distribution phénologique à sa première valeur et peut même être biaisé si les effectifs échantillonnés varient d'une année sur l'autre (Tryjanowski & Sparks 2001; Miller-Rushing *et al.* 2008a; van Strien *et al.* 2008). Des estimateurs plus robustes comme les dates moyennes de comptages (moyenne des dates de comptages pondérées par les abondances relevées lors de ces comptages) pourraient être utilisés. Cependant, leur sens de variation dépend de la forme de la distribution des comptages (voir Moussus et al. 2009 pour une démonstration). Par conséquent il fallait mettre au point un estimateur qui prenne si possible l'ensemble de l'information phénologique disponible c'est-à-dire la totalité de la distribution des comptages et dont les variations soient identiquement interprétables pour l'ensemble des espèces. Nous avons proposé une méthode d'estimation qui répond à ces critères (**Article 2**). Elle repose sur l'utilisation conjointe de modèles additifs généralisés (GAM) et du maximum de vraisemblance. Elle permet d'estimer le décalage temporel entre deux distributions de comptages de formes semblables. Les GAM permettent grâce à des fonctions de lissage de type spline de modéliser les distributions de comptages. Ainsi le modèle GAM suivant

Comptages~spline(Date)

En assumant une distribution de Poisson pour les comptages, on produit une distribution saisonnière lissée de ces comptages.

Le nombre de degrés de libertés associés à la fonction de lissage permet d'ajuster au mieux le modèle. Le principe est le suivant : si l'on admet que les deux distributions de comptages modélisées par un GAM ont une forme identique, et qu'elles ne diffèrent que par leur positionnement dans le temps, alors l'ajustement d'un GAM à l'ensemble des données de comptages de ces deux distributions réunies sera parfait si l'on a imposé aux comptages de l'une des distributions un décalage égal à l'opposé du décalage qui les séparaient. En effet pour cette unique valeur de décalage imposé, les deux distributions seront parfaitement superposées. Il suffit d'ajuster de façon itérative le modèle suivant aux données de comptages de deux années de suivi STOC EPS :

Comptages~spline(Date + t)

En assumant une distribution de Poisson pour les comptages et où t vaut 0 pour les données de comptages d'une des deux années comparées (que l'on qualifiera de référence) et prend successivement des valeurs comprises dans un intervalle de temps choisi raisonnablement (par exemple -30 à +30 jours avec un pas de 1 jour) pour les données de comptage de l'autre année (que l'on qualifiera d'année testée). L'ajustement du modèle GAM pour chacune des valeurs de t est suivi grâce au critère d'information d'Akaike (AIC) qui vaut $-L+2k$ où L correspond au logarithme de la vraisemblance du modèle et k à son nombre de paramètres (Akaike 1981). Cette façon de procéder est pratique dans la mesure où le nombre de paramètres associés à chacun des GAM ajusté étant constant (k est constant), minimiser l'AIC (c'est-à-dire rechercher le meilleur ajustement) revient à maximiser la vraisemblance. Ainsi, en relevant les valeurs de l'AIC correspondant à chaque t, on peut reconstituer la fonction de vraisemblance du modèle et sa dépendance vis-à-vis de t. La détermination du minimum global de la fonction AIC= f(t) permet de trouver la valeur de t qui permet la superposition des deux distributions de comptage. Mais plus encore, l'erreur associée à l'estimation de ce décalage peut elle aussi être quantifiée. En effet cette erreur est donnée par l'opposé de la dérivée seconde de la fonction AIC=f(t) évaluée au minimum global. Dans notre cas cette fonction peut être approximée autour du minimum global par un polynôme du second degré de type $AIC=at^2+ bt + c$. Par conséquent, le minimum global est donné par –b/2a et l'erreur associée à ce minimum global est donnée par $1/a$. En comparant les distributions de comptages de chacune des années qui composent le jeu de données avec toutes les autres années du jeu de données, on peut ainsi calculer l'anomalie de phénologie printanière pour chaque espèce et chaque année (**figure 9**). Le modèle appliqué aux données phénologiques est relativement souple puisqu'il permet de tenir compte d'une variabilité entre sites, ou entre années des effectifs comptés, simplement en intégrant ces variables dans le modèle comme des effets fixes ou aléatoires.

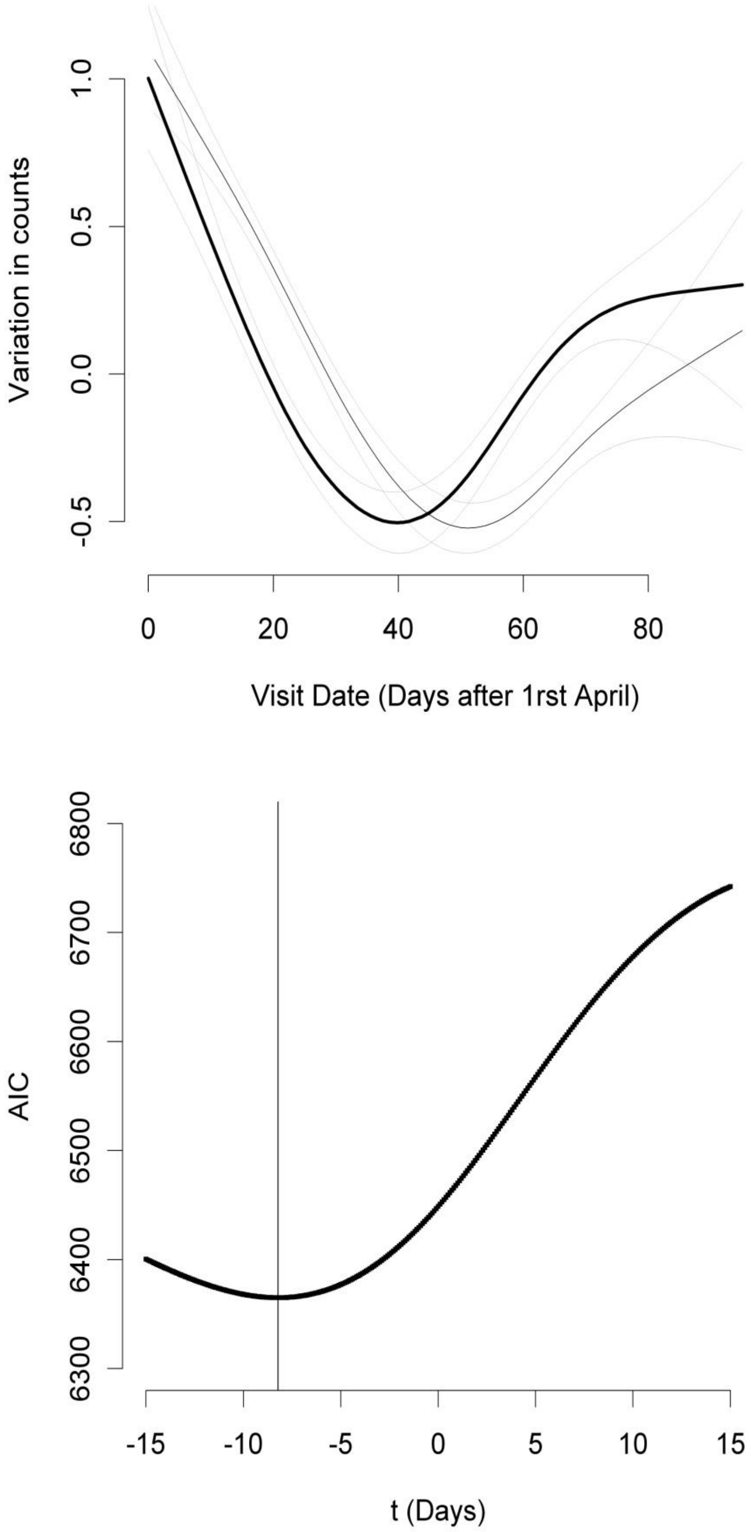


Figure 9. Illustration du fonctionnement de la méthode GAM pour estimer le décalage temporel entre les distributions de comptages de deux années différentes. En haut figurent les distributions de comptages pour la Sittelle torchepot (*Sitta europaea*) pour 2005 (courbe en gras) et 2006 (trait normal). On observe que la distribution des comptages de 2006 est retardée par rapport à celle de 2005 d'une dizaine de jours. Après avoir ajusté le modèle GAM Comptages~ spline (Date de comptage +*t*) ou *t* varie entre -15 et + 15 jours avec un pas

de 0.1 jour, on enregistre les 301 valeurs d'AIC correspondantes. La relation entre AIC et *t*, en bas, admet un minimum global pour la valeur de *t* qui correspond au décalage temporel des deux distributions, ici l'estimation est de 8.23 ± 0.98 jours de retard pour les comptages de 2006 par rapport à 2005. Figure extraite de l'article 2 Moussus et al. (2009).

1.1.3. Précision de l'estimateur phénologique GAM

Nous avons testé la robustesse de cet estimateur à différents paramètres caractérisant les distributions phénologiques dans une étude comparative de 10 estimateurs et sur la base de distributions phénologiques simulées (**Article 3**). Les propriétés des différents estimateurs phénologiques utilisés dans la littérature avaient pour certaines été discutées, les estimateurs basés sur les dates de premières apparitions avaient fait l'objet de vives critiques (Tryjanowski & Sparks 2001; Miller-Rushing *et al.* 2008a; Miller-Rushing *et al.* 2008b; van Strien *et al.* 2008). Toutefois ces critiques avaient été faites sur la base de jeux de données réels, où la valeur attendue, c'est-à-dire la variation phénologique réelle demeurait inconnue. Nous avons donc pris le parti de créer des distributions phénologiques simulées pour lesquelles le décalage phénologique était une quantité connue fixée comme un paramètre de simulation. Pour chaque combinaison de paramètres décrivant les distributions phénologiques, deux jeux de données décalés d'un temps connu étaient donc simulés. Les estimations de ce décalage, connu à l'avance, produites par les 10 estimateurs étaient ensuite comparées. Les résultats de cette étude montrent clairement que les dates de premières apparitions constituent des estimateurs très peu fiables, pouvant même être biaisés par des variations de taille d'échantillons entre les deux distributions comparées. Par ailleurs l'ensemble des simulations identifient deux estimateurs comme étant les plus robustes, c'est-à-dire les moins variables (1000 simulations pour chaque combinaison de paramètres étaient effectuées) et les moins biaisés selon le critère de l'erreur quadratique moyenne (RMSE). Ces deux estimateurs sont la date moyenne et l'estimateur basé sur les GAM décrit précédemment. La qualité des estimations produites par la méthode GAM est notamment peu sensible à des détériorations de la probabilité de détection. De plus, la méthode fonctionne également lorsque le jeu de données n'est pas complet, c'est-à-dire quand certains jours les comptages ne peuvent pas être effectués. Enfin, lorsque les données font apparaître une distribution bimodale, la méthode GAM est plus précise que la date moyenne. Par conséquent, les données phénologiques simulées montrent que la méthode basée sur le GAM et qui tient compte de l'ensemble de la distribution des comptages est un outil solide pour estimer la variation phénologique inter annuelle.

Nous avons également appliqué cette méthode en collaboration avec Ondine Filippi-Codaccioni aux données de l'observatoire de la migration postnuptiale sur les grands cols pyrénéens (Devisse & Urcun 1994) (**Article 4**). Depuis presque 30 ans (début en 1981), sur une période allant du 15 juillet au 15 novembre, des observateurs bénévoles chevronnés comptent selon un protocole standardisé les grands migrateurs (essentiellement les rapaces ainsi que les cigognes et les grues cendrées) sur trois cols pyrénéens. Nous avons estimé les anomalies phénologiques de passage postnuptial au col d'Organbidexka de 14 espèces de rapaces diurnes pour la période 1981-2008 et montré une tendance significative à l'avancement chez les migrateurs transsahariens alors que ce n'est pas le cas des migrateurs non transsahariens. Ce résultat est cohérent avec celui trouvé par Jenni et Kéry en 2003 sur la migration post nuptiale des passereaux. En effet, dans leur étude ces auteurs trouvent que les passereaux transsahariens ont significativement avancé leur migration post nuptiale alors que les passereaux non transsahariens l'on significativement retardée (Jenni & Kery 2003). Par ailleurs, la variance interspécifique de l'évolution temporelle de la phénologie de migration chez les espèces transsahariennes est beaucoup plus faible que chez les espèces non transsahariennes. Ce résultat semble indiquer que les espèces transsahariennes forment un groupe dans lequel la réponse au changement climatique est relativement homogène alors que les réponses des espèces on transsahariennes sont très différentes les unes des autres. Par conséquent, la stratégie transsaharienne paraît plus contraignante en termes de réponse phénologique que les autres stratégies migratoires, ce qui est en accord avec plusieurs études concernant la phénologie de migration des passereaux (Gwinner 1996; Both & Visser 2001; Gordo 2007; Both 2010). Cette étude a été réalisée pour comparaison en utilisant les deux estimateurs (date moyenne et méthode GAM). Les résultats présentés dans l'article sont ceux obtenus en utilisant la date moyenne. En effet dans le cas de jeux de données de migration, la distribution phénologique prend toujours la forme d'une gaussienne donc les dates moyennes sont très facilement estimables et il n'y a pas de problème quant à l'interprétation de leurs variations. Cependant, les résultats obtenus avec la méthode GAM sont identiques dans le cas de cette étude ce qui confirme la capacité de cette méthode à mesurer la variation phénologique.

La méthode GAM a aussi été appliquée aux données de passage post nuptial de Grue cendrée (*Grus grus*) sur les cols d'Organbidexka, Lindux et Lizarietta (**Article 5**). L'objectif était d'une part de quantifier l'évolution temporelle de la phénologie de migration de la Grue cendrée sur la période 1981-2008 pour Organbidexka, 1987-2008 pour Lindux et 1988-2008 pour Lizarietta mais surtout de comparer les estimations obtenues pour chacun des cols afin de tester la cohérence du message phénologique global. Les résultats montrent une grande cohérence de l'avancement significatif constaté de la migration post nuptiale chez la Grue cendrée puisque l'avancement estimé sur la période 1981-2008 est de 20.7 jours pour Organbidexka, 20.4 jours pour Lindux et 17.4 jours pour Lizarietta. Lorsque les variables météorologiques comme la direction et la force moyenne des vents à l'échelle annuelle sont prises en compte dans les modèles de régression, on trouve un avancement cohérent de 18 jours environ pour les trois sites. On constate donc que malgré le bruit potentiel associé à des régimes météorologiques locaux différents pour ces trois sites de suivi migratoire, des données de comptage indépendantes d'un même phénomène donnent en utilisant l'estimateur GAM des estimations phénologiques tout à fait cohérentes. Par ailleurs, la Grue cendrée semble avancer très fortement sa phénologie malgré une stratégie de migration non transsaharienne. Ce résultat a aussi été trouvé pour l'Alouette des champs (*Alauda* *arvensis*), une autre espèce non transsaharienne, en utilisant les données de baguage françaises (Travaux de Master 2 de Pascaline Lebreton).

Pour conclure sur les tests pratiqués pour évaluer l'estimateur phénologique basé sur les GAM, les estimations produites sur des jeux de données phénologiques simulés et les jeux de données de migration permettent d'être confiant dans l'application de cette méthode aux données issues du STOC.

1.2. Ajustement de la phénologie de reproduction à la température et taux de croissance à long terme des populations de passereaux communs.

Comme cela a été évoqué en introduction, le climat et notamment la température jouent un rôle fondamental dans le déclenchement des cycles de reproduction au printemps (Buse *et al.* 1999; Cleland *et al.* 2007; van Asch & Visser 2007). Le contrôle du débourrement des bourgeons au printemps se trouve sous le contrôle de la photopériode et de la température (Schaber & Badeck 2003). De même, le contrôle de la sortie de diapause chez les lépidoptères est aussi assuré par la température et la photopériode (Buse et al. 1999). L'abondance de ces proies va donc être distribuée autour d'un pic lors du printemps, tout comme leur qualité nutritive puisque les chenilles tardives consommeront des feuilles beaucoup plus concentrées en tannins et seront donc de plus faible valeur nutritive pour les oiseaux qui les consomment (Scriber & Slansky 1981; Buse *et al.* 1999). Par conséquent, il existe une forte pression pour que les prédateurs synchronisent les besoins de leur progéniture avec l'abondance de leurs proies (Durant *et al.* 2005; Visser *et al.* 2006; Durant *et al.* 2007; van Asch & Visser 2007). Si l'on admet l'existence d'une possible désynchronisation des chaînes alimentaires chez les espèces incapables d'ajuster correctement leur phénologie de reproduction à celle de leurs proies, alors les effets de cette désynchronisation devraient être visibles sur les taux de croissance à long terme de ces espèces (Both et al. 2006b). Dans une étude récente Moller et ses collaborateurs ont tenté de vérifier cette hypothèse. En considérant uniquement le groupe des oiseaux migrateurs transsahariens, ils ont collecté un grand nombre de tendances phénologiques à long terme d'avancement du retour migratoire disponibles dans la littérature (Moller et al. 2008). Dans cet article, ils mettent en évidence une relation significativement négative entre la tendance à l'avancement du retour migratoire et le taux de croissance à long terme considéré selon des classes qualitatives. Ainsi les espèces migratrices transsahariennes qui ont le moins avancé leur retour printanier connaissent les déclins les plus prononcés. Cette étude est importante car c'est la première qui teste cette hypothèse à grande échelle mais elle laisse deux questions en suspens : cette tendance temporelle à l'avancement est-elle indépendante de l'augmentation des températures liée au réchauffement climatique actuelle ou bien reflète-t-elle les ajustements annuels de la phénologie migratoire aux anomalies de températures ? Ce lien entre phénologie printanière et taux de croissance des populations existe-t-il aussi chez les espèces sédentaires et migratrices non transsahariennes ? Pour répondre à ces deux questions, nous avons mené une étude sur la phénologie de la reproduction de 20 espèces de passereaux communs en utilisant les données de l'observatoire STOC capture (**Article 6**). Tout comme les données de l'observatoire STOC EPS, les données STOC capture comportent aussi un message phénologique. En effet, la période couverte par les séances de capture à l'échelle de la France s'étend depuis début mai jusqu'à mi juillet. Au début de cette période, les juvéniles n'ont pas encore pris leur envol et ne sont donc pas détectés dans les captures. Ils vont faire leur apparition dans les captures dès la fin du mois de mai pour les espèces nicheuses précoces (des espèces sédentaires) et plus tard pour les espèces nicheuses tardives (notamment les migrateurs transsahariens). La proportion de jeunes dans les captures est donc variable au cours de la période de suivi. Nous avons fait l'hypothèse que l'apparition des jeunes dans les captures reflétait la phénologie de reproduction des adultes. Nous avons donc considéré la phénologie d'apparition des jeunes dans les captures comme une approximation de la date de ponte, donc de la réponse des femelles aux conditions environnementales. Une étude sur la Mésange charbonnière montre que celles-ci sont capable après la ponte de corriger la date d'éclosion en jouant sur la durée de l'incubation (Cresswell & McCleery 2003). Toutefois, cet ajustement reste mineur par rapport à celui de la date de ponte elle-même. En revanche, il demeure vrai que notre mesure de phénologie de reproduction n'est représentative que de la partie de la population qui parvient effectivement à se reproduire avec succès puisque nous en détectons la progéniture dans les captures. En appliquant la méthode GAM, nous avons donc estimé les anomalies de phénologie d'apparition des juvéniles dans les captures pour 20 espèces de passereaux communs pour la période 1989-2008. Ces anomalies montrent tout d'abord une relation négative avec la température printanière moyenne (nous avons choisi la période Janvier-Mai pour moyenner les températures). Plus ces températures sont élevées, plus les oiseaux se reproduisent tôt (**figure 10**). Ce résultat confirme la qualité de l'estimateur phénologique utilisé dans la mesure où de nombreuses études montrent un lien de corrélation entre date de ponte et température printanière (Vannoordwijk *et al.* 1995; Crick & Sparks 1999; Dunn & Winkler 1999; Visser *et al.* 2009a). Par ailleurs, pour l'ensemble des espèces, il y a une tendance temporelle à l'avancement de la phénologie de reproduction, ce qui est également en accord avec les résultats d'études menées à long terme notamment au Royaume-Uni (Crick et al. 1997). Nous avons donc testé la relation entre les réponses de la phénologie de reproduction de chaque espèce à la température et les tendances populationnelles sur la même période. Nous avons fait de même avec la tendance temporelle à long terme de la phénologie de reproduction.

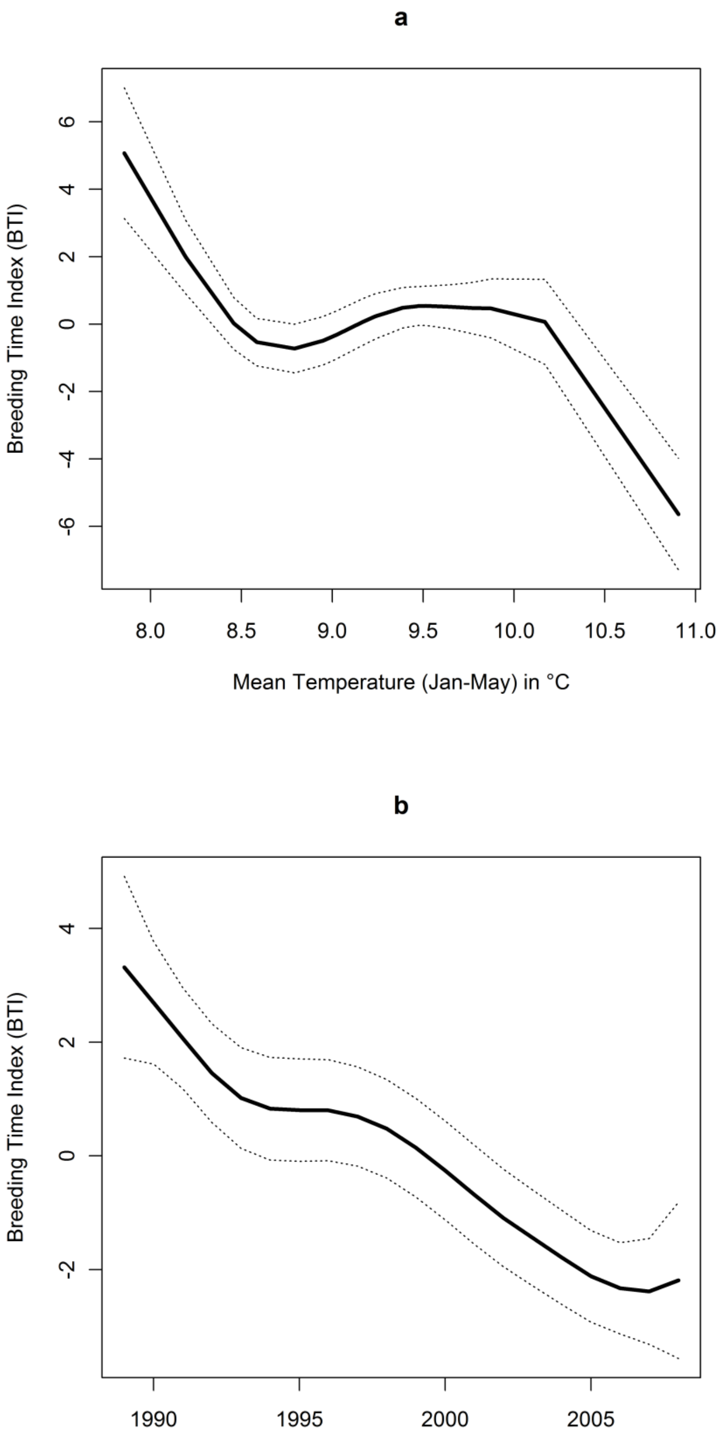
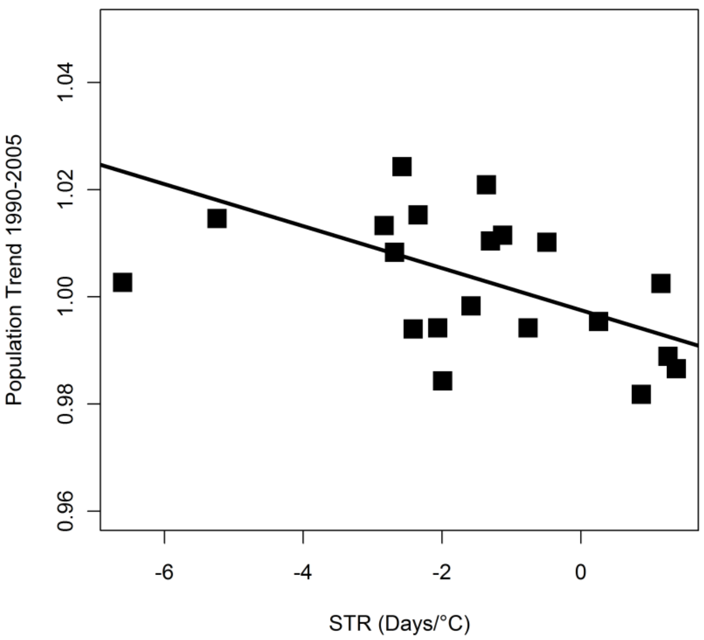


Figure 10. Anomalies de phénologie de reproduction chez 20 espèces de passereaux communs entre 1989 et 2008 estimées partir des données de l'observatoire STOC-capture. La figure (a) présente la relation entre ces anomalies phénologiques et la température journalière moyenne de janvier à mai pour la France. La figure (b) présente l'évolution temporelle des anomalies de phénologie au cours de la période d'étude (1989-2008).

Nous disposions des tendances à long terme mesurées pour la France sur la même période en utilisant les données STOC EPS. Toutefois, une étude complémentaire montre que les estimations d'abondance produites à partir des données STOC EPS sont biaisées par la phénologie des espèces. En effet, du fait de l'existence des variations saisonnières de la détectabilité qui ont été décrites précédemment, on compte significativement moins d'oiseaux pour les espèces à distribution saisonnière de comptages décroissante durant les années où leur phénologie est précoce. L'inverse est vrai dans une moindre mesure pour les espèces à distribution saisonnière des comptages croissantes. Ces variations phénologiques biaisent donc les estimations d'abondance notamment en prédisant de trop fortes diminutions chez les espèces à distribution décroissante, c'est-à-dire en majorité des espèces sédentaires (**Box 1**). Nous avons donc choisi de tester la relation entre réponse de la phénologie de reproduction à la température et taux de croissance à l'échelle européenne grâce aux données issues du programme paneuropéen de suivi des oiseaux communs (Pan European Common Bird Monitoring, PECBM). En effet, les tendances qui sont calculées dans ce cadre intègrent les données de l'ensemble des suivis mis en place à l''échelle européenne (Jiguet et al. 2009), ce qui probablement d'une part minimise le biais associé à la phénologie et d'autre part gomme les spécificités locales des tendances populationnelles pour faire potentiellement mieux apparaître les effets se produisant à l'échelle continentale comme le climat. Nous avons distingué trois types de réponses phénologiques à la température. La première correspond à la pente de régression de l'effet température printanière d'un modèle *Anomalie phénologique~Année*. Cette réponse ne fait pas la distinction entre l'ajustement réel à la température et un avancement graduel de la phénologie. Elle correspond en cela à la variable avancement phénologique de Moller et al. Pour faire cette distinction, nous avons estimé d'une part la pente de régression de l'effet température printanière ajusté à une tendance temporelle linéaire et d'autre part cette tendance phénologique temporelle dans un modèle *Anomalie phénologique~Température + Annee*. C'est la capacité de réponse à l'anomalie de température (c'est-à-dire la pente de régression de l'effet température dans ce dernier modèle) qui est significativement négativement corrélée à la tendance populationnelle à long terme. La tendance temporelle de la phénologie de reproduction n'est pas corrélée aux tendances populationnelles (**figure 11**).



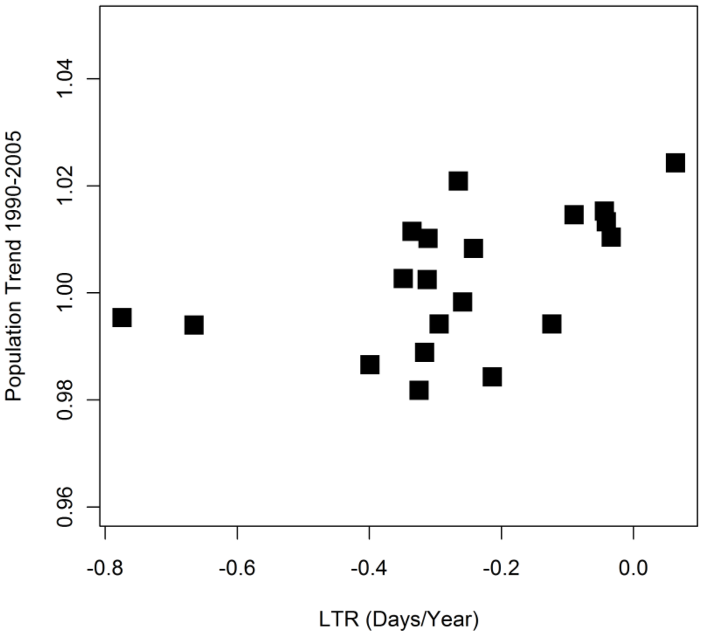
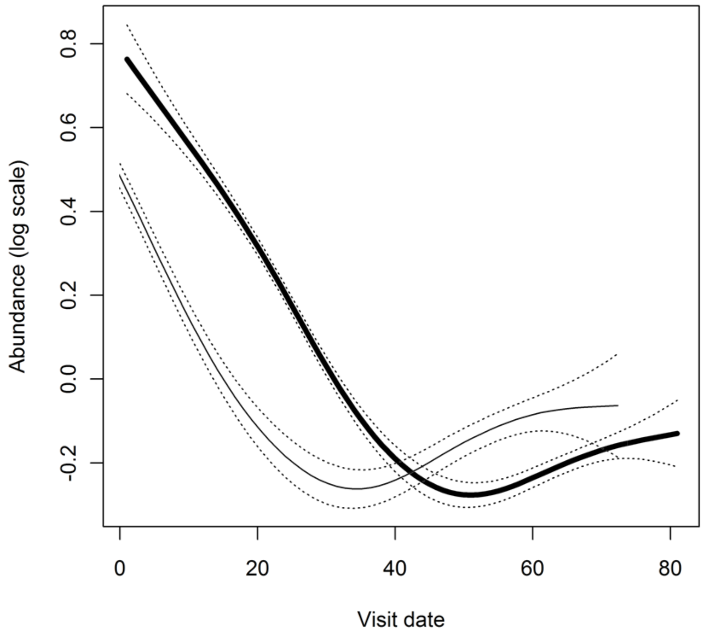


Figure 11. Relation entre les différents types de réponses phénologiques et les taux moyens de croissance à long terme de 20 espèces de passereaux communs. En (a), on observe la relation entre l'ajustement phénologique à la température annuelle, la droite de régression est figurée en trait continu (la relation est significativement négative). En (b) figure la relation entre l'évolution temporelle de la phénologie au cours de la période d'étude (1989-2008) et les taux moyens de croissance à long terme estimés pour l'Europe pour la période 1990-2005. Noter qu'il n'y a aucune évidence pour une relation négative comme dans Moller et al (2008).

Ces résultats aboutissent à une conclusion importante quant aux mécanismes de l'influence climatique à long terme sur les taux de croissances au travers de la phénologie. C'est bien la capacité d'ajustement de l'espèce à l'anomalie de température chaque année qui est corrélée à la croissance de la population à long terme. Cette croissance, ou ces déclins sur la période considérée, reflètent donc la somme des ajustements annuels à la température. Ces résultats sont les premiers à mettre en évidence ce mécanisme d'influence climatique à l'échelle d'un si grand nombre d'espèces communes. Ils identifient bien le climat comme un facteur important du devenir des populations par le biais de la phénologie pour des espèces qui appartiennent certes toutes à l'ordre des passériformes mais qui ont des traits d'histoire de vie très différents, notamment en termes de stratégie d'hivernage, de nombre de couvées, de régime alimentaire, de niche thermique ou de spécialisation pour l'habitat. En revanche, et c'est un point majeur à préciser parce qu'il n'a pas toujours été compris à la lecture de ce manuscrit, ces résultats ne permettent pas de conclure quant aux mécanismes pouvant expliquer l'ajustement phénologique à la température. En effet, deux mécanismes différents peuvent séparément ou conjointement expliquer la variabilité phénologique en réponse à la variabilité des températures (Gienapp et al. 2007; Pulido 2007). D'une part, cette flexibilité peut résulter de la plasticité phénotypique des individus qui composent la population. Ainsi, la date de ponte peut varier chez un même individu d'une année sur l'autre en réponse aux conditions environnementales (Przybylo *et al.* 2000; Both *et al.* 2004; Nussey *et al.* 2007). Un même individu, donc un même génotype peut produire différents phénotypes en fonction de l'environnement dans lequel on le place. Les différents génotypes produits constituent la norme de réaction à l'environnement (Pigliucci 2005). Cependant, dans un contexte de réchauffement à long terme, et sachant que la date de ponte est un caractère fortement héritable (Vannoordwijk *et al.* 1981; Sheldon *et al.* 2003), la sélection naturelle peut favoriser les individus qui se reproduisent tôt parce que ces individus contribueraient en moyenne davantage à la génération suivante que les individus qui se reproduisent tard. On peut dans ce cas s'attendre à l'échelle d'une population à observer une tendance linéaire vers des dates de pontes plus précoces. Dans un contexte climatique de plus en plus variable, la sélection naturelle peut même favoriser les individus possédant la plus grande plasticité phénotypique au niveau de leur date de ponte, c'est-à-dire conduire à des populations dont les individus sont en moyenne de plus en plus plastiques du point de vue de leur ajustement phénologique (Nussey *et al.* 2005; Charmantier *et al.* 2008). Pour être en mesure de s'intéresser à ces mécanismes, il faut étudier les populations à l'échelle individuelle, en utilisant des suivis longitudinaux de la phénologie de reproduction de plusieurs dizaines d'individus dont les relations de parenté sont connues. Cette configuration n'est pas du tout celle de notre étude, nous ne rentrons donc pas dans ce débat. En d'autres termes, l'ajustement phénologique aux anomalies annuelles de température ne peut pas être relié au mécanisme de la plasticité phénotypique moyenne de l'espèce. Pareillement, la tendance phénologique à long terme ne reflète pas obligatoirement un phénomène de sélection naturelle. Cette étude montre aussi que si la flexibilité phénologique semble un mécanisme important pour expliquer les taux de croissance à long terme des espèces, elle n’a pas de contribution indépendante forte à ces tendances comme le suggèrent les analyses en partition hiérarchique de variance. On peut penser que la capacité d’ajustement phénologique est partiellement corrélée à certains traits ou certaines caractéristiques inclus dans les analyses. Cette flexibilité phénologique est donc certainement davantage un mécanisme qui résulte de l’action conjointe de nombreux facteurs que nous avons cherché à déterminer par la suite.

Box 1. Les estimations d’abondance issues des programmes de point d’écoute sont-elles biaisées par les variations phénologiques printanières ?

Nous avons mis en évidence l’existence de variations saisonnières très marquées des évènements de détection sur les protocoles de type point d’écoute. Ces variations sont imputables à des variations du nombre d’oiseaux présents sur les lieux d’échantillonnages mais aussi de la probabilité de détection des oiseaux sachant leur présence. L’objectif premier des suivis à large échelle est de permettre la mise en place d’indicateurs d’abondance annuelle de façon à évaluer la santé des populations d’oiseaux à long terme. La standardisation du protocole, la couverture spatiale importante et l’effort de représentativité des habitats échantillonnés ont pour vocation de limiter le nombre de biais pouvant fausser la valeur des messages des indicateurs produit à partir des variations d’abondance estimées de ces données (Julliard & Jiguet 2002; Greenwood 2007). La question du biais phénologique dans les données de comptage a fait l’objet d’une étude par Selmi et ses collaborateurs. Dans ce travail les auteurs évaluent la variation saisonnière de l’estimation de la richesse spécifique par des points d’écoute au niveau d’oasis en Tunisie. En utilisant des analyses de type CMR (présence/absence de l’espèce sur les points d’écoute), ils montrent que la richesse spécifique estimée est fonction de la période à laquelle se déroulent les comptages et insistent sur la prise en compte de cette variable dans les estimations de richesse spécifique (Selmi & Boulinier 2003). C’est notamment parce que les variations saisonnière de détection sont connues qu’au moins deux passages sont effectués sur chacun des points d’écoute ou transects et que dans la plupart des cas c’est la valeur maximale des comptages à chaque point qui est utilisée pour estimer l’abondance annuelle. Cependant, nous avons mis en évidence que les distributions saisonnières de détection, pouvaient être décalées dans le temps d’une année sur l’autre en relation avec les variations phénologiques propres à chaque espèce. La simulation de courbes imitant les deux types de distributions observées (décroissantes et croissantes) montre que l’on s’attend pour les espèces possédant une distribution décroissante et une phénologie printanière précoce une année donnée, à une estimation d’abondance pour cette année plus faible par simple artefact phénologique. L’inverse est aussi vrai pour les espèces qui présentent des distributions saisonnières de détection croissantes. Toutefois pour ces dernières on s’attend à un effet moins fort du fait de la convergence des distributions à la fin de la période de comptage (**figure 12**).



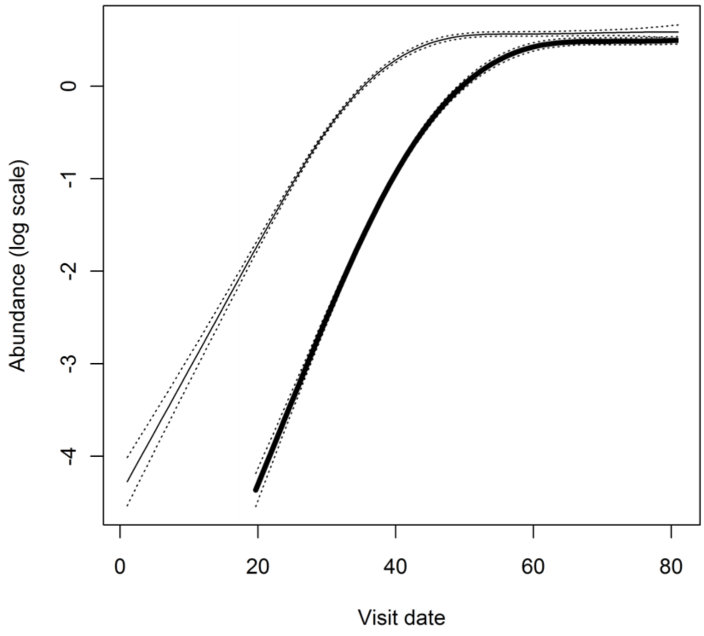


Figure 12. Illustration du biais phénologique attendu dans les estimations d'abondance en fonction de la forme de la distribution saisonnière des détections. En haut, pour des distributions décroissantes, on constate que le nombre total (ou maximal) d'oiseaux détectés est plus faible lorsque la phénologie printanière est précoce (courbe claire) que lorsque celle-ci est tardive (courbe foncée). Ce cas de figure concerne principalement les espèces sédentaires (exemple du Geai des chênes *Garrulus glandarius* ici). En bas, pour une phénologie croissante, le nombre total (ou maximal) d'oiseaux comptés est plus faible lorsque la phénologie est tardive (courbe foncée) que lorsqu'elle est précoce (courbe claire). L'effet semble moins important que pour les distributions décroissantes du fait de la convergence des deux courbes à la fin de la période de comptage (le décalage temporel est

identique sur les figures du haut et du bas). Ce dernier cas de figure concerne en majorité les espèces migratrices et notamment migratrices transsahariennes (exemple de la Tourterelle des bois *Streptopelia turtur* ici).

Nous avons donc testé les relations entre les indices d'abondance spécifiques produits à partir des données STOC EPS et les anomalies phénologiques estimées par la méthode GAM. Nos résultats montrent un fort effet des anomalies de phénologie annuelles sur les estimations d'abondance. Cet effet est d'ailleurs comme attendu plus marqué pour les espèces dont la distribution saisonnière des détections est décroissante. Pour ces espèces, plus la phénologie est précoce moins on compte d'oiseaux alors que c'est l'inverse pour les espèces qui montrent une distribution saisonnière des détections croissante. De plus l'effet est d'autant plus fort que la variation temporelle intra saisonnière des comptages est importante. Il existe donc bien un biais phénologique dans les estimations d'abondance telles qu'elles sont produites par les protocoles de type STOC. La quantification de ce biais pour chaque espèce est nécessaire pour tenter d'apporter une correction « phénologique » aux indices d'abondance. Cette correction est indispensable. En effet, la vocation des indicateurs de biodiversité, dont font partie les indicateurs fondés sur les tendances temporelles des abondances d'oiseaux est de fournir une information sans équivoque de la santé des populations indicatrices (Gregory et al. 2005; Gregory et al. 2008). Cette information est ensuite utilisée par les décideurs pour mettre en place des mesures de gestion en faveur de la biodiversité. Toutefois dans le cas des suivis type STOC, il se pourrait que des déclins trop prononcés soient prédits du fait d'un simple artefact phénologique dans les données. En réalité, pour des espèces qui parviennent à ajuster leur phénologie printanière aux conditions environnementales, et nous avons montré que ces espèces bénéficient de cet ajustement sur le long terme, on estime probablement des baisses de taux de croissance ou des augmentations trop faibles de celui-ci. La variabilité du climat devant augmenter au cours des prochaines décennies (IPCC 2007), on s'attend à des réponses phénologiques de plus en plus marquées et de plus en plus variables au moins chez les espèces qui montrent actuellement un ajustement phénologique important à la température (Primack et al. 2009). Si la correction phénologique des indices d'abondance n'est pas appliquée pour ces espèces, le message fournit par les indicateurs qui les prennent en compte pourrait devenir de plus en plus flou.

1.3. Variation interspécifique des capacités d'ajustement de la phénologie de reproduction à la température et traits d'histoire de vie des espèces.

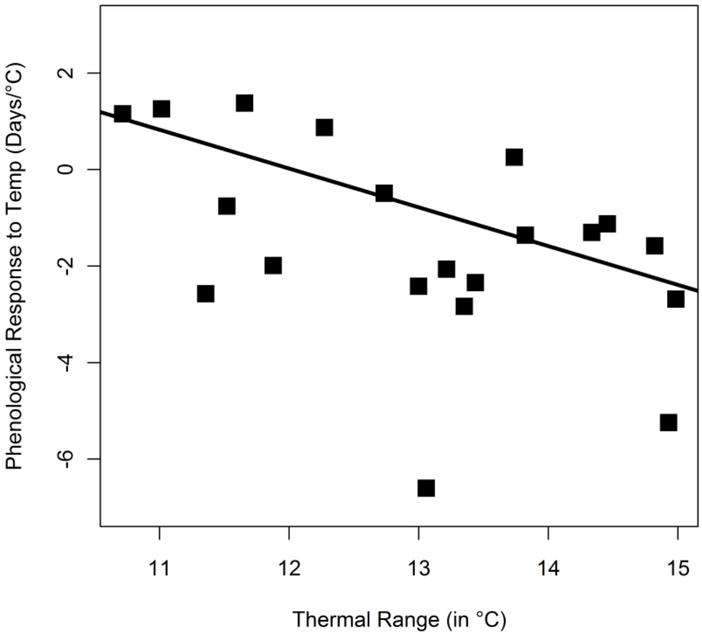
L'étude concernant la relation entre phénologie et taux de croissance à long terme des populations montre d'une part une certaine variabilité interspécifique des anomalies de phénologie annuelles, d'autre part de la capacité d'ajustement de la phénologie de reproduction à la température. Il est peu probable que la capacité d'ajustement phénologique soit distribuée aléatoirement parmi les différentes espèces considérées. Or comprendre comment se répartit cette flexibilité phénologique revêt une grande importance pour identifier les espèces qui pourraient subir le plus d'impact du changement climatique actuel. Pour explorer la variabilité des capacités d'ajustement phénologique, on peut distinguer deux types de contraintes (**Article 7**).

La première catégorie de contraintes regroupe les traits d'histoire de vie qui sont directement en relation avec le cycle de vie des espèces. Plusieurs travaux identifient à ce titre le groupe des migrateurs transsahariens comme des espèces à risque face au changement climatique (Gwinner 1996; Both & Visser 2001; Gordo & Sanz 2008; Both 2010; Jones & Cresswell 2010). En effet, d'une part, du fait de leur stratégie migratoire, le « planning » printanier est très chargé chez ces espèces puisqu'à leur retour tardif sur les lieux de reproduction succède immédiatement l'ensemble des étapes de la reproduction, c'est-à-dire la recherche d'un territoire, la recherche d'un partenaire et la reproduction au sens strict. On peut donc supposer que les contraintes temporelles très fortes liées à ce mode de vie limitent les possibilités d'ajustement de grande ampleur aux conditions environnementales locales (Jones & Cresswell 2010). La deuxième contrainte imposée par une stratégie migratoire transsaharienne est liée à l'acquisition, en fin d'hiver, d'informations concernant les conditions environnementales sur les quartiers de reproduction alors que les oiseaux se trouvent à de très grandes distances de ces lieux. De nombreux travaux attribuent à un contrôle endogène le départ des lieux d'hivernage vers les quartiers de reproduction (Berthold & Querner 1981; Berthold 1984; Berthold & Terrill 1991). Une étude suggère cependant l'existence d'un couplage climatique entre les conditions climatiques sur les lieux d'hivernage en Afrique et les conditions climatiques sur les lieux de reproduction en Europe (Saino & Ambrosini 2008). Toutefois, même si ce couplage existe et qu'il donne une certaine quantité d'information, il est peu probable qu'il en fournisse autant que des indices directement mesurables pour les espèces qui sont présentes toute l'année sur les lieux de reproduction ou à proximité. Enfin, quand bien même les migrateurs transsahariens auraient acquis l'information nécessaire pour arriver en temps et en heure sur les lieux de reproduction, le retour est lui aussi soumis aux aléas climatiques, ce qui limite encore les possibilités d'ajustement (Marra *et al.* 2005; Huppop & Winkel 2006; Tottrup *et al.* 2008; Both 2010). On peut donc faire l'hypothèse que la distance de migration est un facteur majeur de la capacité d'ajustement phénologique des espèces. Autre variable directement liée aux cycles de vie des espèces, le nombre moyen de couvées qu'elles élèvent chaque année. Dans les populations de Mésange charbonnière qui élèvent deux couvées, la date de ponte n’est pas reliée au pic d’abondance des insectes alors que c’est le cas dans les populations qui n’élèvent qu’une seule couvée (Verboven et al. 2001). On peut supposer que la pression à l’ajustement phénologique est plus élevée chez les espèces ou les populations qui n’élèvent qu’une couvée car celle-ci peut ne dépendre que d’une seule ressource alors que les espèces qui produisent deux couvées peuvent dépendre de plusieurs ressources différentes (Jiguet et al. 2007). On pourrait donc attendre une relation d’autant moins importante entre phénologie de la reproduction et température que l’espèce produit moins de couvées par an.

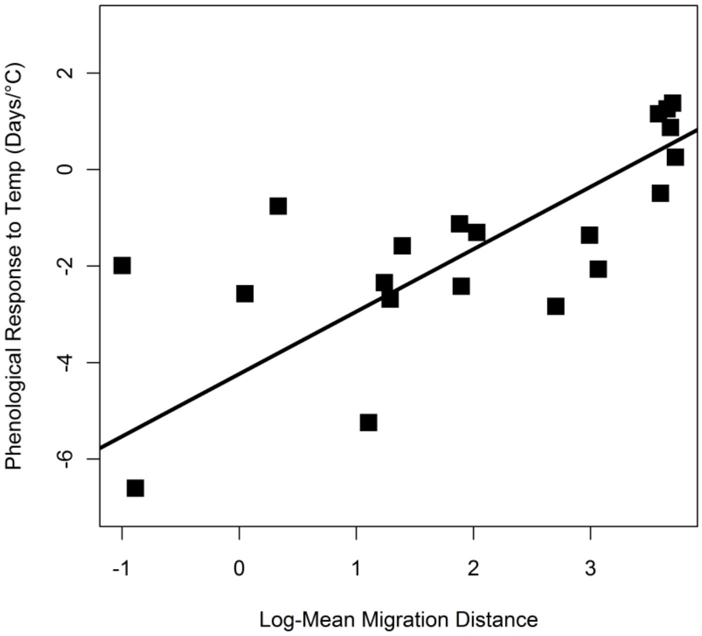
Le second groupe de contraintes dont on peut penser qu’elles influencent la capacité des espèces à ajuster leur phénologie au climat, est lié à leur capacité intrinsèque à exploiter leur environnement, c'est-à-dire à leur niche écologique. En effet, la capacité de réponse à un environnement changeant est fonction de la largeur de la niche écologique des espèces (Hutchinson 1957; Levins 1962; MacArthur et al. 1967; Scheiner 1993). En d’autres termes, dans un contexte de changement en cours, on attend que les espèces généralistes soient favorisées par rapport aux espèces spécialistes dont on pense qu’elles sont le résultat d’une évolution dans un contexte environnemental stable dans le temps et l’espace. En effet, la largeur de la niche écologique est considérée comme le résultat d’un compromis évolutif entre la variété des conditions environnementales permettant le maintien d’une espèce et son efficacité d’exploitation de chacune de ces conditions environnementales (Futuyma & Moreno 1988; Kawecki 1994; Kassen 2002). Ces prédictions ont été plusieurs fois vérifiées pour différents groupes taxonomiques parmi lesquels, les plantes (Fischer & Stocklin 1997), les insectes (Kotze & O'Hara 2003), les poissons (Munday 2004), les mammifères (Fisher et al. 2003) et les oiseaux (Julliard *et al.* 2004a; Jiguet *et al.* 2006). Chez ces derniers, deux dimensions (pas forcément indépendantes) ont été identifiées comme des facteurs important des tendances populationnelles à long terme : d’une part la tolérance des espèces vis-à-vis de l’habitat (Julliard et al. 2004a) et d’autre part la tolérance des espèces vis-à-vis de la température (Jiguet *et al.* 2006; Jiguet *et al.* 2009). Dans les deux cas, les espèces ayant une niche écologique et/ou thermique étendues voient leurs populations croître davantage que les espèces pour lesquelles ces niches sont plus restreintes. Par ailleurs, dans le contexte du réchauffement climatique actuel, les espèces qui ont une limite haute de niche thermique élevée sont celles qui se portent le mieux et ce à l’échelle du continent européen (Jiguet et al. 2007). Il semble donc que les espèces flexibles, tolérantes, généralistes soient avantagées dans le contexte des changements globaux ce qui conduit à un remplacement progressif de nombreuses espèces plus ou moins spécialistes par un nombre beaucoup plus faible d’espèces généralistes (Olden & Poff 2004; Devictor *et al.* 2007). On nomme ce phénomène l’homogénéisation biotique fonctionnelle (car basé sur les caractéristiques de la niche écologique des espèces). Nous avons montré dans l’étude précédente que la flexibilité phénologique des espèces était également une composante de leur taux de croissance à long terme. On peut donc se poser la question de l’existence d’un véritable syndrome de flexibilité qui préjugerait de l’avenir des espèces concernées. Ainsi, on peut faire l’hypothèse que les espèces généralistes pour la température et pour l’habitat sont celles qui sont aussi les plus flexibles du point de vue phénologique, elles seraient donc dotées des meilleures capacités d'ajustement à la température pour positionner leur cycle de reproduction. Nous avons donc inclus dans cette étude l'indice de spécialisation pour l'habitat estimé à partir des données de STOC EPS (Julliard et al. 2006), la largeur de la niche thermique. En effet, on peut penser que les populations situées proche de leur limite thermique pourraient montrer de plus faibles capacités d'ajustement parce qu'elles se trouvent dans un environnement suboptimal. Comme évoqué précédemment, cet ajustement nécessite l'acquisition d'information disponible dans l'environnement parce que le déclenchement de la reproduction se fait bien avant que ne survienne le pic d'abondance de la ressource et les besoins correspondant de la progéniture (Bourgault et al. 2006; Bourgault et al. 2009). On peut supposer que le décodage temporel de l'environnement qui se produit pour de nombreuses espèces à la fin de l'hiver ou au tout début du printemps repose sur des capacités cognitives variables selon les espèces. Deux études au moins suggèrent en effet que les espèces qui possèdent une masse cérébrale importante relative à leur taille se portent mieux que les espèces dotées d'encéphales plus réduits (Shultz et al. 2005; Sol et al. 2007). Une autre étude montre que les espèces qui possèdent les masses cérébrales relatives les plus élevées survivent mieux après avoir été introduites dans de nouveaux environnements (Sol et al. 2005). Nous avons par conséquent testé si la masse cérébrale relative au poids moyen pouvait être corrélée à la capacité d'ajustement phénologique des espèces aux conditions environnementales. Enfin, en relation avec la largeur de la niche écologique, nous avons inclus comme variable explicative dans nos modèles, le régime alimentaire. En effet, la réussite de la reproduction étant particulièrement sensible à la quantité et à la qualité de la ressource fournie à la progéniture, les espèces qui possèdent un régime alimentaire omnivore pourraient être favorisées et se trouver moins sous la pression de l'ajustement phénologique que les espèces insectivores strictes. On peut donc penser que la phénologie des premières sera moins sensible aux conditions environnementales que celle des secondes.

Les résultats de cette étude montrent que quatre des variables testées sont significativement reliées aux capacités des espèces à ajuster leur phénologie à la température printanière. Tout d'abord, la distance moyenne de migration est très fortement négativement corrélée à la capacité d'ajustement phénologique. Ainsi, les migrateurs transsahariens ajustent bien moins leur phénologie à la température printanière que les sédentaires et les migrateurs non transsahariens. Ensuite, les espèces qui ont une niche thermique et une niche habitat étendue ajustent significativement davantage leur phénologie de reproduction au climat que les espèces spécialistes thermiques. Enfin, les espèces possédant une masse cérébrale élevée relativement à leur poids ajustent également davantage leur phénologie à la température printanière que les espèces aux capacités cognitives plus limitées (**figure 13**). Toutefois, les effets de la spécialisation pour l'habitat et de la taille relative du cerveau ne demeurent pas lorsqu'ils sont ajusté aux deux précédents. En effet ils sont corrélés respectivement à la spécialisation thermique (une espèce spécialiste pour la température est aussi une espèce spécialiste pour l'habitat) et à la distance de migration (les espèces migratrices ont un cerveau plus petit que les espèces sédentaires). De ces trois facteurs, c’est la distance de migration qui contribue le plus à la variabilité interspécifique des capacités d’ajustement phénologique tout en sachant que c’est cette variable qui montre la plus importante variation interspécifique.

a


Phenological Response to Temp (Days/°C)
2
0
-2
-4
-6
11
12
13
14
15
Thermal Range (in °C)

b


Phenological Response to Temp (Days/°C)
2
0
-2
-4
-6
-1
0
1
2
3
Log-Mean Migration Distance

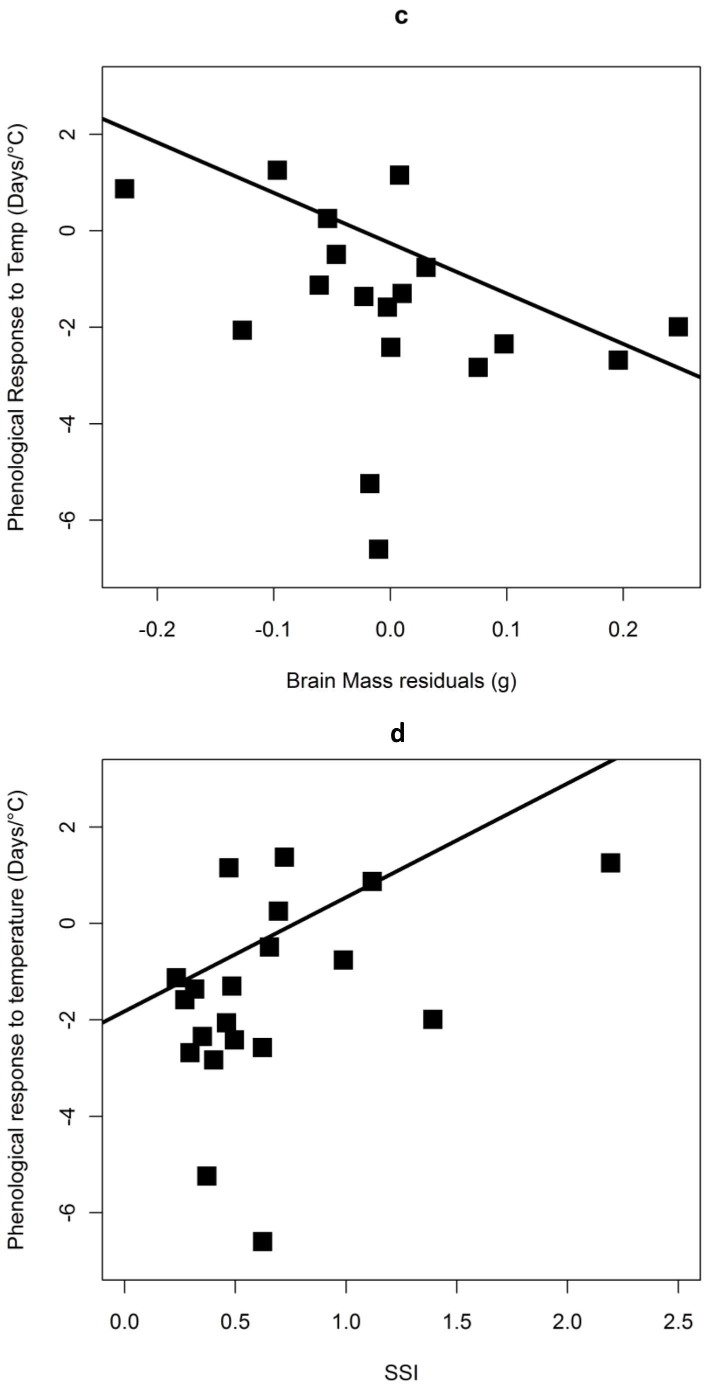


Figure 13. Relations entre les capacités d'ajustement de la phénologie de reproduction de 20 espèces de passereaux communs à la température moyenne journalière de janvier à mai pour la période 1989-2008 et (a) le degré de spécialisation thermique soit la différence entre la température moyenne des 5 pourcents de sites les plus chauds et la température moyenne des 5 pourcents de sites les plus froids où l'espèce est présente à l'échelle européenne, (b) la distance moyenne de migration (échelle logarithmique), (c) la masse cérébrale relative au poids moyen de l'espèce estimée par les résidus d'une régression linéaire entre la masse cérébrale brute et le poids moyen de l'espèce et (d), l'indice de spécialisation de l'espèce pour l'habitat mesurée à partir des données du STOC EPS.

Par ailleurs, les migrateurs transsahariens montrent tous des capacités d'ajustement phénologique à la température proche de 0. En d'autres termes, le groupe des migrateurs transsahariens apparaît très homogène au regard des autres espèces. Ce résultat confirme donc l'hypothèse d'une stratégie très contraignante du point de vue phénologique et offrant de très faibles possibilités de flexibilité (Gwinner 1996). Ce manque de souplesse phénologique pourrait être l'un des mécanismes prévalant au déclin des migrateurs transsahariens constaté dans plusieurs études en Europe (Sanderson *et al.* 2006; Pearce-Higgins *et al.* 2009). Elle pose également question sur la capacité des espèces migratrices à évoluer vers davantage de plasticité phénologique. La sélection naturelle de la plasticité phénotypique a été démontrée chez la Mésange charbonnière mais cette espèce est sédentaire (Nussey *et al.* 2005; Charmantier *et al.* 2008). La stratégie migratoire longue distance pourrait imposer une forte contrainte évolutive sur la sélection d'individus fortement plastiques. La relation significative entre le degré de spécialisation thermique et la capacité d'ajustement phénologique suggère l'existence d'un syndrome de tolérance ou de flexibilité. Les espèces aux niches écologiques (la température fait partie des dimensions de la niche écologique) étendues sont flexibles du point de vue phénologique. Par conséquent l'ajustement phénologique pourrait être l'un des mécanismes expliquant la bonne santé de ces espèces à l'échelle continentale. Mais plus encore, l'existence de ce « syndrome » et de la relation forte qui lie flexibilité ou largeur de niche avec les taux de croissance des populations, constitue un élément très probant du fait même que les écosystèmes se trouvent dans un contexte changeant (Kassen 2002). Comme nous l'avons déjà explicité, les espèces spécialistes ont évolué en réponse à des environnements stables et exploitent très efficacement leur niche (Futuyma & Moreno 1988). Néanmoins, la théorie de la spécialisation PREDIT que les espèces généralistes seront favorisées dans un contexte changeant (Kawecki 1994; Kassen 2002). Par conséquent, on peut dire que ces résultats, conjointement à ceux qui ont déjà été mis en évidence sur cette thématique attestent de l'intensité des perturbations auxquelles sont actuellement soumis les écosystèmes. Enfin, le fait que la capacité d'ajustement phénologique des espèces soit reliée à leur masse cérébrale relative laisse penser que cette flexibilité est reliée à des facultés cognitives susceptibles de permettre aux espèces de suivre l'avancement printanier de l'environnement avec précision (Dall & Cuthill 1997). Plusieurs études ont abordé le problème des indices environnementaux pouvant aiguiller les oiseaux dans l'ajustement de leur phénologie de reproduction. Si l'influence directe de la température sur le réglage de la date de ponte semble possible comme le démontre une étude en dispositif expérimental (Visser et al. 2009a), il n'en demeure pas moins que selon l'environnement dans lequel se trouve la population, l'ajustement phénologique peut faire intervenir des types d'information variés comme le montre une étude récente sur la date de ponte de la Mésange bleue (Thomas et al. 2010). Dans cette étude, les auteurs montrent que dans les forêts de chênes à feuillage caduc, où les femelles pondent leurs œufs tôt au printemps, la phénologie de la végétation ou des insectes règle la date de ponte. Dans les forêts de chênes à feuillage persistant, où la reproduction se produit plus tard en saison, les femelles passent d'un système de repères principalement basés sur la phénologie à un système de repères basés surtout sur la température. Les résultats de notre étude supportent l'idée d'une grande complexité de l'information à acquérir pour ajuster la phénologie de reproduction de façon optimale aux conditions environnementales. Toutefois, il n'est pas surprenant que cet effet de la masse cérébrale ne soit pas significatif ajusté aux deux autres effets. En effet, les espèces migratrices transsahariennes de notre étude ont des masses cérébrales plus faibles que les espèces sédentaires et migratrices non transsahariennes. Ceci est cohérent avec une étude précédente qui montre que les encéphales d'espèces migratrices sont moins grands que ceux des espèces sédentaires (Sol et al. 2010). Dans leur article, les auteurs proposent comme explication à cette différence la perte de fonctions cognitives non nécessaires une fois la migration apparue. Ces facultés pourraient par conséquent correspondre à l'acquisition d'information disponible sur les lieux de reproduction en hiver. En effet, chez les migrateurs, on observe non pas un changement de comportement alimentaire saisonnier mais un changement spatial. Par conséquent, il est possible que la capacité des espèces sédentaires à varier leur régime alimentaire au cours des saisons soit liée à leur capacité à ajuster leur phénologie de reproduction au climat printanier. Les espèces migratrices qui ont développé une stratégie basée sur une variation spatiale seraient donc moins flexibles.

1.4. Conclusion partielle : influence du climat sur la démographie par le biais de la phénologie.

Pour conclure sur les mécanismes d'influence du climat via l'ajustement phénologique des espèces, nous avons montré qu'une partie des variations d'abondance mesurées grâce aux programmes de suivis nationaux à l'échelle continentale, est très certainement imputable à la somme des ajustements phénologiques de chaque espèce au climat printanier. Il apparaît que certains groupes d'espèces, notamment les migrateurs transsahariens d'une part et les espèces spécialistes écologiques d'autre part, sont davantage susceptibles de subir les conséquences du changement climatique actuel et tout particulièrement de l'augmentation attendue de la variabilité interannuelle du climat. Pour ces espèces sous haute « pression phénologique », on peut se demander dans quelle mesure elles pourront s'adapter (au sens évolutif du terme) au changement climatique étant donné les contraintes évolutives importantes qui s'exercent sur elles. Des changements de stratégie de migration sont en cours chez plusieurs espèces (Berthold et al. 1992; Rivalan et al. 2007; Visser et al. 2009b) mais pas une seule d'entre elle ne figure dans la catégorie des migrateurs transsahariens. On peut donc nourrir de vives inquiétudes quand à l'avenir de ce groupe. Quant aux espèces spécialistes écologiques, leur faible capacité à faire face à la variabilité climatique est à l'image de la capacité des espèces spécialistes à faire face aux perturbations d'une manière plus générale. Ainsi, les espèces généralistes qui semble-t-il présentent un « syndrome de flexibilité » paraissent beaucoup plus à même de résister voire de bénéficier de la perturbation climatique actuelle et à venir. Elles pourraient d'ailleurs bénéficier de la relaxation de compétition face aux espèces spécialistes suite au déclin de celles-ci.

2. Vers une prise en compte de la sensibilité de la démographie au climat dans les modèles prédictifs de distribution sous scénario climatique.

2.1. Prédire l'aire de distribution future d'une espèce sous scénario climatique : principe de la modélisation de niche.

Si la dernière décennie a vu se multiplier les études mettant en évidence les conséquences des changements climatiques sur les populations d'oiseaux, au moyen de longues séries temporelles passées, elle a également vu se développer une discipline tournée vers l'avenir : la « modélisation de niche » (Guisan & Thuiller 2005). En effet, la connaissance des mécanismes de l'influence climatique sur la démographie est indispensable pour identifier des espèces ou des groupes d'espèces à risque face à la perturbation à venir. Toutefois, le cadre de la niche écologique permet une projection, dans le futur, de la niche écologique actuelle des espèces, en prenant en compte ce que l'on peut prédire de l'évolution des paramètres climatiques à grande échelle spatiale (Peterson *et al.* 2002; Pearson *et al.* 2007). Le principe de la « modélisation de niche » découle donc directement de la théorie de la niche écologique (Hutchinson 1957). Elle suppose la capacité à estimer la largeur de la niche écologique relative à N paramètres environnementaux (Pearson & Dawson 2003; Thuiller *et al.* 2005; Araujo & Guisan 2006). Cette largeur de la niche écologique réalisée définit donc par projection sur un territoire donné une surface possible pour la présence de l'espèce. Plusieurs travaux ont effectué cette modélisation pour les oiseaux mais également pour d'autres taxons (Thuiller *et al.* 2005; Pearson *et al.* 2007; Green *et al.* 2008; Huntley *et al.* 2008). Dans un premier temps, pour caractériser la niche écologique d'une espèce, une distribution actuelle ou passée des présences/absences de cette espèce est modélisée en relation avec des variables environnementales connues à l'échelle de la zone étudiée. Si l'on considère l'exemple climatique, cette première étape permet donc d'estimer une probabilité d'adéquation climatique corrélée à la présence d'une espèce. Idéalement, plusieurs types de modèles sont utilisés et c'est une prédiction consensuelle qui est formulée (Ensemble forecasting) (Thuiller *et al.* 2005; Thuiller *et al.* 2009). La deuxième étape correspond à la validation de la niche modélisée par la prédiction de l'aire de distribution actuelle (connue) de l'espèce. La troisième étape correspond à l'utilisation des corrélations entre présence de l'espèce et variables environnementales, mises en évidence lors de la première étape, ainsi que des prédictions climatiques spatiotemporelles (telles que celles formulées par le GIEC) pour déterminer les zones de présence possibles de l'espèce à plus ou moins long terme en assumant que ces exigences climatiques vont demeurer constantes. Par conséquent, comme le décrivent Thuiller et al. dans leur article (2009), la méthode repose sur un « espace écologique » où l'on exploite des données relatives à l'espèce et aux paramètres environnementaux et un « espace prédictif » (**figure 14**) qui utilise des prévisions concernant les paramètres environnementaux pour fournir l'aire de distribution future possible de l'espèce (Thuiller et al. 2009).

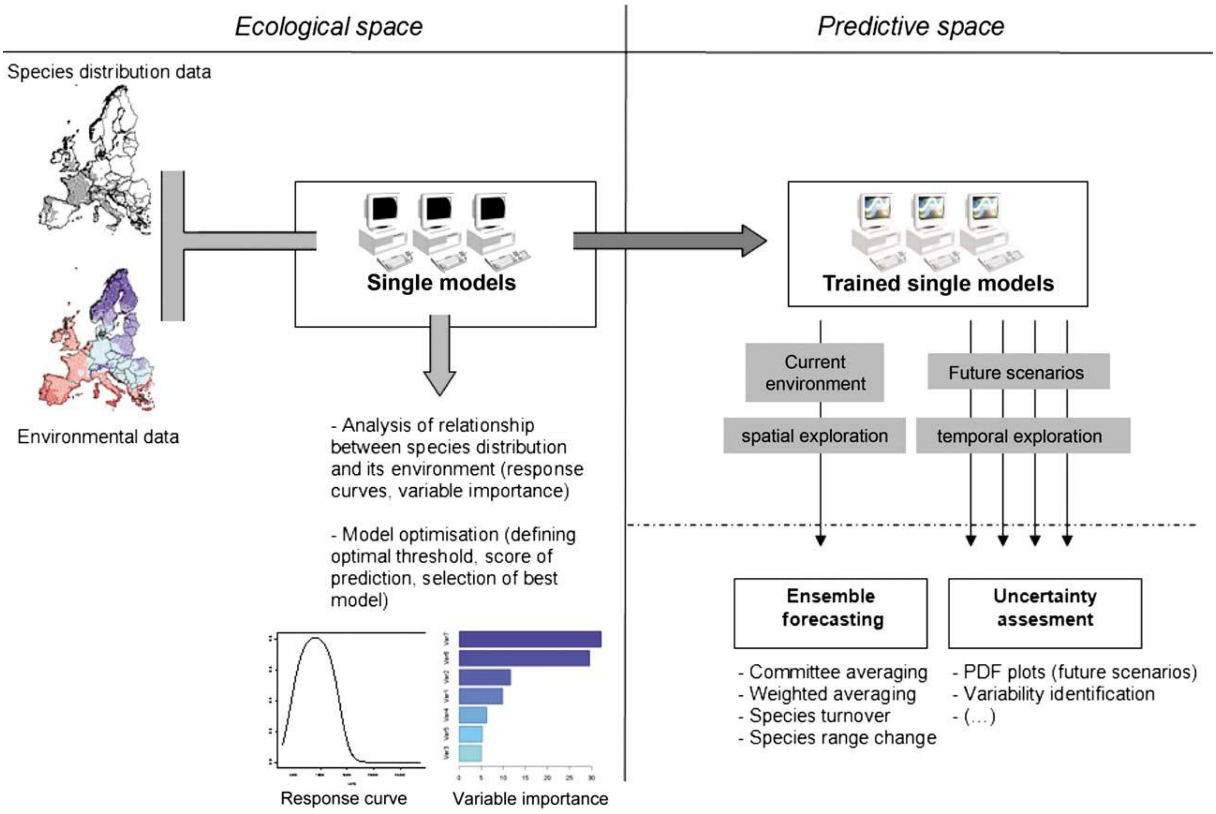


Figure 14. Principe de l' « Ensemble Forecast » permettant de formuler des prédictions concernant la distribution future d'espèces sous différents scénarios environnementaux (changement climatique, changement de l'habitat…). Cette méthode repose sur deux étapes bien distinctes puisque la première repose sur l'utilisation de données avérées alors que la seconde utilise des prédictions pour les paramètres environnementaux ainsi que les relations de dépendances de la présence d'une espèce vis-à-vis des paramètres environnementaux mises en évidence lors de la première étape. Figure extraite de Thuiller et al. (2009).

2.2. Application des modèles de niche à l'avifaune européenne et limites.

Cette méthode a été appliquée à l'échelle européenne à plus de 400 espèces d'oiseaux nicheurs (Huntley *et al.* 2007; Huntley *et al.* 2008). Cet ouvrage modélise les distributions actuelles et à l'horizon 2100 pour l'ensemble des espèces de la zone concernée. Par ailleurs, c'est en utilisant les distributions prédites par ce travail qu'un indicateur d'impact du réchauffement climatique sur les oiseaux a été publié par Gregory et al. en 2009. En effet, ces auteurs ont calculé pour chaque espèce le rapport de surface de l'aire de distribution future sur l'aire actuelle et corrélé ces rapports aux taux de croissance à long terme des espèces à l'échelle européenne. Ainsi, les espèces dont on prédit qu'elles vont voir leur aire de distribution s'élargir sont actuellement celles qui montrent des taux de croissance, mesurés par les données de suivis nationaux similaires au STOC sur 18 pays, les plus élevés. De plus, les capacités de ces modèles à rétroprédire les tendances populationnelles passées apportent un crédit intéressant à cette méthode (Green et al. 2008). Toutefois, elle est insuffisante à plusieurs égards.

Tout d'abord, les incertitudes relatives aux prédictions produites par ces modèles sont très importantes (Araujo & Guisan 2006; Buisson *et al.* 2010). En effet, les intervalles de confiances qui encadrent les scénarios climatiques sont larges (Murphy *et al.* 2004; Stainforth *et al.* 2005; Heikkinen *et al.* 2006). Par conséquent cette incertitude climatique est mécaniquement retrouvée au niveau des prédictions d'aires de distribution. De plus, actuellement, les prédictions formulées par les modèles de niches ne reflètent que les corrélations entre la présence/absence de l'espèce et les paramètres abiotiques considérés (ici des paramètres climatiques). Ainsi, il est encore difficile de produire des prédictions tenant compte les interactions biotiques qui sont pourtant un facteur majeur de la distribution des espèces (Connell 1961; Silander & Antonovics 1982; Davis *et al.* 1998; Araujo & Pearson 2005), si ce n'est en intégrant comme variable la distribution de l'espèce interagissant avec l'espèce d'intérêt (Heikkinen et al. 2007). Il faudrait pour cela être en mesure de quantifier à grande échelle spatiale des phénomènes de compétition, de prédation (au sens large) ou de facilitation. Ces données ne sont pas encore disponibles à l'heure actuelle. Enfin, la plupart des modèles de niche tels qu'ils fonctionnent actuellement utilisent des données de présence/absence et non des données d'abondance (Les approches de type Modèle Linéaire Généralisé ou Modèles Additifs Généralisés pourraient utiliser l'abondance). Le corollaire de ce fonctionnement est que l'on assume une sensibilité identique de l'espèce aux conditions environnementales dans l'ensemble de l'aire de distribution. Or la démographie d'une espèce le long de son aire de distribution n'est pas uniforme (Brown *et al.* 1996; Mehlman 1997; Angert 2006, 2009). A titre d'exemple, certaines populations qui se trouvent dans des zones très favorables produisent un excès d'individus, alors que d'autres populations localisées dans des zones en marge de la niche écologique de l'espèce ne doivent leur persistance qu'à une arrivée d'oiseaux issus des populations localisées en zones favorables, par dispersion (Brown 1969; Dias 1996). La dynamique des populations sources (les premières) diffèrent ainsi de celle des populations puits (les secondes). Or les données de présence/absence utilisées pour modéliser l'aire de distributions futures des espèces sous scénario climatique ne permettent pas de distinguer entre différents types de populations. La conséquence de cette approximation est une probable surestimation de la taille de la niche écologique d'une espèce (Pearson & Dawson 2003; Svenning & Skov 2004). En effet, dans le cas d'un système de populations fonctionnant en dynamique sources-puits, la niche écologique réalisée, mesurée par la présence de l'espèce sur le terrain, dépasse la niche fondamentale théorique puisque certaines populations ne peuvent se maintenir que par apport récurrent d'individus issus de la dispersion (Pulliam 1988, 2000).

2.3. Vers une intégration de la sensibilité différentielle des populations d'oiseaux au climat dans la modélisation de niche.

L'amélioration du pouvoir prédictif des modèles de niche passe nécessairement par une meilleure compréhension de la structuration spatiale de la niche climatique des espèces, c'est-à-dire la projection de cet espace multidimensionnel à la surface du globe. Les modèles de niche tels qu'ils sont appliqués actuellement reposent sur l'hypothèse que la distribution actuelles des espèces, c'est-à-dire leur niche climatique réalisée représente une bonne approximation de leur niche climatique fondamentale ou alors qu'elle est incluse dans la niche fondamentale. Cette conception renvoie aux origines de la théorie de la niche écologique (Hutchinson 1957; James et al. 1984). Ainsi, dans une vision classique, la niche écologique fondamentale définit un ensemble d'espaces possibles pour la présence de l'espèce. Cependant, l'espèce, notamment parce qu'elle peut-être limitée par ses capacités à disperser, peut ne pas occuper la totalité de cette niche fondamentale (Svenning & Skov 2004). Dans ce cas, la niche réalisée est de taille inférieure à celle de la niche fondamentale. Il s'ensuit qu'utiliser la distribution des espèces pour modéliser leurs exigences écologiques peut conduire à une prédiction pessimiste de leur distribution future. Cependant, il a été proposé il y a une vingtaine d'année que la niche écologique réalisée puisse dans certains cas outrepasser la niche fondamentale. Dans son article en 1988, Ronald Pulliam propose en effet un modèle dans lequel il distingue deux types de fonctionnements populationnels (Pulliam 1988). D'une part, il y aurait des populations situées dans la niche fondamentale de l'espèce et qui du fait de bonnes conditions pourraient produire un excès d'individus. D'autre part, des populations situées hors de la niche écologique fondamentale pourraient persister au moins de façon temporaire grâce à la dispersion des jeunes produits en excès dans les populations situées dans la niche fondamentales (Dias 1996). Ces dernières sont qualifiées par lui de populations sources alors que les populations hors niche fondamentale sont qualifiées de populations puits dépendantes du taux d'immigration. Dans ce cas, la niche réalisée est donc plus grande que la niche fondamentale, ce qui là encore peut avoir des conséquences quant à la qualité des prédictions de distributions futures qui pourraient ainsi se trouver surestimées (Pulliam 2000). C'est cette question des relations entre niches écologiques fondamentales et réalisées que nous allons aborder dans cette dernière partie et ce notamment pour la niche climatique qui définit la distribution des espèces à une échelle plus importante que celui de la niche écologique dans sa conception classique. Nous avons pour cela formulé deux hypothèses relatives à la distribution observée des espèces d'oiseaux et mis au point une méthode permettant de trancher entre ces deux hypothèses. Dans le cas d'une niche fondamentale incluant la totalité de la niche réalisée, on peut s'attendre à observer une sensibilité des taux démographiques, et notamment du taux de croissance des populations, croissante en fonction des variables environnementales et notamment climatiques. Cette hypothèse est suggérée par plusieurs études sur le terrain concernant des plantes et des oiseaux (Mehlman 1997; Angert 2006, 2009). La deuxième hypothèse suggère l'existence de populations en dehors de la niche fondamentale et une dynamique de populations de type source-puits. Toutefois, il est évident que la notion de sources-puits s'applique au niveau local (Howe *et al.* 1991; Thomas & Kunin 1999) étant donné les distances de dispersion natales réduites chez la plupart des passereaux (Paradis et al. 1998). Cependant, on peut supposer l'existence de la proportion de population sources et de populations puits le long de l'aire de distribution et d'un gradient d'adéquation climatique. Ainsi l'aire de distribution ferait apparaître un cœur composé essentiellement de populations sources et une aire marginale où seraient localisées une proportion croissante de populations puits au fur et à mesure que les conditions climatiques s'éloigneraient des frontières de la niche fondamentale (**figure 19**). Nous avons étudié la plausibilité de chacune de ces hypothèses pour trois espèces modèles dont les traits d'histoire de vie suggèrent le climat comme un facteur majeur de la dynamique temporelle des populations (Robinson et al. 2007b). De plus, ces trois espèces se trouvent en limite septentrionale de leur aire de distribution au niveau de la France. Ce sont la Bouscarle de Cetti (*Cettia cetti*), la Cisticole des joncs (*Cisticola juncidis*) et la Fauvette pitchou (*Sylvia undata*). Contrairement à la plupart des autres Sylvidés, elles demeurent sur ou proche de leurs zones de reproduction pendant l'hiver où l'on prédit que leur régime insectivore strict rend leur survie hivernale dépendante du climat. Par ailleurs, ces espèces sont connues pour les fluctuations importantes montrées par leurs tailles de populations ou aires de distribution au cours des dernières décennies et notamment des replis très importants suite à des hivers particulièrement rigoureux (Robinson et al. 2007b). En revanche, malgré leurs similitudes sur le plan de la stratégie migratoire et du régime alimentaire, ces trois espèces fréquentent des milieux différents puisque la Bouscarle de Cetti niche dans les milieux buissonnants en bordure de zones humides, la Cisticole des Joncs dans les prairies humides et la Fauvette Pitchou dans les landes plutôt sèches et épineuses (Bibby 1976). Nous avons dans un premier temps établi la relation supposée entre climat hivernal et abondance estimée grâce aux données STOC EPS au printemps. La température moyenne hivernale est significativement corrélée à l'abondance de ces trois passereaux au printemps. Nous avons cherché à expliquer ces variations d'abondance au printemps par un mécanisme démographique. Ceci était possible pour l'une de ces trois espèces, la Bouscarle de Cetti, à partir des données du STOC-capture qui nous ont permis d'estimer les paramètres de survie et de productivité.

2.3.1 Relier les variations d'abondance à des mécanismes démographiques : estimer la survie annuelle à partir des données STOC.

2.3.1.1 Les techniques de capture-marquage-recapture : des suivis longitudinaux.

Les données.

L'estimation du taux de survie moyen à l'échelle d'une ou plusieurs populations a donné lieu à d'importants développements statistiques au cours des dernières décennies (Cormack 1964, 1989; Cormack & Jupp 1991; Lebreton *et al.* 1992; Anderson *et al.* 1994; Anderson *et al.* 2000). Avant de présenter succinctement le principe de l'estimation d'un taux de survie, passons quelques instants à décrire les données nécessaires à cette estimation. La mesure de la mortalité requiert une prise d'information à l'échelle individuelle. Elle suppose que l'on échantillonne un certain nombre d'individus que l'on estime représentatifs de l'ensemble de la population. Par conséquent, on va réaliser un suivi longitudinal des nombreux individus. Afin de distinguer les individus qui forment l'échantillon des autres mais aussi pour reconnaître chacun des individus, ceux-ci vont être « marqués » de façon unique. Pour les passereaux qui nous concernent ici, la marque est une bague portant un numéro unique. L'individu, une fois capturé, marqué et relâché, appartient à l'échantillon et ce sont les évènements ultérieurs de recapture de ce même individu identifiable (et de l'ensemble des autres individus de l'échantillon) qui vont permettre l'estimation du taux de survie. En effet, chaque fois que l'observateur se rendra sur le terrain pour capturer des oiseaux, il sera susceptible de capturer ou non un individu donné déjà marqué. On pourra alors construire pour chacun des individus une histoire de vie, c'est-à-dire une suite de 0 et de 1 qui représentent respectivement les évènements de non capture et de capture à chaque fois que l'observateur s'est rendu sur le terrain pour tenter de capturer. Les individus marqués lors d'une session de capture donnée forment une cohorte.

Le programme STOC capture, outre les informations qu'il fournit sur le succès reproducteur, peut être envisagé comme un protocole de capture-marquage-recapture à grande échelle spatiale. En effet, chaque printemps, sur chaque site, les bagueurs effectuent entre trois et cinq sessions de capture pendant lesquelles sont marqués un certain nombre d'individus et repris un certain nombre d'autres individus déjà marqués. Il est donc possible de reconstruire les histoires de capture de chacun des oiseaux marqués dans le cadre du programme STOC à l'échelle de chaque site.

Les paramètres modélisés.

Le lien entre les évènements de capture (ou de non capture) et le taux de survie moyen sur un site donné suppose la décomposition de la détection (ou non) d'un oiseau déjà marqué lors d'une session de capture en deux composantes (Lebreton et al. 1992). L'interprétation d'une capture d'un oiseau marqué est sans équivoque, elle signifie que l'oiseau est vivant ET présent sur le site. En revanche, l'absence de capture d'un individu peut signifier trois choses. L'individu peut être physiquement mort, il ne sera plus jamais capturé dans ce cas. Il peut aussi avoir définitivement quitté le site auquel cas il ne sera jamais revu, il est donc dans ce cas « localement mort ». L'individu peut enfin être vivant, présent sur le site, mais ne pas être capturé lors d'une session donnée. En effet la probabilité de détection (ici nommée probabilité de recapture) déjà évoquée en première partie, est dans la très grande majorité des cas inférieure à 1 et même très inférieure à 1. Si l'on regroupe dans une même classe les oiseaux physiquement morts et localement morts parce qu'il est impossible à l'échelle d'un site de distinguer entre ces deux phénomènes, le problème de l'estimation du taux de survie « locale » se résume à tenter de faire la différence entre les absences de captures dues à la disparition définitive de l'individu de l'échantillon et la présence non détectée des individus. Par conséquent, ce ne sont pas un mais deux paramètres que l'on estime lorsque l'on recherche le taux de survie : le taux de survie d'une part, la probabilité de recapture d'autre part. Pour un individu donné et une session de capture donnée, les évènements de recapture et de non recapture forment un système complet d'évènements. En d'autres termes, le résultat de la session pour cet individu se résume à un jeu de pile ou face à la différence près que la pièce n'est dans ce cas pas équilibrée. Ainsi, la probabilité de capturer l'individu n'est pas 0.5 mais le taux de survie multiplié par la probabilité de détection de l'individu sachant qu'il est « localement vivant ». Comme pour le jeu de pile ou face, cette situation peut-être résumée par une loi de Bernoulli de probabilité *P=Survie x Probabilité de détection*. Si l'on considère maintenant non plus un mais tous les individus marqués précédemment sur le site, le nombre d'individus marqués capturés lors d'une session peut être représenté par un tirage dans une loi binomiale dont l'effectif vaut le nombre d'individus marqués précédemment et la probabilité d'un succès c'est-à-dire de capturer un individu vaut *P* (**figure 15**).

Formalisation des histoires de vie et probabilités associées.

On peut élargir ce modèle à une succession de sessions de capture dont les résultats peuvent être modélisés par un tirage dans une loi multinomiale (Cormack 1989; Cormack & Jupp 1991). Pour ce faire, on peut résumer l'intégralité de l'information comprise dans le jeu de données en construisant le M-array (**tableau 1**), c'est-à-dire un tableau dont la première colonne contient à chaque ligne le nombre d'individus relâchés à chaque session (Grosbois et al. 2009). Les colonnes suivantes forment une matrice de terme générique a_{ij} valant le nombre d'individus relâchés à la session *i* et repris pour la première fois lors de la session *j*. La dernière colonne prend à chaque ligne pour valeur le nombre d'individus relâchés à la session *i* et jamais revu par la suite.

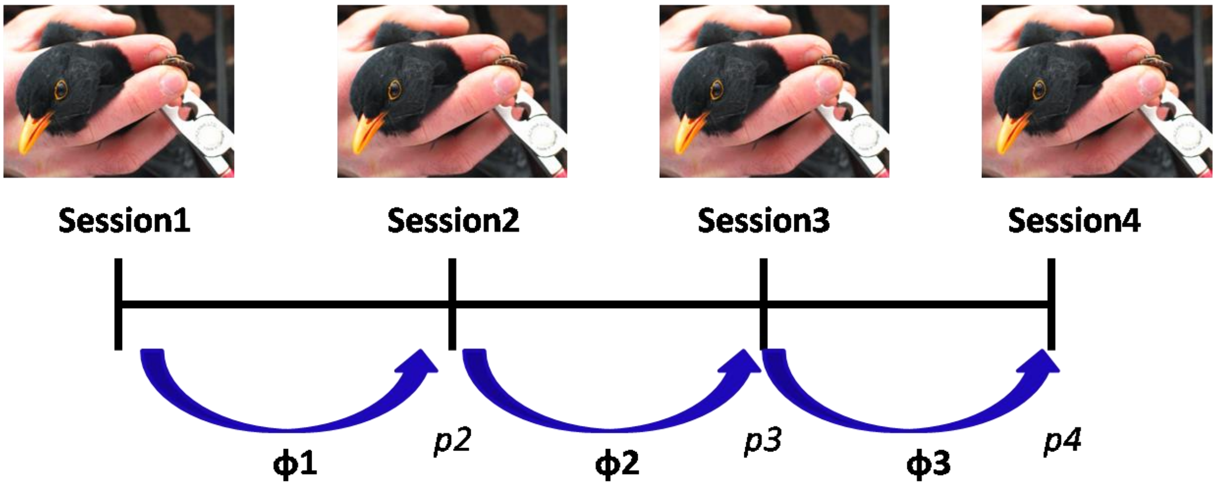


Figure 15. Illustration d’un suivi de population par capture-marquage-recapture. Dans cet exemple, on réalise 4 sessions de capture. Pour qu’un individu marqué soit recapturé durant une session donnée, il faut qu’il survive depuis la session à laquelle il a été marqué (paramètres ϕ et flèches bleues) et qu’il soit recapturé (paramètres *p*).

Session	Individus relâchés	S2	S3	S4	Jamais revus
1	54	20	3	1	**30**
2	25	0	21	1	**2**
3	67	0	0	32	**33**

Tableau 1. Exemple de M-array pour un échantillonnage comprenant 4 sessions de capture. Seuls les individus marqués lors des 3 premières sessions sont informatifs au regard de l’estimation des paramètres de survie et de probabilité de recapture.

Session	S2	S3	S4	Jamais Revu
1	ϕ1*p2	ϕ1*(1-p2)*ϕ2*p3	ϕ1*(1-p2)*ϕ2*(1-p3)*ϕ3p4	1-C1
2	0	ϕ2*p3	ϕ2*(1-p3)*ϕ3*p4	1-C2
3	0		ϕ3*p4	1-C3

Tableau 2. Expression des différents termes du M-array en fonction des deux paramètres d’intérêt, les taux de survie (ϕ) et les probabilités de recapture (p). La probabilité qu’un individu ne soit jamais repris vaut 1 moins la probabilité d’avoir été repris au moins une fois. Cette dernière probabilité vaut la somme des termes de chaque ligne (C).

Session	S2	S3	S4	Jamais Revu
1	$[\phi 1*p2]^{20}$	$[\phi 1*(1-p2)*\phi 2*p3]^{3}$	$[\phi 1*(1-p2)*\phi 2*(1-p3)*\phi 3p4]^{1}$	$[1-C1]^{30}$
2	0	$[\phi 2*p3]^{21}$	$[\phi 2*(1-p3)*\phi 3*p4]^{1}$	$[1-C2]^{2}$
3	0		$[\phi 3*p4]^{32}$	$[1-C3]^{33}$

Tableau 3. Application des expressions du tableau précédent à l'exemple proposé. En considérant l'indépendance des histoires de captures de chacun des individus, la probabilité d'observer *n* fois un évènement vaut la probabilité de l'observer une fois à la puissance *n*.

On peut montrer que chacun des termes du M-Array est une fonction non complexe des paramètres de survie et de probabilité de recapture (**tableau 2**). Toutefois, on peut faire un certain nombre d'hypothèses simplificatrices :

- Les individus sont indépendants, c'est-à-dire qu'il n'y a pas de relations entre la recapture d'un individu et la recapture d'un autre individu.
- Les individus sont identiques, c'est-à-dire que les taux de survie et les probabilités de recapture s'appliquent à l'ensemble des individus de l'échantillon.
- Les évènements successifs de capture d'un même individu sont indépendants, c'est-à-dire que la probabilité de capture d'un individu à une session ne dépend pas de ses captures précédentes.

Au prix de ces hypothèses qui forment le modèle de Cormack-Jolly-Seber (Cormack 1989), on peut écrire la vraisemblance du jeu de données, c'est-à-dire du M-array, comme le produit de l'ensemble de ses termes, chacun d'entre eux étant élevé à la puissance de l'effectif qui constitue chacune des cases (**tableau 3**). L'estimation des paramètres peut alors être effectuée par maximum de vraisemblance ou en utilisant des statistiques bayésiennes (Grosbois et al. 2008).

2.3.1.2 Estimer la survie annuelle et la productivité à partir de données multi-sites : application aux données STOC pour la Bouscarle de Cetti.

Le cadre général présenté dans la partie précédente s'applique à des jeux de données récoltés à l'échelle d'un site pour une espèce. Le programme STOC-capture intègre des données de plus de 200 sites. De plus, tous les sites n'ont pas été échantillonnés sur une période identique. A titre d'exemple, parmi les 13 sites qui ont commencé à être suivis en 1989, cinq sont encore actifs à ce jour. Cette situation produit un jeu de données en plan incomplet puisque l'ensemble des sites ne produit pas de données pour chacune des années. L'estimation de la composante moyenne de la survie à l'échelle du pays nécessite la modélisation de la variabilité entre les sites. Toutefois, le plan factoriel étant incomplet, il convient de traiter l'effet site comme un effet aléatoire. Les modèles mixtes ne sont pas encore implémentés dans les logiciels classiques qui estiment les paramètres par maximum de vraisemblance. Nous avons donc utilisé des méthodes bayésiennes basées sur des méthodes de Monte Carlo par chaînes de Markov (Grosbois et al. 2008). Une fois la vraisemblance du modèle explicitée, et les distributions initiales et valeurs initiales des paramètres choisies, l'estimation des paramètres est effectuée grâce à l'algorithme d'échantillonnage de Gibbs. Outre la possibilité d'inclure des effets aléatoires dans les modèles, les méthodes d'estimation bayésiennes facilitent le développement de modèles hiérarchisés couplant des jeux de données indépendants. Le modèle utilisé pour estimer les survies annuelles de chaque espèce est le suivant :

Les taux de survie sont modélisés comme une fonction du temps et du site :

$$\text{logit}\,(\phi_{\text{ik}}) = \log\left(\frac{\phi_{\text{ik}}}{1-\phi_{\text{ik}}}\right) = \mu_{\text{i}} + \alpha_{\text{k}}$$

Où ϕ_{ik} est la probabilité qu'un individu appartenant au site *k* survive de l'année *i* à l'année *i+1*, μ_{i} correspond à l'effet fixe de l'année *i* sur le taux de survie ϕ_{ik} et α_{k} est l'effet aléatoire du site *k* sur le taux de survie ϕ_{ik}. Les α_{k} sont supposes être distribués normalement α_{k}~N(0, σ^2_{site}) où σ^2_{site} est la variance à estimer.

Les probabilités de recapture sont modélisées comme une fonction du site :

$$logit(p_{i,k}) = \beta_k$$

Où $p_{i,k}$ est la probabilité de détection d'un individu donné durant l'année *i* au site *k* et β_k est la probabilité de détection moyenne au site *k*. Nous avons fait l'hypothèse que les probabilités de détection ne variaient pas d'une année sur l'autre pour une même espèce dans la mesure où le protocole STOC est à effort constant c'est-à-dire que chaque année les bagueurs volontaires effectuent un nombre identique de sessions de captures, en disposant un nombre de filets identique, à des emplacements identiques.

En plus de permettre l'estimation des taux de survie locale annuels, les données STOC permettent d'estimer la productivité, c'est-à-dire la proportion moyenne de juvéniles dans les captures totales :

$$Prod_{i,k} = \frac{Juv_{i,k}}{Juv_{i,k} + Ad_{i,k}}$$

Ainsi, le succès de reproduction $Prod_{i,k}$ est modélisé comme un ratio entre le nombre de jeunes $Juv_{i,k}$ et le nombre d'adultes $Ad_{i,k}$ capturés une année *i* sur un site *k* donné. Ce succès de reproduction peut ensuite être modélisé comme une fonction du temps et du site :

$$\text{logit}\,(Prod_{i,k}) = \log\left(\frac{Prod_{i,k}}{1-Prod_{i,k}}\right) = \pi_{\text{i}} + \rho_{\text{k}}$$

Où $Prod_{i,k}$ est le succès de reproduction au site *k* à l'année *i*, π_i correspond à l'effet fixe de l'année *i* sur le succès de reproduction $Prod_{i,k}$ et ρ_k est l'effet aléatoire du site *k* sur le succès de reproduction $Prod_{i,k}$. Les ρ_k sont supposes être distribués normalement $\rho_k \sim N(0, \sigma^2_{site})$ où σ^2_{site} est la variance à estimer.

L'influence des covariables climatiques sur les taux de survie et le succès de reproduction peut aussi être modélisée en utilisant des modèles linéaires mixtes :

$$\mathrm{logit}\,(\mathrm{Taux}_{ik}) = \beta_0 + \beta_1 \times \mathrm{climat}_i + \alpha_k + \varepsilon_{i,k}$$

Où Taux_{ik} représente soit un taux de survie soit un succès de reproduction, climat_i une variable climatique associée à l'année *i*. Les coefficients β représentent les coefficients de la régression linéaires à estimer, tandis que $\alpha_k$et $\varepsilon_{i,k}$ représentent respectivement l'effet aléatoire du site et le terme d'erreur résiduelle également modélisé comme un effet aléatoire.

Ces modèles appliqués aux données de capture de Bouscarle de Cetti (*Cettia cetti*) pour la période 2000-2009 montrent une corrélation significative entre les taux de survie et la température moyenne d'Octobre à Mai (**figure 17 et Article 8**). Le succès de reproduction ne semble pas dépendant de la température et ne montre d'ailleurs que très peu de variations interannuelles. Nous avons par ailleurs mis en relation les estimations d'abondance issues du programme STOC EPS avec les deux taux démographiques estimés avec les données du STOC capture. L'intérêt d'une telle démarche est la comparaison du message populationnel fourni par deux jeux de données complètements indépendants opérant à des échelles géographiques similaires mais sur des sites distincts et au moyen de protocoles complètement différents. Alors que la productivité d'une année ne semble pas significativement corrélée aux indices d'abondances au printemps suivant, le taux de survie y est lui très fortement corrélé comme le montre le R^2 du modèle qui relie les deux mesures et qui vaut 72 % (**figure 16**).

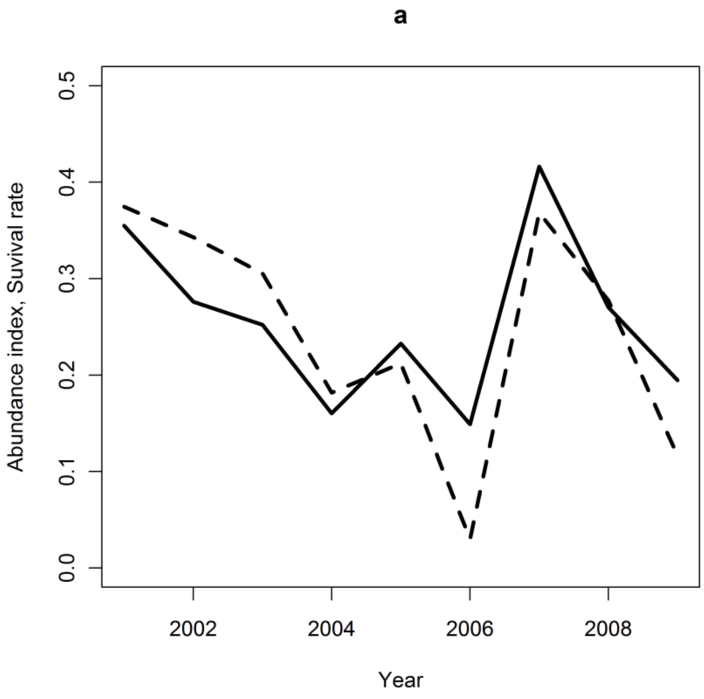


Figure 16. Couplage entre les indices d'abondance annuels estimés (Courbe en pointillés) à partir des données STOC EPS et les taux de survie locale annuels (Courbe en trait plein) estimés à partir des données STOC capture pour la période 2002-2009 chez la Bouscarle de Cetti (*Cettia cetti*). Les incertitudes associées à ces estimations ne sont pas représentées afin d'améliorer la clarté de la figure.

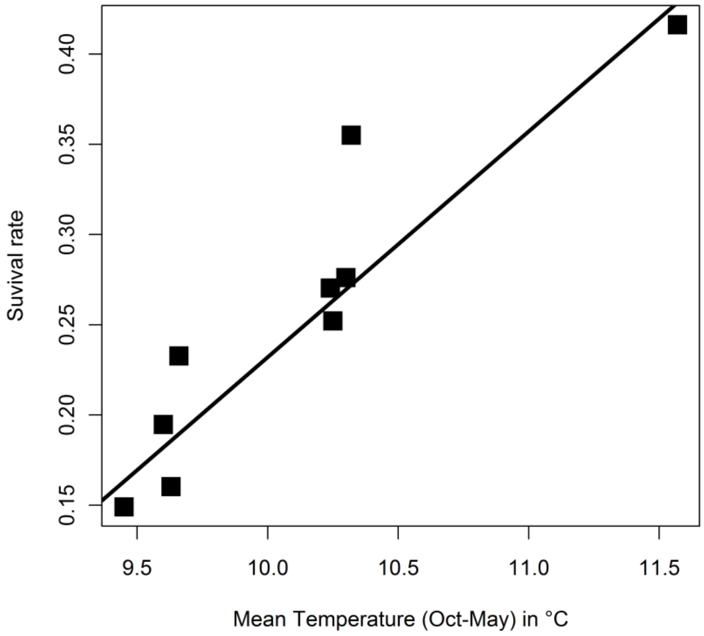


Figure 17. Relation entre la température moyenne d'octobre à mai et le taux de survie locale annuel moyen de la Bouscarle de Cetti (*Cettia cetti*) estimé à partir des données STOC capture sur 20 sites pour la période 2002-2009. Les incertitudes associées à ces estimations ne sont pas représentées afin d'améliorer la clarté de la figure. La relation est statistiquement significative.

Ces résultats ne constituent pas en soi une nouveauté dans la mesure où les observations naturalistes témoignent depuis longtemps de la sensibilité des effectifs printaniers de cette espèce à la rigueur de l'hiver. Toutefois, ici, cette dépendance est estimée à plus grande échelle et surtout, le mécanisme démographique supposé est mis en évidence, à savoir la survie. Ainsi, ces résultats peuvent être considérés comme une base solide pour l'étude de la variation spatiale de la sensibilité démographique au climat. Par ailleurs, on constate aussi pour cette espèce la grande cohérence du message biologique apporté par deux jeux de données complètement indépendants que sont le STOC EPS et le STOC capture.

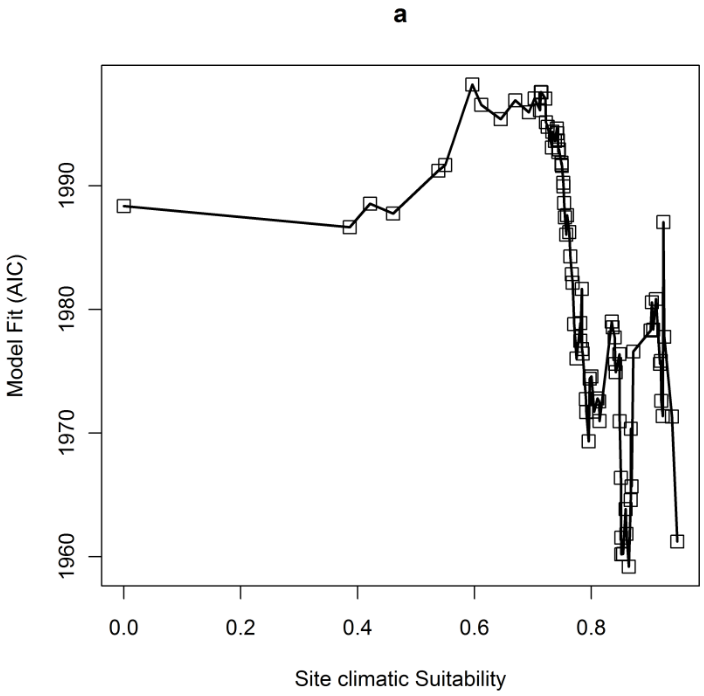
2.3.2. Sensibilité différentielle de la démographie au climat le long de l'aire de distribution.

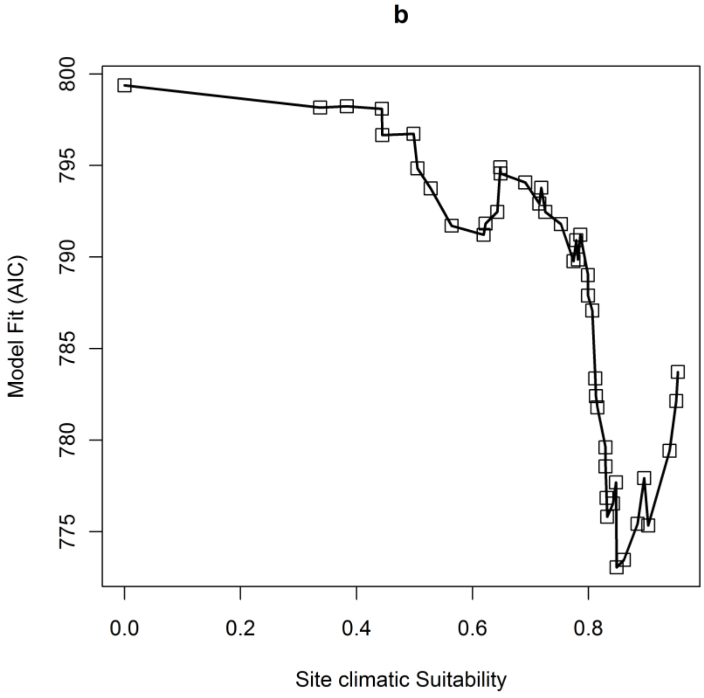
Le mécanisme démographique principalement responsable des variations d'abondance au printemps chez la Bouscarle de Cetti est donc la survie hivernale. Compte tenu des traits communs avec les deux autres espèces considérées, il est fort probable que ce même mécanisme régisse les taux de croissance chez la Cisticole des joncs et la Fauvette Pitchou. Nos résultats montrent en effet également une corrélation significative entre température moyenne hivernale et les effectifs printaniers comptés par le STOC EPS (**Article 9**). Nous allons maintenant aborder la description de la méthode permettant le test des hypothèses présentée en introduction de cette partie. Dans le cas d'une niche fondamentale supérieure ou égale à la niche réalisée, on peut attendre une sensibilité croissante de la démographie (modélisée par les variations d'abondance) lorsque l'on s'approche de la frontière de la niche fondamentale. Dans le cas d'une niche réalisée supérieure à la niche fondamentale, la sensibilité *réelle* des populations aux fluctuations climatique devrait aussi croître selon un gradient d'adéquation climatique. Cependant, on peut attendre que les zones situées en marge de l'aire de distribution fonctionnent selon des dynamiques source-puits très prononcées. Par conséquent, il est possible que des processus d'extinctions locales (suite à des évènements climatiques défavorables) et de recolonisation masquent la sensibilité réelle des populations au climat. En effet, si des épisodes climatiques défavorables conduisent à la disparition d'une population de type puit à un site donné (témoignant ainsi de la sensibilité *réelle* de la population au climat), la période s'étalant depuis cette extinction jusqu'à la recolonisation du site par des individus issus de populations sources sera marquée par une sensibilité *apparente* nulle au climat car l'abondance sera nulle. Par conséquent, la première hypothèse conduirait plutôt à une interaction négative entre température et adéquation climatique du site pour expliquer l'abondance. La seconde hypothèse conduirait plutôt à une interaction positive (sensibilité *apparente* et réelles *équivalentes*), c'est-à-dire une sensibilité *apparente* de l'abondance au climat décroissante selon un gradient décroissant d'adéquation climatique, voire à l'existence d'un seuil de sensibilité apparente au climat. Nous avons estimé pour chaque site une probabilité de présence dépendante du climat et mesurant ainsi l'adéquation climatique de chacun des sites de comptage. Cette mesure de l'adéquation climatique du site pour l'espèce est obtenue par modélisation de niche de type « Ensemble Forecast » basée sur des données de présences/absences actuelles et sur un certain nombre de variables climatiques

Pour les trois espèces, il existe une interaction significativement positive entre adéquation climatique du site et climat hivernal. Nous avons donc cherché à mettre en évidence un seuil de sensibilité apparente au climat susceptible de révéler la frontière entre niche fondamentale et niche réalisée dans la distribution observée des trois espèces. Pour cela, le modèle suivant a été ajusté aux données d'abondance issues du programme STOC EPS :

$$\log(\eta_{i,k}) = \beta_0 + \beta_1 \times \mathrm{climat}_i + \nu_k + \varepsilon_{i,k}$$

Où $\eta_{i,k}$ est l'abondance au site *k* à l'année *i*, climat_i correspond à la valeur de la variable climatique (Température) de l'année *i.* Afin de déterminer un seuil de sensibilité au climat pouvant refléter des différences de dynamiques de populations, le coefficient β_1 est fixé à 0 pour toutes les données qui concernent les sites dont l'adéquation climatique est inférieure à une valeur S que l'on fait varier itérativement entre 0 et 1. Pour chaque valeur de S, l'ajustement du modèle est observé par son AIC. On prédit que l'AIC du modèle sera le meilleur lorsque l'on aura séparé les sites de sensibilité *apparente* faible au climat des sites à sensibilité *apparente* forte c'est-à-dire équivalente à la sensibilité *réelle* (**figure 18**).


a
Model Fit (AIC)
1960
1970
1980
1990
0.0
0.2
0.4
0.6
0.8
Site climatic Suitability


b
Model Fit (AIC)
775
780
785
790
795
800
0.0
0.2
0.4
0.6
0.8
Site climatic Suitability

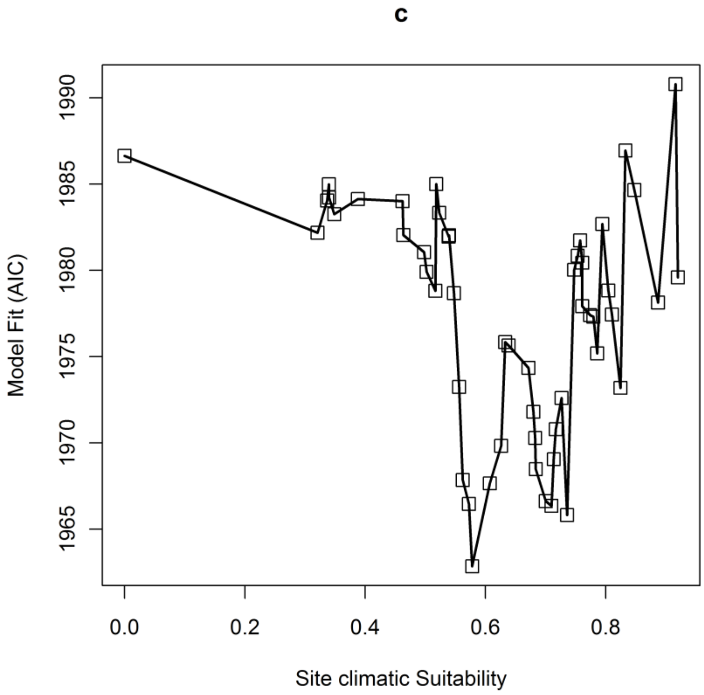


Figure 18. Mise en évidence d'un seuil de sensibilité démographique *apparente* au climat hivernal chez (a) la Bouscarle de Cetti (*Cettia cetti*), (b) la Fauvette pitchou (*Sylvia undata*) et (c) la Cisticole des joncs (*Cisticola juncidis*). Les figures représentent la qualité de l'ajustement du modèle $\log(\eta_{i,k}) = \beta_0 + \beta_1 \times \mathrm{climat_i} + \nu_k + \varepsilon_{\mathrm{i,k}}$ où β_1 est fixé à 0 pour les sites dont l'adéquation climatique est inférieure à une valeur S que l'on fait varier entre 0 et 1. Le meilleur ajustement est obtenu pour un modèle qui ne prend en compte que les populations sources dont la sensibilité apparente au climat est la plus forte.

Les résultats semblent indiquer que pour ces trois espèces, c'est la seconde hypothèse qui rend le mieux compte des distributions géographiques observées. L'interprétation la plus vraisemblable des seuils de sensibilité mis en évidence pour les trois espèces, est qu'ils représentent la frontière d'adéquation climatique qui sépare les niches climatiques fondamentales et réalisées. Il semble donc qu'il existe une zone marginale plus ou moins importante de l'aire de distribution actuelle de ces espèces fortement dépendantes du climat qui soit hors de leur niche climatique fondamentale. Dans cette zone, la proportion de populations instables serait croissante en se rapprochant de la limite observée de la distribution. On peut supposer que lorsque les conditions environnementales sont trop inadéquates, il ne pourrait demeurer que des populations puits, ce qui n'est pas possible sur une zone géographique très large étant donnée la distance faible de dispersion natale chez ces espèces.

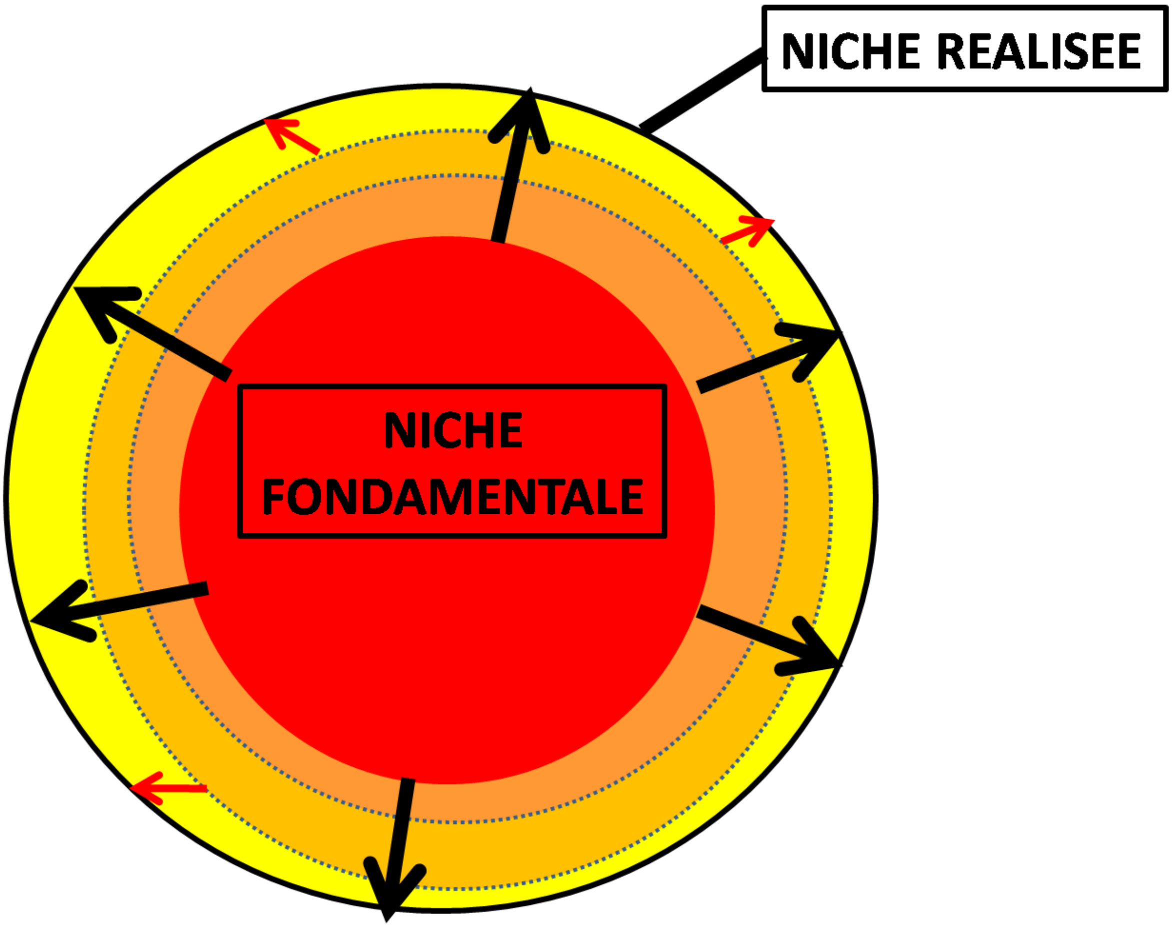
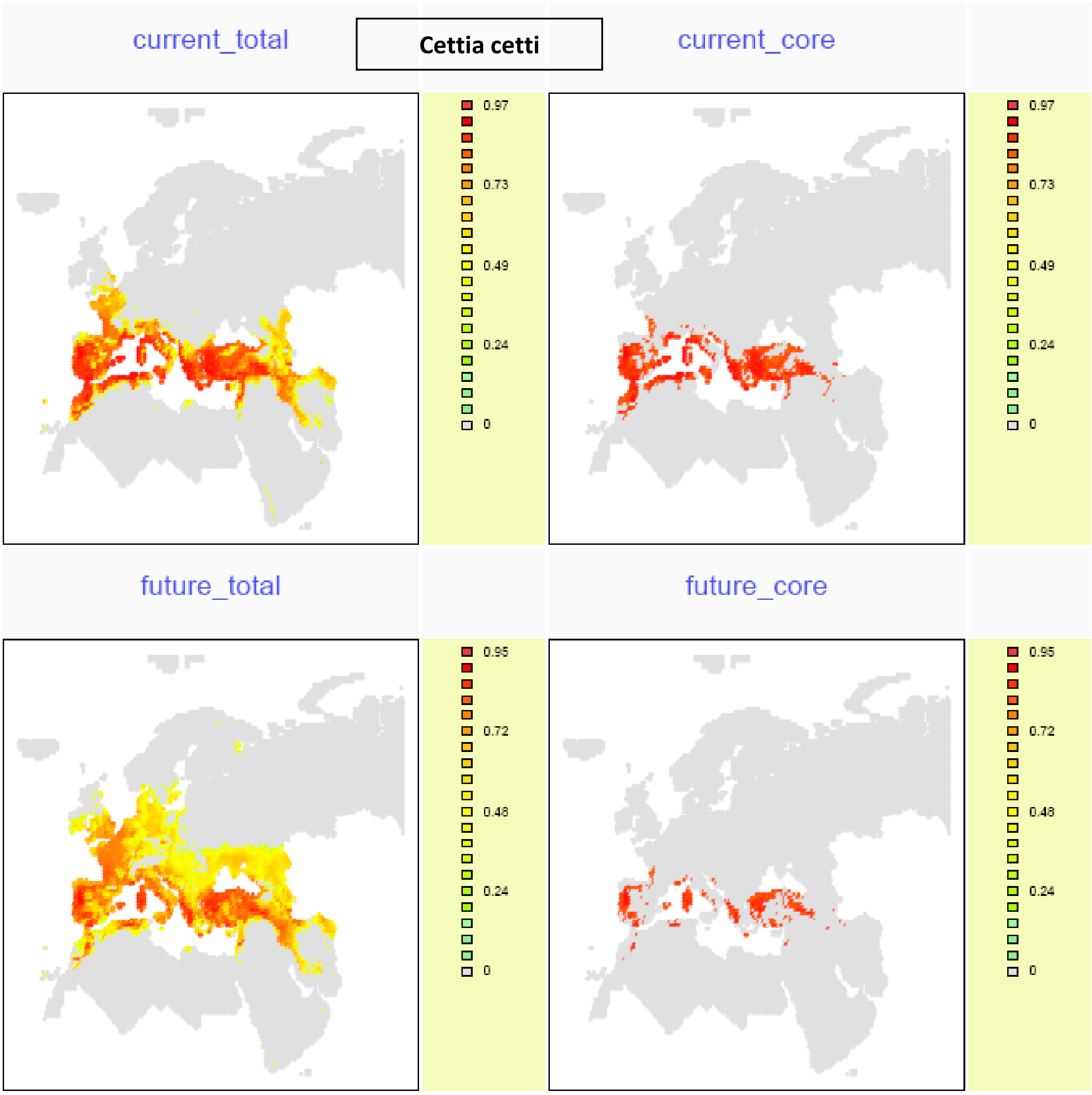
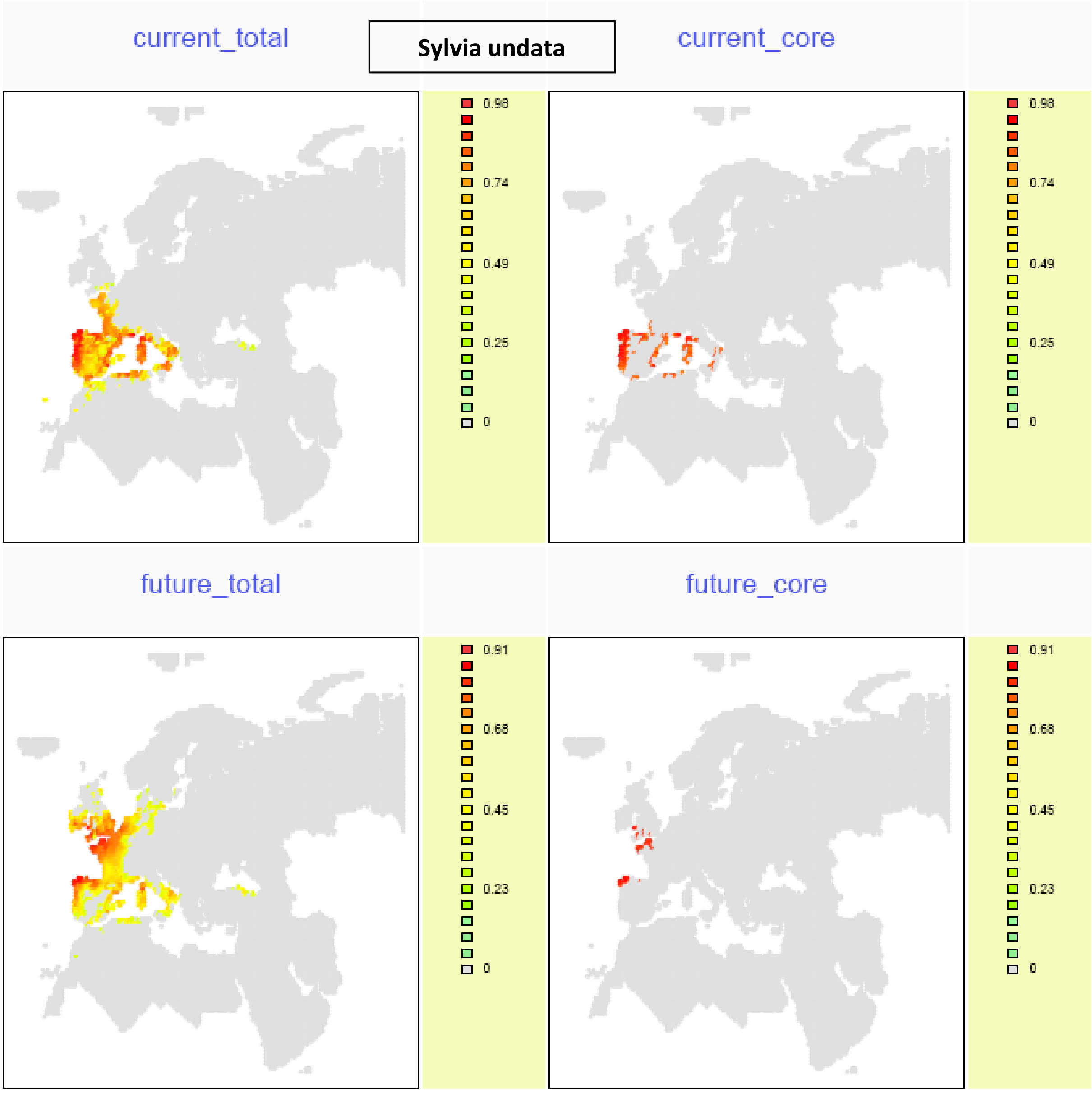


Figure 19. Interprétation de l'existence d'un seuil d'adéquation climatique pour la sensibilité démographique aux variations climatiques annuelles. La distribution observée de l'espèce c'est-à-dire sa niche réalisée (entourée de noir) comprendrait sa niche fondamentale (en rouge) et un ensemble de zones où la proportion de populations instables type Puits serait croissante (dégradé de couleurs et flèches noires). La limite d'aire de distribution serait définie par la position des dernières populations sources et par la distance de dispersion natale de l'espèce (flèches rouges).

Il est possible de comparer les distributions actuelles et futures basées d'une part sur la totalité des données (niche réalisée) et sur les données que l'on peut supposer comprises dans la niche fondamentale (sites avec une adéquation climatique supérieure à la valeur seuil). Ainsi, toutes les zones dont la probabilité de présence est inférieure à ce seuil ne sont plus représentées sur la distribution qui ne comprend alors plus que les zones dont on prédit qu'elles forment ou formeront le cœur de l'aire de distribution (**figure 20**).




Sylvia undata

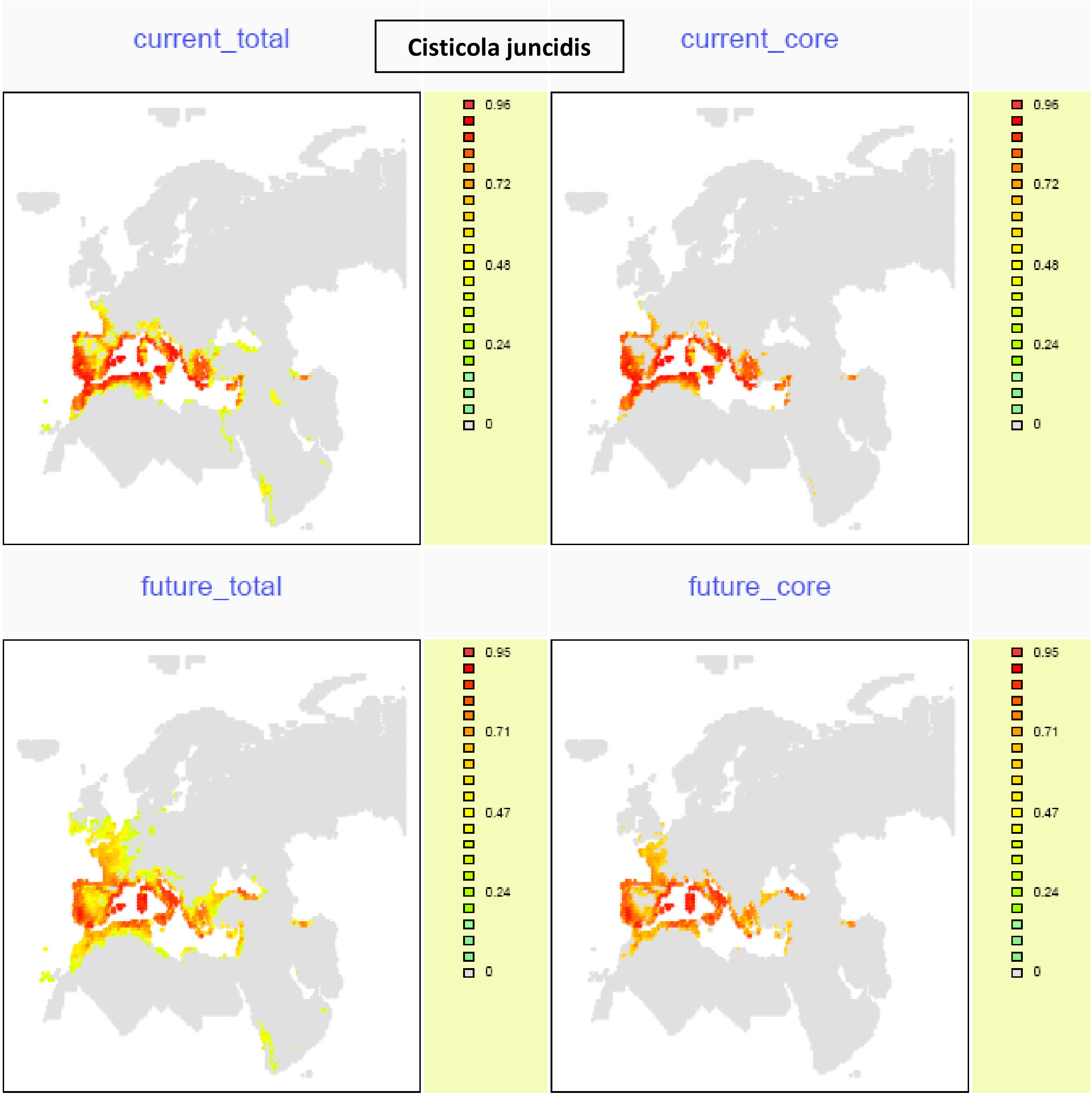


Figure 20. Modélisation des aires de distribution actuelles et futures sous scénario climatique pour trois espèces, la Bouscarle de Cetti (*Cettia cetti*), la Fauvette Pitchou (*Sylvia undata*) et la Cisticole des Joncs (*Cisticola juncidis*). Pour chacune des espèces, la figure représente sur la première ligne l'aire de distribution actuelle totale (current_total) et l'aire de distribution des populations localisées sur des sites d'adéquation climatique supérieure au seuil estimé (current_core). Sur la deuxième ligne sont représentées les aires de distributions futures possibles pour l'ensemble des populations (futur_total) et pour les populations localisées sur des sites d'adéquation climatique supérieure au seuil estimé, représentant le cœur de distribution (futur_core).

Cette méthode, appliquée aux trois espèces, fournit des résultats semblant indiquer que leur niche climatique réalisée, et donc leur distribution, est plus large que leur niche climatique fondamentale. En effet, pour chacune d'entre elles, l'ajustement du modèle Abondance~Température est plus fort lorsque des sites ayant une adéquation climatique inférieure à une valeur S ne sont pas pris en compte pour évaluer la sensibilité de la démographie au climat. Cette valeur S est relativement élevée pour la Bouscarle de Cetti et la Fauvette pitchou (respectivement 0.85 et 0.83) alors qu'elle est plus faible pour la Cisticole des joncs (autour de 0.58). Lorsque des modèles de type « Ensemble Forecasting » sont appliqués aux données de présence/absence pour modéliser les aires futures sous scénario climatique, un seuil de confiance est aussi classiquement appliqué aux prédictions. Toutefois, cette valeur seuil classiquement utilisée est estimée sur la base d'hypothèses concernant la modélisation des aires actuelles (Liu et al. 2005). Elle correspond à la probabilité de présence qui maximise le nombre de sites où l'on prédit la présence de l'espèce sachant qu'elle est effectivement présente (d'après la distribution de données de présences/absences) tout en minimisant le nombre de sites pour lesquels on prédit la présence de l'espèce sachant qu'elle n'est pas présente (toujours d'après les distributions actuelles connues). Cette valeur seuil ne tient absolument pas compte de la dynamique de populations ou de l'abondance dans l'aire de distribution. Si l'on applique les valeurs seuils issues de la méthode basée sur la sensibilité à la température, on obtient des distributions futures sensiblement différentes pour les trois espèces. Ces distributions ne représentent toutefois pas la même chose que les distributions classiquement établies par les modèles de niche. Dans ce cas, on prédit la distribution des populations de type Source (ou cœur de distribution) alors qu'en appliquant un seuil statistique classique, on prédit la distribution la plus raisonnable possible de l'ensemble des populations sans faire de distinction fonctionnelle (Svenning & Skov 2004; Pearson *et al.* 2007). Les distributions futures de l'ensemble des populations font apparaître de larges zones de probabilités de présence seulement légèrement supérieures à la valeur seuil statistique. Il est peu probable qu'une espèce puisse être présente sur d'aussi larges étendues surtout si ce sont des populations de type Puits qui, pour se maintenir, doivent bénéficier d'un apport régulier d'oiseaux en provenance de population Sources. Pour la Fauvette Pitchou et la Bouscarle de Cetti, l'application d'un seuil basé sur la sensibilité climatique aboutit à des prédictions de réduction importante du cœur de l'aire de distribution, alors que l'application d'un seuil classique conduit à des prédictions d'augmentation de la distribution notamment vers le nord et l'est. Pour la Cisticole des Joncs, les deux types de prévisions sont plus proches les unes des autres. Le positionnement de la limite entre populations situées au cœur de la niche climatique et population en marge (et donc moins stables) est, au regard de cette étude encore relativement imprécise. En revanche, ces résultats suggèrent que l'influence du climat sur la démographie est variable le long de l'aire de distribution et que la prise en compte de cette variation fait sensiblement varier le message fourni par les prédictions de distributions issues de la modélisation de niche. Les travaux qui visent à prédire l'évolution de la biodiversité en un site donné sous scénario climatique se fondent actuellement sur une approche statistique pour déterminer le seuil de présence d'une espèce sur surface géographique donnée. La prise en compte de la dynamique de populations différentielle le long de l'aire de distribution pourrait substantiellement changer les prédictions de richesse spécifique en un endroit donné.

Conclusion générale

1. Synthèse des principaux résultats

Les principaux résultats de ce travail de thèse complètent partiellement le schéma contextuel proposé en fin d'introduction générale. Tout d'abord, la question de l'influence du climat sur le succès reproducteur d'espèces de passereaux a été abordée essentiellement par le biais de la réponse phénologique de ces espèces à la température. L'échelle spatiale, l'échelle temporelle ainsi que le nombre d'espèces pour lesquelles le programme STOC fournit des informations a effectivement permis d'explorer la variabilité interspécifique de ces réponses phénologiques. D'une part, l'intensité de couplage entre phénologie et climat apparaît comme facteur de la croissance des populations à l'échelle régionale. Ce résultat conforte donc l'hypothèse du mécanisme phénologique comme une voie d'influence du réchauffement climatique sur la démographie aviaire. Plus encore, il identifie l'ajustement annuel de la phénologie de reproduction et non la tendance à long terme de celle-ci comme un déterminant du taux de croissance à grande échelle spatiale. Si l'on se réfère au schéma proposé en introduction, c'est donc l'existence et la nature des flèches qui lient successivement phénologie, succès de reproduction et taux de croissance régional qui se trouvent en partie explicités. La variabilité interspécifique des capacités d'ajustement phénologique trouve également dans ce travail une certaine organisation. En identifiant la stratégie de migration, la largeur de la niche écologique et de la taille du cerveau comme des corrélats de la flexibilité de la phénologie de la reproduction, ce travail met en évidence des catégories d'espèces davantage susceptibles de pâtir des changements climatiques. De plus, la mise en évidence de l'importance de la largeur de niche thermique pour la capacité d'ajustement phénologique, inscrit ce travail dans la lignée des études identifiant les espèces spécialistes comme plus vulnérables face aux perturbations, et témoigne de la réalité de cette perturbation.

Concernant la modélisation des conséquences futures des changements climatiques sur les populations d'oiseaux et donc leur distribution géographique, cette thèse propose un cadre de travail pouvant, à terme, fonder les prédictions d'aires de distribution non plus seulement sur des distributions actuelles, mais sur des informations relatives au fonctionnement des populations. Ainsi, le travail préliminaire effectué sur trois espèces modèles permet dans un premier temps d'identifier des différences de dynamiques de l'abondance en relation avec un positionnement différent de ces populations dans la niche climatique de l'espèce. En fournissant des informations sur le cœur de l'aire de distribution et son évolution future, cette approche n'affine pas stricto sensu les prédictions déjà réalisées dans d'autres études, elle fournit des indications différentes et plus fonctionnelles de ce que pourraient devenir les distributions des espèces d'oiseaux concernées sous scénario climatique. En outre, elle ouvre la voie à l'exploitation des données issues d'observatoires, tels que le Suivi Temporel des Oiseaux Communs, pour ce type de modélisation. Ces outils de suivis de la biodiversité à grande échelle apparaissent donc à la lumière de ce travail comme des éléments indispensables pour l'étude des conséquences passées et à venir de perturbations qui de toute façon, opèrent à des échelles supra régionales.

2. Perspectives.

2.1. Mécanismes de l'influence des changements climatiques sur la démographie.

Si des réponses ont pu être apportées à certaines hypothèses et questions de départ de ce travail, d'autres aspects de l'influence climatique sur le cycle de vie des passereaux communs n'ont pas pu être abordés pendant la durée de cette thèse et demeurent ainsi comme des questions en suspens. Tout d'abord, le rôle du climat sur la qualité et la quantité de la ressource pour expliquer les variations temporelles du succès reproducteur n'a pas fait l'objet de recherches poussées. Des analyses préliminaires suggéraient pourtant un certain degré de synchronisation à grande échelle pour de nombreuses espèces communes. Toutefois, il est probable qu'à l'instar de ce que l'on observe pour les données d'abondance issues du STOC EPS, la méthode retenue pour estimer la productivité soit aussi sensible à la variation phénologique interannuelle. Ce biais pourrait masquer une part de la variation du succès reproducteur non lié à la phénologie. L'influence du climat sur la qualité de la reproduction (hors mécanismes phénologiques déjà décrits) pourrait faire l'objet d'une modélisation impliquant des modèles matriciels hiérarchisés. Les paramètres estimés pour chaque espèce pourraient dans ce cadre également faire l'objet d'une analyse comparative visant aussi à identifier des traits corrélés à la sensibilité et donc à identifier des groupes d'espèces à risque.

Une analyse aboutie et détaillée des variations interannuelles de la survie en relation avec des variables climatiques manque également à ce travail. En réalité, les estimations de survie annuelles pour la période 1989-2008 ont pu être effectuées pour 19 des 20 espèces étudiées pour les analyses phénologiques. Si une certaine synchronie semble exister pour les espèces sédentaires, l'identification de déterminants climatiques majeurs apparaît plus délicate. Sans doute serait-il plus judicieux d'estimer les contributions relatives du succès reproducteur et de la survie aux taux de croissance des populations de chacune de ces espèces communes. C'est peut-être davantage dans la variabilité interspécifique de ces contributions que pourraient apparaître les groupes d'espèces plus vulnérables aux changements climatiques. Dans cette optique, les données issues de programmes type STOC (et sans doute également une coopération à l'échelle internationale pour mettre en commun les données de ce type existant dans de nombreux pays européens), couplées à l'utilisation de modèles hiérarchisés où la croissance d'une population peut-être modélisée en utilisant les données de comptages et les paramètres démographiques (productivité et survie) en utilisant des données de capture sur des sites à effort constants, offrent des perspectives très prometteuses pour mettre en relation la dynamique des populations et la perturbation climatique à grande échelle.

2.2. Modélisation des distributions futures sous scénario climatique.

L'efficacité de la modélisation d'une distribution future repose évidemment sur la précision des scénarios climatiques. Mais elle dépend probablement autant du degré de connaissances que l'on peut acquérir concernant la niche écologique au sens large (c'est à dire comprenant les interactions biotiques) de l'espèce. A court terme, c'est probablement cette partie de l'incertitude qu'il est possible de réduire sensiblement. Ainsi, tenir compte de l'abondance et non pas seulement des présences/absences permettrait de mieux établir la relation entre la présence d'une espèce et les variables environnementales. Dans ce cadre, les observatoires pourront fournir des données d'abondance à des échelles pertinentes (nationales et supranationales). L'un des défis les plus importants de ce domaine sera la prise en compte des interactions spécifiques et notamment les interactions de compétition qui pourraient limiter sensiblement la distribution future de nombreuses espèces. Cette étape nécessite déjà la quantification de ces interactions. Or les données de type observatoire pourraient permettre de quantifier des interactions spécifiques au moins de façon préliminaire notamment en étudiant des patrons de cooccurrence ou en mettant en relation les paramètres démographiques de plusieurs espèces, de façon à faire émerger des corrélations négatives pouvant signifier des interactions de compétition. Le troisième défi concerne la dynamique de colonisation et d'extinction depuis la distribution actuelle vers la distribution future. En effet, la méthode actuelle projette un espace multidimensionnel d'une période à une autre sans tenir compte, d'une part de la résilience des populations à des conditions non comprises dans leur niche écologique, d'autre part de la capacité à coloniser des espaces nouvellement favorables suite aux changements climatiques. Ce manque d'un processus dynamique reliant un état initial à un état final constitue aussi un grand défi pour cette discipline et les observatoires type STOC pourraient également jouer un rôle important pour identifier différents types de fonctionnements de populations en relation avec le climat, comme c'est le cas dans le présent travail. Ils pourraient permettre de quantifier la vitesse de déplacement actuelle des aires de distributions, ces vitesses pouvant par la suite être intégrées aux modèles de niche. Pour résumer, ce sont les données fonctionnelles spécifiques issues de programmes de monitoring et mises en relation avec le climat qui devraient conduire dans les années à venir à une nette amélioration de la qualité des prédictions d'aires futures en réponse aux changements climatiques.

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Manuscrits

Manuscrit 1

Accounting for weather and time-of-day parameters when analysing count data from monitoring programs

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ORIGINAL PAPER

Accounting for weather and time-of-day parameters when analysing count data from monitoring programs

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Abstract Problems induced by heterogeneity in species and individuals detectability are now well recognized when analysing count data. Yet, most recent techniques developed to handle this problem are still hardly applicable to many monitoring schemes, and do not provide abundance estimates at the point count scale. Here, we show how using simple weather variables can be a useful surrogate to detect variability in species detectability. We further look for a potential bias or loss in statistical power based on count data while ignoring weather and time-of-day variables. We first used the French Breeding Bird Survey to test how each of the counts of the 97 most common breeding species was influenced by weather and time-of-day variables. We assessed how the estimation of each species response to fragmentation could be influenced by correcting counts with such variables. Among 97 species, 75 were affected by at least one of the five weather and time-of-day variables considered. Despite these strong influences, the relationship between species abundance and fragmentation was not biased when not controlling counts for weather and time-of-day variables and further found no improvement in statistical power when accounting for these variables. Our results show that simple variables can be very powerful to assess how species detectability is influenced by weather conditions but they are inconsistent with any specific bias due to heterogeneous detectability. We suggest that raw count data can be used without any correction in case the sources of variation in detectability could be considered independent to the factor of interest.

Keywords Breeding bird survey · Detectability · Fragmentation · Point counts · Relative abundance · Time-of-day · Weather conditions

Abbreviations

BBS Breeding bird survey

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Introduction

Counts of individuals or species are the result of two processes: a biological process (the true presence or absence of a species or individual), and a methodological filter (the ability of the observer to detect an individual). If variation in detectability among species and/or individuals is not accounted for, an unknown part of the variation in presence or abundance of a given species will result from variation in detectability regardless of its true variation. Therefore, using just the detected bird counts (per unit effort) as an index of abundance is sometimes considered to be neither scientifically sound nor reliable (Burnham 1981). To control the potential bias induced by heterogeneity in detectability, two approaches have been adopted. On the one hand, several methods have been developed to account for the whole detection process and to further directly estimate the probabilities of detection. Yet these methods need either both spatial and temporal replications (Dodd and Dorazio 2004; Royle 2004; Kéry et al. 2005), or temporal replication and marking of individuals (Farnsworth et al. 2002; Alldredge et al. 2007). On the other hand, count data may be corrected with covariables known to be sources of heterogeneity in detectability (Caughley et al. 1976; Link and Sauer 1998, 2002). This approach may be simpler to apply but sources of heterogeneity in detectability may remain unchecked and can still bias the analyses.

Collecting abundance data from incomplete counts may respond to different objectives which involve different strategies to deal with heterogeneity in detectability. First, it is important to note that estimating a species total abundance over an area requires an estimation of detectability even if detectability is constant across sites (Thompson et al. 1998). For these objectives, a direct estimation of detectability seems to perform well (Kéry et al. 2005; Royle et al. 2007). However, most ecological studies do not need an absolute measure of abundance, but rather an index, usually named relative abundance, to infer spatial or temporal variations of species abundance. In these cases, imperfect detection must be accounted for if detectability covaries with the dimension to be compared. Here we focused on the use of count data to infer on abundance variations across spatial variations of an ecological factor, which is a common output of large scale monitoring programs (Jiguet et al. 2006; Julliard et al. 2006; Posthuma and De Zwart 2006; Vaughan et al. 2007). As many ecological factors such as habitat characteristics are measured very locally, these studies often need a measure of relative abundance on a very local scale (e.g. for each point count), which unfortunately precludes using any spatial replication of count data. Thus, in many cases, a direct estimation of detectability is still not possible. In such cases, accounting for factors that potentially affect species detectability could be a valuable proxy in counts analysis (Link and Sauer 1998). Moreover, some of these factors are easily recorded by observers. Here, we focused on time-of-day and weather variables which are more likely directly linked to detection processes rather than to variations in true abundance (Robbins 1981; Verner 1985). We thus provided a framework to test how these simple variables can influence the power of classical analyses based on counts. We specifically addressed two objectives: (i) relating variations in counts to weather and time-of-day factors, (ii) assessing how accounting for these variables could correct bias and/or improve statistical power while testing ecological predictions. For this purpose, we chose to use landscape fragmentation as an ecological factor impacting a wide range of common species (Fahrig 2003; Devictor et al. 2008). Monitoring data came from the French Breeding Bird Survey (Jiguet et al. 2007), which is similar to many classical monitoring programs.

We predict that time-of-day influences detectability of species in either a positive or a negative way depending on the type of activity enhancing detectability (e.g. song activity generally decrease and foraging activities might increase with time after sunrise; Robbins 1981; Lindenmayer et al. 2004). We also predict that weather conditions should affect detectability if they restrain sighting or hearing of individuals or if they influence bird activities (Verner 1985).

Material and methods

The French Breeding Bird Survey

A breeding bird survey (BBS) was started in France in 2001 carried out by volunteer skilled ornithologists and following a standardized protocol with the same sites sampled for several years. Each observer provided a locality from which, within a 10 km-radius, a 2 × 2 km plot to be sampled was randomly selected (i.e. among 80 possible plots). Such random selection ensures the survey of representative habitats (including farmlands, woodlands, suburbs and cities). In each site, observers monitored 10 point-counts separated by at least 300 m. Data collected by observer on each permanent point-count stations were the counts and specific identification of all individuals seen and/or heard during a fixed period of 5 min.

We considered all points surveyed in 2005 for this analysis ($n = 7350$, i.e. from 735 plots). Birds were counted twice (before and after the 8th of May within April to mid-June) in each plot, with 4–6 weeks between the two counts and within 1–4 h after sunrise. Only individuals detected within 100 m of the observer were considered, to avoid bias due to visual detections strongly depending on landscape structure. Habitats were recorded by observers on their point counts, using a standardized code (Julliard et al. 2006). Finally, we retained species for which at least 30 individuals were counted ($n = 97$ species, see Appendix) to conduct the analyses.

Observers were also asked for each point count to note the time of the count start (to the nearest minute) and to describe weather conditions for four variables: cloudiness, rain, wind and visibility. Each of these variables was scored as 1, 2 or 3 (see Table 1). The monitoring recommendations stated that counting during rain, strong wind or deep fog should be avoided, so these extreme meteorological conditions are rarely found in the dataset (mostly when conditions changed during the sampling).

Landscape fragmentation

An estimate of landscape fragmentation within each surveyed plot was obtained using the geographical information system package ArcView 3.2 (ESRI 2000) and the Corine land

Table 1 Criteria used by observers to assess weather conditions for each point counts

Values	Cloudiness (%)	Rain	Wind	Visibility
1	0–33	Absent	Absent	Good
2	33–66	Drizzle	Light	Moderate
3	66–100	Showers	Medium/strong	Poor

Cloudiness is measured in sky covering percentage cover database. CORINE is a national geo-referenced land-cover, based on satellite digital images for the whole country. This land cover layer was created in 2000 to classify, by means of remote sensing, landscape units larger than 25 ha as belonging to one of 44 habitat classes (Bossard et al. 2000). The resolution concerning polygon limits is 20 meters. In other words, the difference between two polygons of different habitat types as well as each polygon complex form was precisely represented by CORINE. The edge density (sum of all contact length between polygons) was thus considered as a good measure of habitat fragmentation (Lausch and Herzog 2002; Devictor et al. 2008). The edge density was highly correlated to the number of polygons and to the average polygon size of the different habitat types enclosed in the landscape (Devictor and Jiguet 2007).

Statistical analyses

We modelled each species counts with two successive statistical models. First, we considered an “uncontrolled model”, i.e. for each species, counts was only a function of period (first or second), habitat type (among 18 classes) and habitat fragmentation using a Generalized Linear Model: Counts vary with Period + Habitat + Fragmentation. Second, we considered a “controlled model” by adding in the previous model the five supplementary predictors supposedly linked to detectability: Counts varies with Period + Habitat + Time + Cloudiness + Rain + Wind + Visibility + Fragmentation.

Time recorded by the observer was converted to time after local sunrise (in min, source: USNO 2007). Time and weather variables were considered as continuous predictors, as we expected the response of each species to each variable to be monotone. These five variables were also standardized by a z-transformation to allow comparisons of their magnitudes. Spearman’s rank correlations between habitat fragmentation, time-of-day and each weather variable were calculated. We found that habitat fragmentation and time-of-day were extremely weakly correlated to other variables (Table 2). As expected, rain, wind and visibility were weakly correlated to each other (Table 2).

We used generalized linear models accounting for “quasipoisson” distribution of errors, differing from Poisson distribution by allowing overdispersion in the count data for a species (McCullagh and Nelder 1989), with log as a link function.

Note that we didn’t account for spatial dependence between point counts (spatial autocorrelation) as statistical models usually run to handle spatial autocorrelation hardly support Poisson regression with large datasets. Despite violating the spatial independence assumption, we assumed that it should impact both models equally (with or without weather variables). Therefore, this problem should not impact the comparison between both models, which is the main focus of our analysis.

Table 2 Spearman’s rank correlations between variables used in this study

	Fragmentation	Time-of-day	Cloudiness	Rain	Wind
Time-of-day	−0.067				
Cloudiness	0.008	−0.005			
Rain	0.049	0.006	0.310		
Wind	0.023	0.094	0.172	0.119	
Visibility	0.041	−0.031	0.319	0.282	0.028

We analysed the effects of the five variables supposedly linked to detectability in two steps. First, we performed for each species and for each variable, a *t*-test of the corresponding slope fitted in the controlled model, compared to zero, to assess which species respond significantly to each variable. Second, we gathered for each variable, the 97 species response slopes and performed *t*-tests compared to zero in order to test more general patterns of response to weather and time-of-day variables. Time-of-day effects were also tested for the "vocal" activities species subset ($n = 73$; species most often detected because of their territorial vocalizations) as time-of-day effects were mostly expected for vocal activities (Lindenmayer et al. 2004; Woltmann 2005).

We further looked for a possible bias in the fragmentation effect estimation for the uncontrolled model by correlating fragmentation parameters of the two models in a paired *t*-test. Finally, we compared the fragmentation effect estimation's accuracy in both models. For this purpose, we calculated, for each species, the statistical power gain as follows:

$$\text{Gain} = (\text{SE}_1 - \text{SE}_2)/\text{SE}_1 \times 100$$

where SE_1 and SE_2 are the standard errors of the fragmentation parameters of respectively the uncontrolled and the controlled model. This metric gave us a potential gain (or a loss if negative) in accuracy of the fragmentation effect estimation, expressed in percentage of the uncontrolled accuracy.

As the amount of available data was expected to affect model fits, we assessed whether both eventual bias and gain in accuracy were related to the species commonness, measured using the log of total number of individuals recorded in the dataset for each species.

Results

Time-of-day and weather effect

Among the 97 species considered, the counts of 38 species were significantly affected by time-of-day (Table 3). These responses were as often positive as negative and the global response of the considered species was not significant (Fig. 1a, b). But, "vocal" species ($n = 73$) responded globally negatively to time-of-day (Table 3). Rain had globally the strongest effect on counts, but only 15 species individually responded significantly (Table 3, Fig. 1c). We also found highly significant negative effects of cloudiness and wind on counts (Table 3, Fig. 1d). However, visibility seemed to affect few species counts, without the expected global positive response (Table 3). Altogether, 75 of the 97 species showed at least one significant response to any of the five variables considered.

Bias and accuracy in fragmentation effect estimation

Fragmentation effect slope was highly correlated between uncontrolled and controlled models ($n = 97$, Pearson correlation coefficient: $\rho = 0.997$, see Fig. 2). Paired *t*-test revealed no significant differences between these two estimations ($t = 1.31$, df = 96, $P = 0.194$), and these slight differences were not linked to species commonness ($t = 0.73$, df = 95, $P = 0.47$).

Moreover there was no gain in accuracy in the estimation of fragmentation effect (average gain = −0.7%, $t = -1.33$, df = 96, $P = 0.186$), and there was no significant link between these gains and species commonness ($t = 0.238$, df = 95, $P = 0.812$).

Table 3 Effects of Time-of-day and Weather variables on counts

Variable	Species responses						
	−	(−)	(+)	++	Total significant	Average slope	*P*
Time-of-day							
Total	22	32	27	16	38	−0.001	0.974
Vocal species	19	28	19	7	26	−0.039	**0.014**
Cloudiness	21	43	24	9	30	−0.070	**<0.001**
Rain	9	37	45	6	15	−0.340	**0.013**
Wind	23	44	26	4	27	−0.072	**<0.001**
Visibility	5	35	46	11	16	0.041	0.50

The −, (−), (+) and ++ columns refer to the number of species that respectively respond significantly negatively, non-significantly negatively, non-significantly positively and significantly positively to the corresponding variable. Total significant column refers to the total number of species which respond significantly to each factor (either positively or negatively). Average slope column refers to the average response among species to the corresponding variable, and last column refers to the *P*-value from the *t*-test of the Average slope compared to zero

Bold values are significant test with $P < 0.05$

Discussion

Weather and time-of-day effects on detection

Among the 97 species we studied, 75 responded at least to one of the five variables potentially linked to detectability. Time-of-day seemed to be the less influential variable but the even distribution and large variability of this variable within the dataset showed many significant responses for individual species and, as expected, a global negative trend for vocal species (Lindenmayer et al. 2004; Woltmann 2005). Conversely, the four weather variables showed stronger global effects but affected fewer species, most likely because there were only three categorical values and very unequal sample sizes, as observers were told to avoid rainy, windy and misty conditions as much as possible. This resulted in only 6% of the counts made in both rainy and strong wind conditions and only 1% in poor visibility. Yet, many species still responded significantly to these variables, showing that standardizing field methods in monitoring programs does not still guarantee a constant detectability across sites (Verner 1985; Thompson 2002).

These results also showed that very easily recorded variables can provide valuable information for practical issues. Similar analyses could help to provide strong recommendations to new monitoring schemes, for example by recording time-of-day and weather conditions to find optimal detection conditions of a targeted species. Such variables could also be useful for more theoretical purposes. For example, these monitoring data could be used to test predictions on the time-of-day specialization of song activities (Cody and Brown 1969; Brumm 2006). In this latter case, we show that one should account for the variation in counts induced by variation in the time of the records.

Implication for fragmentation effect estimation

We found no bias induced by weather conditions on the fragmentation effect. Indeed, the fragmentation effect was remarkably robust to time-of-day and weather variables (Fig. 2).

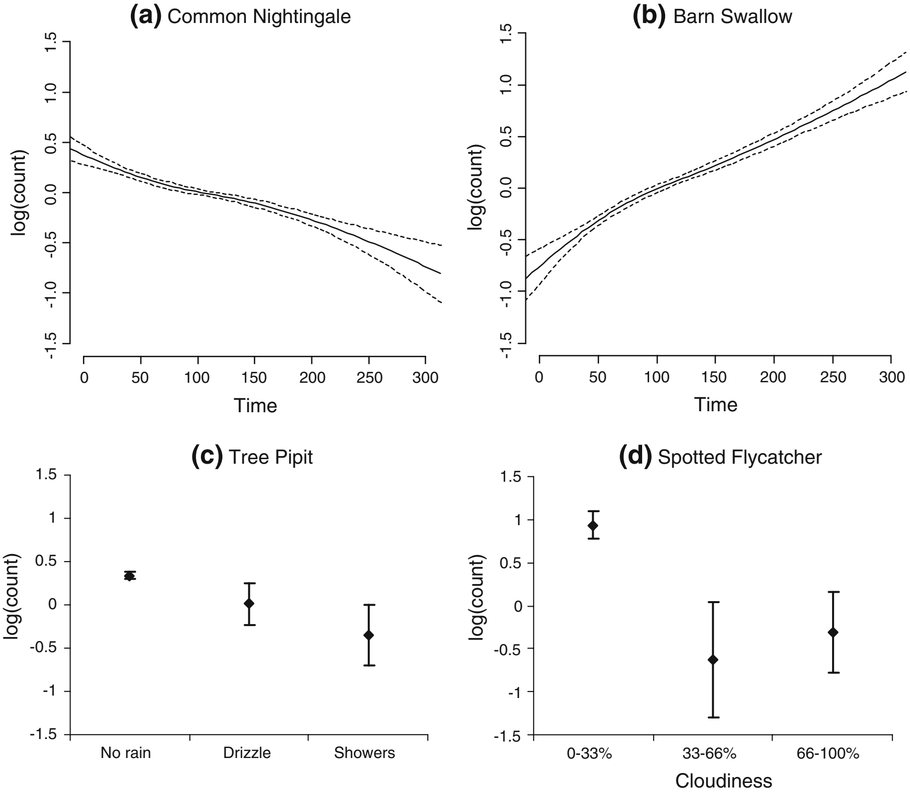
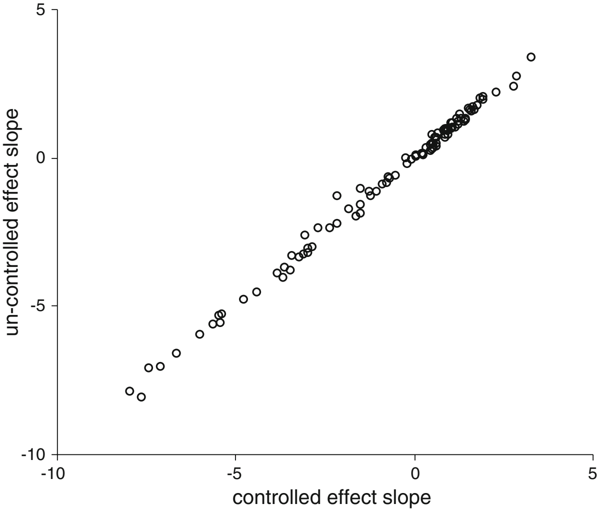


Fig. 1 Examples for differential detectability under different conditions. (**a**, **b**) The relationship between counts and time after sunrise for (**a**) Common Nightingale (*Luscinia megarhynchos* Brehm), a species detected almost exclusively by its song and for (**b**) Barn Swallow (*Hirundo rustica* L.) whose detection is linked to its prey activity (dipterans). Fit from a non-parametric spline function with 4 df, adjusted to habitat, count period and weather; dotted lines show ±1 SE. (**c**) The relationship between counts and rain conditions for Tree Pipit (*Anthus trivialis* L.), a species whose detection is linked to territorial display activity which is strongly inhibited by rain. Note that rain was here considered as a discrete variable, its effect was adjusted to habitat, count period, time-of-day and weather; bars show ±1 SE. (**d**) The relationship between counts and cloudiness for Spotted Flycatcher (*Muscicapa striata* Pallas), a species detected mostly when sallying out from vegetation hunting flying insects (Cramp and Perrins 1993). Cloudiness was here considered as a discrete variable, its effect was adjusted to habitat, count period, time-of-day and weather; bars show ±1 SE

Thus, this result suggests that when heterogeneity in detectability is not correlated to the process of interest, there should be no bias in ecological correlations using raw counts. However, Gu and Swihart (2004) found strong bias in habitat relationships with simulated occurrence data, even when detectability was independent of habitats. We emphasize that this pattern could be induced when considering occurrence data. Indeed, sites with very few individuals should exhibit critically low detection probabilities which may stronger impact occurrence than abundance potential bias. Thus, we argue that although counts may include more sources of unchecked variations, using counts should be more robust than presence-absence data to detectability heterogeneity.

Fig. 2 The relationship between uncontrolled and controlled estimation of the fragmentation effect for the 97 species (points)



Moreover, we also found no gain in accuracy when accounting for time-of-day and weather covariates. Thus in this example, there was no need to account for weather and time-of-day covariates to answer our ecological question.

To conclude, we showed that raw counts can be influenced by weather and time-of-day conditions even if the monitoring design intends to standardize field methods. Yet, we also showed that these variations in detectability did not induce any bias nor any lack of statistical power while estimating species response to habitat fragmentation. We suggest that this example is representative of many ecological analyses performed on large raw counts dataset. Obviously, sources of variation in detectability may be more diverse than weather and time-of-day alone (Bart and Schoultz 1984; Schieck 1997; Norvell et al. 2003) and can give wrong ecological messages if not carefully addressed (Moilanen 2002; Mazerolle et al. 2005). We thus strongly recommend to at least list potential bias induced by heterogeneity in detectability. Then, we suggest that counts from classic monitoring scheme may still be used without any correction when relating species abundance to ecological factor, whenever variations in detectability can be safely considered as independent of the ecological factor of interest.

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Appendix

List of the 97 species used in the analysis

Scientific name	Vocal	Time-of-day	Cloudiness	Rain	Wind	Visibility
Aegithalos caudatus	0	0.118 ± 0.062	0.059 ± 0.068	−0.109 ± 0.076	0.01 ± 0.065	−0.04 ± 0.062
Alauda arvensis	1	0.093 ± 0.018	0.018 ± 0.02	−0.038 ± 0.023	0.015 ± 0.018	−0.024 ± 0.019
Alectoris rufa	1	−0.053 ± 0.08	−0.021 ± 0.084	0.144 ± 0.07	−0.362 ± 0.097	−0.067 ± 0.071
Anthus campestris	1	−0.158 ± 0.083	−0.366 ± 0.114	−5.477 ± 314	−0.075 ± 0.083	5.693 ± 292
Anthus pratensis	1	−0.247 ± 0.08	−0.197 ± 0.089	−0.061 ± 0.094	0.386 ± 0.065	−0.022 ± 0.084
Anthus trivialis	1	0.042 ± 0.037	0.005 ± 0.04	−0.136 ± 0.05	−0.078 ± 0.04	−0.032 ± 0.036
Apus apus	0	0.188 ± 0.094	−0.591 ± 0.162	0.27 ± 0.093	0.089 ± 0.098	−0.088 ± 0.138
Burhinus oedicnemus	1	0.083 ± 0.129	−0.029 ± 0.146	0.167 ± 0.115	−0.47 ± 0.167	−0.144 ± 0.111
Buteo buteo	0	0.158 ± 0.059	−0.059 ± 0.068	−0.15 ± 0.096	−0.094 ± 0.066	0.064 ± 0.074
Carduelis cannabina	1	0.127 ± 0.047	−0.032 ± 0.054	0.04 ± 0.048	0.092 ± 0.045	−0.001 ± 0.05
Carduelis carduelis	1	0.02 ± 0.034	−0.017 ± 0.037	−0.002 ± 0.035	−0.018 ± 0.034	−0.017 ± 0.035
Carduelis chloris	1	−0.096 ± 0.026	−0.006 ± 0.027	−0.003 ± 0.025	−0.015 ± 0.026	0.027 ± 0.027
Certhia brachydactyla	1	−0.092 ± 0.031	0 ± 0.032	−0.013 ± 0.032	−0.103 ± 0.034	−0.023 ± 0.029
Certhia familiaris	1	−0.17 ± 0.111	−0.294 ± 0.134	−0.116 ± 0.151	0.366 ± 0.104	−0.178 ± 0.098
Cettia cetti	1	−0.557 ± 0.086	−0.003 ± 0.085	0.034 ± 0.073	−0.003 ± 0.076	−0.205 ± 0.061
Cisticola jucundis	1	−0.038 ± 0.064	−0.028 ± 0.075	−0.188 ± 0.101	−0.05 ± 0.062	−0.201 ± 0.06
Coccothraustes coccothraustes	0	−0.202 ± 0.093	0.183 ± 0.087	−0.152 ± 0.112	−0.278 ± 0.114	−0.077 ± 0.07
Columba livia	1	−0.208 ± 0.086	−0.369 ± 0.122	0.117 ± 0.075	0.066 ± 0.094	−0.094 ± 0.112
Columba oenas	1	−0.082 ± 0.189	−0.178 ± 0.218	−0.25 ± 0.4	−0.308 ± 0.251	−0.054 ± 0.213
Columba palumbus	1	−0.107 ± 0.021	0.008 ± 0.023	0.015 ± 0.021	−0.074 ± 0.022	−0.006 ± 0.022
Corvus corone	0	0.021 ± 0.036	−0.005 ± 0.039	0.021 ± 0.036	−0.01 ± 0.036	−0.005 ± 0.036
Corvus frugilegus	0	0.207 ± 0.141	−0.442 ± 0.22	0.115 ± 0.186	0.074 ± 0.14	−0.009 ± 0.207
Corvus monedula	0	0.249 ± 0.104	−0.166 ± 0.129	0.116 ± 0.106	−0.216 ± 0.126	−0.118 ± 0.112

Appendix continued

Scientific name	Vocal	Time-of-day	Cloudiness	Rain	Wind	Visibility
Coturnix coturnix	1	−0.278 ± 0.071	0.031 ± 0.075	−0.036 ± 0.094	−0.007 ± 0.063	−0.26 ± 0.121
Cucculus canorus	1	−0.09 ± 0.035	−0.074 ± 0.038	0.015 ± 0.035	−0.131 ± 0.039	−0.153 ± 0.029
Delichon urbicum	0	−0.073 ± 0.132	−0.338 ± 0.179	−0.425 ± 0.403	−0.207 ± 0.157	−0.104 ± 0.166
Dendrocopos major	1	−0.038 ± 0.032	0.057 ± 0.034	−0.058 ± 0.039	−0.169 ± 0.037	0.036 ± 0.035
Dendrocopos medius	1	0.15 ± 0.073	−0.137 ± 0.081	−0.399 ± 0.18	−0.289 ± 0.105	−0.31 ± 0.051
Dendrocopos minor	1	0.073 ± 0.118	−0.014 ± 0.13	−0.015 ± 0.132	−0.218 ± 0.141	0.004 ± 0.127
Dryocopos martius	1	−0.063 ± 0.121	0.133 ± 0.123	0.012 ± 0.123	−0.019 ± 0.131	0.112 ± 0.141
Emberiza cia	1	−0.291 ± 0.163	0.283 ± 0.157	−0.318 ± 0.226	−0.045 ± 0.164	−0.111 ± 0.135
Emberiza cirlus	1	−0.066 ± 0.039	−0.117 ± 0.043	0.046 ± 0.04	−0.071 ± 0.039	0.003 ± 0.04
Emberiza citrinella	1	−0.047 ± 0.027	−0.013 ± 0.029	−0.028 ± 0.031	0.007 ± 0.026	0.018 ± 0.028
Emberiza hortulana	1	0.234 ± 0.168	−0.19 ± 0.228	−5.607 ± 623	0.213 ± 0.164	−0.081 ± 0.213
Erithacus rubecula	1	−0.08 ± 0.015	0.036 ± 0.016	−0.01 ± 0.015	0.005 ± 0.016	−0.002 ± 0.015
Falco tinnunculus	0	0.116 ± 0.062	0.046 ± 0.068	0.017 ± 0.066	0.068 ± 0.06	0.096 ± 0.075
Fringilla coelebs	1	0.044 ± 0.01	0.02 ± 0.011	0.015 ± 0.01	0.01 ± 0.01	0.021 ± 0.011
Galerida cristata	1	−0.117 ± 0.103	−0.459 ± 0.133	−5.375 ± 265.9	−0.576 ± 0.15	−0.193 ± 0.092
Garrulus glandarius	0	0.041 ± 0.035	−0.089 ± 0.039	0.019 ± 0.037	−0.05 ± 0.038	0.08 ± 0.041
Hippolais polyglotta	1	−0.128 ± 0.036	−0.117 ± 0.043	−0.023 ± 0.047	−0.061 ± 0.037	−0.063 ± 0.041
Hirundo rustica	0	0.341 ± 0.043	0.138 ± 0.048	0.034 ± 0.042	−0.164 ± 0.048	0.076 ± 0.051
Jynx torquilla	1	0.052 ± 0.124	−0.307 ± 0.149	0.062 ± 0.127	−0.125 ± 0.138	−0.093 ± 0.114
Lanius collurio	0	0.17 ± 0.068	−0.108 ± 0.093	−0.006 ± 0.105	−0.136 ± 0.076	0.119 ± 0.125
Locustella naevis	1	−0.123 ± 0.107	0.063 ± 0.106	−0.039 ± 0.101	−0.01 ± 0.104	−0.116 ± 0.084
Lullula arborea	1	0.067 ± 0.048	−0.131 ± 0.055	0.042 ± 0.054	−0.159 ± 0.053	0.058 ± 0.056
Luscinia megarhynchos	1	−0.193 ± 0.023	−0.064 ± 0.024	0.011 ± 0.023	−0.078 ± 0.023	−0.039 ± 0.021
Merops apiaster	0	1.182 ± 0.15	−0.454 ± 0.272	−5.473 ± 629	−0.613 ± 0.287	0.167 ± 0.375
Miliaria calandra	1	−0.028 ± 0.039	−0.007 ± 0.043	0.004 ± 0.046	−0.015 ± 0.037	−0.017 ± 0.041

Appendix continued

Scientific name	Vocal	Time-of-day	Cloudiness	Rain	Wind	Visibility
Milvus migrans	0	−0.207 ± 0.139	−0.141 ± 0.153	0.142 ± 0.117	0.046 ± 0.128	0.158 ± 0.177
Motacilla alba	1	−0.011 ± 0.041	0.062 ± 0.043	0.047 ± 0.036	0.016 ± 0.039	−0.001 ± 0.041
Motacilla flava	1	−0.031 ± 0.05	0.035 ± 0.054	−0.075 ± 0.068	0.008 ± 0.046	0.055 ± 0.059
Muscicapa striata	0	0.286 ± 0.104	−0.467 ± 0.167	−5.22 ± 299.411	−0.082 ± 0.126	0.067 ± 0.199
Oenanthe oenanthe	0	0.192 ± 0.085	−0.046 ± 0.098	0.065 ± 0.084	−0.073 ± 0.09	−0.216 ± 0.064
Oriolus oriolus	1	−0.017 ± 0.045	−0.051 ± 0.051	0.005 ± 0.054	−0.113 ± 0.049	0.132 ± 0.063
Parus ater	1	0.175 ± 0.041	−0.082 ± 0.051	0.05 ± 0.047	0.09 ± 0.047	0.031 ± 0.047
Parus caeruleus	1	0.03 ± 0.019	−0.018 ± 0.02	−0.015 ± 0.02	−0.037 ± 0.02	0.028 ± 0.02
Parus cristatus	0	0.243 ± 0.061	−0.04 ± 0.077	−0.29 ± 0.144	−0.05 ± 0.079	−0.08 ± 0.071
Parus major	1	−0.025 ± 0.015	0.027 ± 0.016	0.028 ± 0.014	−0.095 ± 0.016	0.041 ± 0.016
Parus montanus	1	−0.045 ± 0.114	0.067 ± 0.128	0.117 ± 0.095	−0.028 ± 0.122	0.141 ± 0.096
Parus palustris	1	0.109 ± 0.062	0.122 ± 0.066	0.019 ± 0.063	−0.274 ± 0.08	0.001 ± 0.062
Passer domesticus	0	0.001 ± 0.021	−0.092 ± 0.024	0.072 ± 0.02	0.028 ± 0.021	0.028 ± 0.025
Passer montanus	0	−0.246 ± 0.104	−0.343 ± 0.125	0.067 ± 0.12	−0.207 ± 0.112	−0.165 ± 0.093
Perdix perdix	0	0.012 ± 0.058	0.074 ± 0.062	0.013 ± 0.065	−0.087 ± 0.057	0.003 ± 0.061
Phasianus colchicus	1	−0.286 ± 0.061	−0.053 ± 0.061	0.02 ± 0.059	−0.085 ± 0.06	−0.009 ± 0.056
Phoenicurus ochruros	1	−0.06 ± 0.031	−0.004 ± 0.033	0.047 ± 0.029	−0.116 ± 0.033	0.118 ± 0.038
Phoenicurus pheonicurus	1	0.027 ± 0.057	−0.13 ± 0.066	−0.085 ± 0.075	−0.062 ± 0.063	−0.001 ± 0.063
Phylloscopus bonelli	1	0.091 ± 0.05	−0.254 ± 0.064	0.034 ± 0.066	−0.249 ± 0.066	0.018 ± 0.061
Phylloscopus collybita	1	−0.006 ± 0.015	0.031 ± 0.016	−0.053 ± 0.016	0.007 ± 0.016	−0.013 ± 0.015
Phylloscopus sibilatrix	1	−0.014 ± 0.108	0.175 ± 0.109	0.118 ± 0.098	−0.348 ± 0.146	0.092 ± 0.118
Phylloscopus trochilus	1	0.223 ± 0.047	0.243 ± 0.05	−0.149 ± 0.059	−0.063 ± 0.054	−0.075 ± 0.044
Pica pica	0	−0.045 ± 0.032	−0.005 ± 0.035	−0.064 ± 0.039	−0.046 ± 0.033	0.003 ± 0.037
Picus viridis	1	−0.002 ± 0.039	−0.001 ± 0.042	0.041 ± 0.036	−0.101 ± 0.042	−0.015 ± 0.038
Prunella modularis	1	−0.058 ± 0.028	−0.048 ± 0.03	0.023 ± 0.026	0.076 ± 0.027	−0.027 ± 0.027

Appendix continued

Scientific name	Vocal	Time-of-day	Cloudiness	Rain	Wind	Visibility
Pyrrhula pyrrhula	0	0.098 ± 0.077	0.012 ± 0.087	0.02 ± 0.08	0.014 ± 0.082	0.003 ± 0.082
Regulus ignicapillus	1	−0.013 ± 0.051	−0.028 ± 0.056	0.078 ± 0.046	−0.147 ± 0.06	−0.056 ± 0.047
Regulus regulus	1	0.028 ± 0.054	−0.041 ± 0.062	0.061 ± 0.057	−0.157 ± 0.066	0.055 ± 0.06
Saxicola rubetra	1	−0.275 ± 0.113	−0.238 ± 0.129	−0.042 ± 0.139	0.112 ± 0.1	0.072 ± 0.132
Saxicola torquatus	1	0.024 ± 0.039	−0.009 ± 0.042	0.059 ± 0.039	−0.092 ± 0.039	0.028 ± 0.041
Serinus serinus	1	−0.09 ± 0.036	−0.016 ± 0.038	−0.024 ± 0.038	−0.053 ± 0.037	−0.016 ± 0.037
Sitta europaea	1	0.058 ± 0.034	−0.034 ± 0.038	−0.095 ± 0.048	−0.141 ± 0.04	0.052 ± 0.041
Streptopelia decaocto	1	−0.064 ± 0.025	0.029 ± 0.026	0.042 ± 0.022	−0.092 ± 0.026	−0.001 ± 0.025
Streptopelia turtur	1	−0.014 ± 0.032	0.015 ± 0.035	−0.085 ± 0.042	−0.072 ± 0.033	−0.064 ± 0.035
Sturnus vulgaris	1	0.025 ± 0.045	0.117 ± 0.048	0.039 ± 0.04	−0.03 ± 0.045	−0.075 ± 0.043
Sylvia atricapilla	1	−0.019 ± 0.011	0.009 ± 0.011	−0.008 ± 0.011	−0.037 ± 0.011	0.016 ± 0.011
Sylvia borin	1	0.06 ± 0.045	0.125 ± 0.049	−0.175 ± 0.067	0.033 ± 0.046	−0.018 ± 0.052
Sylvia cantillans	1	−0.121 ± 0.093	−0.791 ± 0.158	0.456 ± 0.08	−0.235 ± 0.114	0.236 ± 0.158
Sylvia communis	1	0.004 ± 0.028	−0.004 ± 0.031	−0.069 ± 0.035	0.039 ± 0.027	−0.072 ± 0.028
Sylvia curruca	1	0.029 ± 0.128	−0.282 ± 0.166	0.258 ± 0.111	−0.099 ± 0.135	0.215 ± 0.196
Sylvia melanocephala	1	−0.106 ± 0.067	−0.033 ± 0.072	−0.033 ± 0.072	−0.231 ± 0.079	−0.136 ± 0.059
Sylvia undata	1	0.049 ± 0.097	0.188 ± 0.112	−5.568 ± 383	−0.117 ± 0.116	0.261 ± 0.153
Troglodytes troglodytes	1	−0.138 ± 0.014	0.063 ± 0.014	−0.023 ± 0.014	0.025 ± 0.014	0.013 ± 0.014
Turdus merula	1	−0.062 ± 0.011	0.035 ± 0.011	0.029 ± 0.01	−0.044 ± 0.011	−0.003 ± 0.011
Turdus philomelos	1	−0.141 ± 0.023	0.097 ± 0.023	−0.046 ± 0.023	−0.029 ± 0.024	−0.036 ± 0.021
Turdus pilaris	1	−0.013 ± 0.137	−0.034 ± 0.152	0.072 ± 0.104	0.34 ± 0.122	−0.252 ± 0.097
Turdus viscivorus	1	−0.023 ± 0.05	−0.13 ± 0.056	0.085 ± 0.044	0.029 ± 0.051	−0.131 ± 0.042
Upupa epops	1	−0.237 ± 0.068	−0.252 ± 0.074	0.021 ± 0.065	0.029 ± 0.064	−0.278 ± 0.046
Vanellus vanellus	0	0.396 ± 0.161	−0.301 ± 0.236	0.234 ± 0.164	−0.321 ± 0.2	−0.022 ± 0.197

Vocal column shows which species have been considered as “vocal” (1) or not (0), i.e. whose detections are mainly due to territorial vocalizations. The last five columns show species response slopes (±SE) to the five weather and time-of-day z-transformed variables in the controlled model

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Manuscrit 2

A method to estimate phenological variation using data from large-scale abundance monitoring programmes

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A method to estimate phenological variation using data from large-scale abundance monitoring programmes

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Capsule Large-scale abundance monitoring programmes can be used to estimate annual phenological shifts.

Aims Phenology refers to the timing of any annually repeated biological event. The method developed here aims at measuring phenological variation in an indirect way by modelling seasonal abundance variations. Thus, it provides the opportunity to use a large number of datasets which have rarely been used in phenological studies. Phenological variations computed using this standardized method are comparable between species.

Methods The data used for the development of this method originates from the French Breeding Bird Survey, a large-scale abundance monitoring programme launched in 2001. For each species, the phenological shift between two seasonal abundance trends is computed using maximum likelihood.

Results Phenological shifts relative to the year 2005 (reference year) were estimated for 46 species over a 5-year period (2001–6). The standard deviations of the shifts do not differ significantly between species with different migratory status. Moreover, at the species level, the computed phenological shifts relate to the shifts of the mean date weighted by abundance. However, mean date, cannot be used in studies incorporating species with different migratory status (e.g. trans-Saharan migrant, sedentary) because of ambiguous changes for the same biological shift in timing.

Conclusions The method described here is of particular value in determining how the phenology of common bird species changes in relation to climate. It offers the opportunity to increase the spatial scale of phenological studies and to include multi-species analyses. This method could be applied to any abundance or constant effort site programme to study the timing of any biological process for which a seasonal distribution is available.

Phenology has become a key research field in the understanding of the effects of climate change on animal or plant populations (Walther *et al.* 2002, Parmesan & Yohe 2003, Crick 2004, Parmesan 2006). However, until now hypotheses concerning the way global change is currently altering the timing of seasonal events of a species mostly originate from sampling protocols dealing with only a few species surveyed intensively at few study sites (Sparks *et al.* 2005, Jonzen *et al.* 2006).

Moreover, most datasets that have until now been analyzed under the phenological framework originate from designs displaying many temporal but very few spatial replicates. This is a result of the trade-off existing between temporal and spatial replicates as the former are too costly to carry out at a large spatial scale. Among birds, for example, although migration studies are numerous, they are usually carried out at specific migration monitoring stations (Sparks & Braslavska 2001, Moller *et al.* 2004, Sparks *et al.* 2005, Croxton *et al.* 2006, Jonzen *et al.* 2006). These monitoring conditions only allow a maximum of a dozen species to be surveyed accurately due to scarcity of data concerning rare or nocturnal migration (but see Jenni & Kery [2003] concerning autumn migration

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*Correspondence author. Email: moussus@mnhn.fr trends). Breeding timing in birds has been followed primarily using nestboxes in localized areas (but see Crick & Sparks 1999).

A major issue about a species phenology is the effective estimation of how early or late it is compared with its average timing over a certain period of time. The aforementioned protocols and their derived methods yield different accuracies for such estimates. On the one hand, it is possible to derive the exact laying dates from nestbox surveys. On the other hand, the first bird seen is a very approximate and unreliable proxy for temporal distribution of migration (van Strien *et al.* 2008). Furthermore, median dates or mean date quantiles might very much depend on the monitoring site and sample sizes (Tryjanowski & Sparks 2001, van Strien *et al.* 2008). However, surveys including many temporal records on few sites allowed estimations concerning gradual advancement of migration arrival dates or laying dates. The accuracy of these approaches has made it possible to compare a species' phenological response to climate change with that of its prey (Visser & Both 2005, Visser *et al.* 2006).

Yet, these approaches raise two different issues. First, they remain spatially limited, and second, they do not tackle the phenological issue for all the species that cannot be surveyed that way. Indeed, staying with the bird example, between 50 and 80 species are fairly common in western Europe depending on the environment. Yet, for most of them, we have hardly any idea of their particular phenology except from data collected by amateurs that may lack standardization and repeatability. Thus, there is a current gap in the knowledge of most common species' temporal responses to climate change.

Here, we propose to take advantage of large-scale abundance monitoring programmes used to survey many different taxa. Most of these sampling protocols are designed to monitor abundance on large spatial scales. Therefore, most of them provide abundance data with many spatial replicates but only few temporal replicates. These data were analyzed using a new method designed to determine for a given species, the temporal phenological shift between two different years, in other words, how a species is late or early in its breeding phenology compared to a reference year. We applied this method to 93 bird species monitored by the French Breeding Bird Survey (BBS) (Jiguet *et al.* 2007). In comparison with costly monitoring methods such as nestbox surveys or permanent migratory counts at a few stations, the dataset analyzed here originates from volunteers' monitoring efforts; counting birds at numerous sites spread across the whole country using a repeatable and standardized protocol. This method can be applied to data gathered through point counts or transects as long as standardization is ensured throughout the study period.

METHODS

Data collection and data processing

The French BBS programme is based on volunteer ornithologists counting birds in spring on permanent plots. Surveyed sites are 2 × 2 km squares randomly selected within a 10 km radius around a locality specified by the volunteer. Random selection (one of about 80 possible squares) ensures that surveyed habitats closely match their actual availability (Jiguet *et al.* 2007). In each square, observers carry out ten point counts (separated by at least 300 m) of 5 minutes duration each. Counts are done twice in spring (from 1 April to 8 May, then from 9 May to the end of June) in order to detect both early and late breeders, with 4–6 weeks between both counts. For a given site, counts are repeated yearly by the same observer at the same points, on approximately the same date (± 7 days within April to mid-June), and at the same time in the day (± 15 minutes). Here, counts for the ten points within each square and each session were summed before analysis. The number of monitored sites varied across the study period: 178 sites in 2001, 616 in 2002, 774 in 2003, 856 in 2004, 886 in 2005 and 873 in 2006.

In order to address statistical problems due to data over-dispersion, we fixed a threshold for the number of birds seen at the same time at ten individuals on the scale of the count point (Julliard *et al.* 2006). Wetland birds were excluded from the study because they are not well monitored by this protocol (Jiguet *et al.* 2007).

Seasonal abundance variation modelling

The purpose for this study was to determine the differences in phenological timing of a species between two years. The BBS data provide us with a count distribution across time within a year of the survey. Thus, for a given species it would be possible to estimate its phenological shifts between two years by using mean or median count dates weighted by abundance (Knudsen *et al.* 2007). However, it is not possible to use such measures, to compare the shifts of different species displaying different shapes of count distributions. Indeed, the sign of the shifts of mean and median dates depends on the type of count distribution the species displays (see Fig. 1 for an example based on two different theoretical abundance

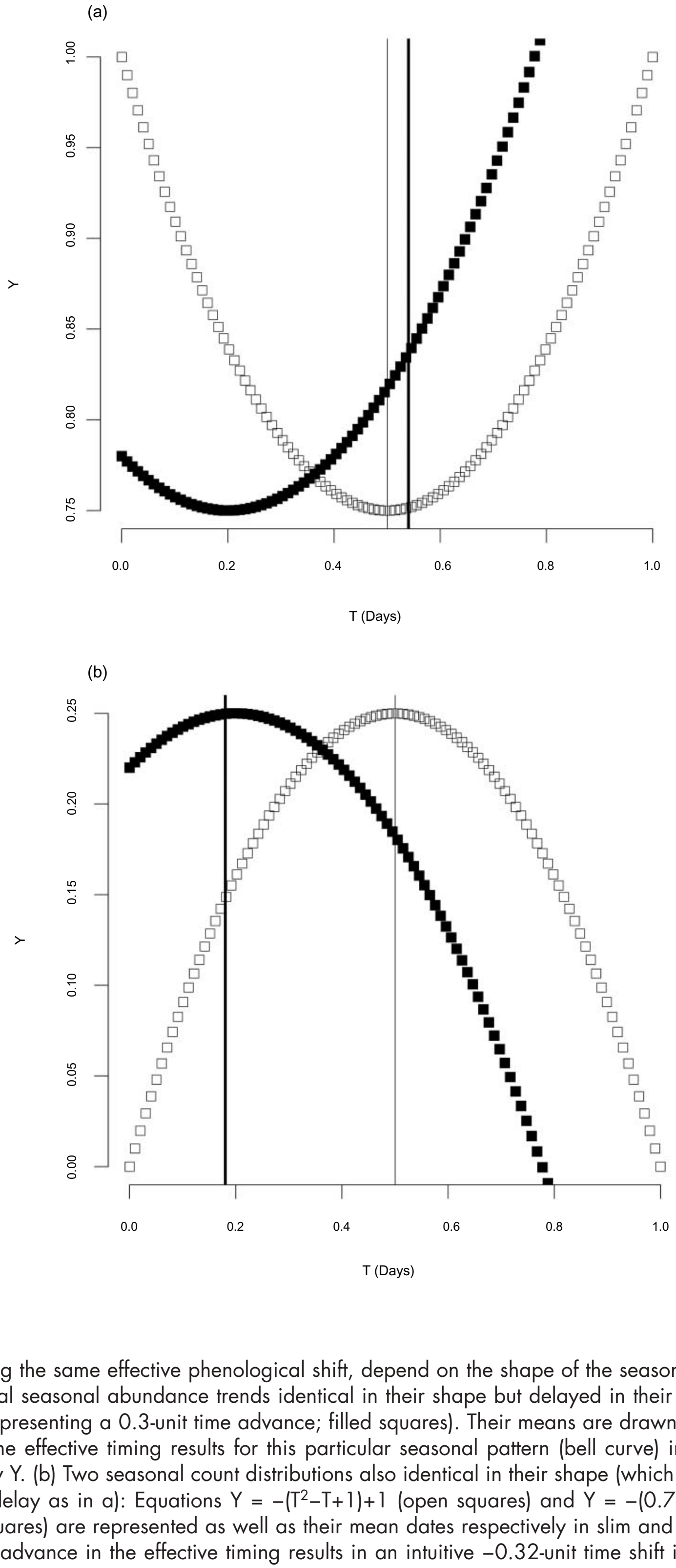


Figure 1. Mean shifts reflecting the same effective phenological shift, depend on the shape of the seasonal count distribution. (a) Two equations representing two theoretical seasonal abundance trends identical in their shape but delayed in their timing: $Y = T^2 – T+1$ (open squares) and $Y = 0.75T^2 – 0.3T+0.78$ (representing a 0.3-unit time advance; filled squares). Their means are drawn respectively in slim and thick lines. This 0.3-unit time advance in the effective timing results for this particular seasonal pattern (bell curve) in a counterintuitive +0.04-unit time shift for the mean T weighted by Y. (b) Two seasonal count distributions also identical in their shape (which is different from the shape in a) but delayed in their timing (same delay as in a): Equations $Y = –(T^2 – T+1)+1$ (open squares) and $Y = –(0.75T^2 – 0.3T+0.78)+1$ (representing a 0.3-unit time advance; filled squares) are represented as well as their mean dates respectively in slim and thick lines. This time, for this shape of distribution the 0.3-unit time advance in the effective timing results in an intuitive –0.32-unit time shift in the mean T weighted by Y. Thus, mean date shifts computed for different species showing different shapes of seasonal abundance patterns (either bell or U curves) are not comparable since the same biological change makes the weighted mean change in opposite ways.

distributions). For this reason it was not possible to use mean dates or given quantile dates as did Sparks *et al.* (2005) or Jonzen (2006). To address this issue we developed a method yielding phenological shifts and from which the signs do not depend on the species life-history traits.The first step is the modelling of a species' annual phenology using the count data. Birds were counted twice a year at a given site. This provides an estimation of the species' seasonal abundance variation for this site. As each species was detected on numerous sites at various dates, then for a given species, pooling data originating from all sites yields a continuous estimation of the species' seasonal abundance variations. We assumed that variation in estimated abundance using raw counts was a proxy for a species' phenology. Indeed, detection probability which determines this count is a function of two variables. First, the number of birds that are to be counted and second, the probability of counting a bird knowing it is actually present (MacKenzie *et al.* 2002, Royle *et al.* 2005). The number of birds to be counted varies with a species' phenology. The probability of detecting a certain bird that is present is a function of its behaviour and of the observer's skill. Behaviour is also highly dependent on phenology (Best & Petersen 1982, Hegelbach & Spaar 2000, Amrhein *et al.* 2004, Kunc *et al.* 2007). Both variables could be to some extent confounded, but this has no major impact on the method. Indeed it is very likely that, for a given species, if detection probability increases with abundance throughout the sampling season, this should happen evenly every year. As under these assumptions, we expected non-linear abundance variations, we fitted a generalized additive model (GAM) to the count data across time using the following model: Counts~(Counting site) + spline function (Counting date) with a Poisson error. The non-linear part of the model (spline function) was assigned three degrees of freedom. Smoothing abundance data to model phenology has recently been suggested (Knudsen *et al.* 2007). For each species and each annual model, relevance was tested and the significance of the smoothed term (Counting date) was recorded.

Repeatability in different abundance patterns in different years is a prerequisite for computation of phenological shifts because year-to-year comparisons require that both annual abundance distributions can be matched. Therefore, this method can only be applied to the species under the assumption that the shape of the seasonal distribution does not change between years. This is also true for any other tested dataset. For this reason, we only calculated temporal shifts for the species for which the counting date had a significant effect on seasonal abundance and similar shapes in abundance distributions in at least 3 years. Thus, 46 species out of 93 were retained.

Estimation of inter-annual temporal shifts

For those species for which seasonal trends in abundance were significantly related to time measured by the counting date, we estimated temporal shifts of the phenology. In order to achieve this we propose a method based on maximum likelihood: the main picture of this method is to compare the timing of two smoothed seasonal abundance trends by setting one as a reference and by shifting the other one temporally until it best matches the first one. In order to achieve this, all estimated temporal shifts were computed between each one of the survey's within-year seasonal trend for each species, and the trend for 2005. This year was set as the reference year because it had the most monitored sites and therefore yielded most data. The algorithm employed the following steps:

(a) Both the tested year's and the reference year's abundance data were pooled into a common dataset comprising dated abundance data.

(b) Onto this dataset we fitted the following GAM: Counts~(Counting site) + spline function (Counting date + t) with a Poisson error, where t was equal to 0 for all the data gathered during the reference year (the trend that remains fixed) and ranged from −15 to +15 days with 0.1-day intervals for the tested year (the trend that is translated temporally until it matches the reference trend). We limited the time interval to 30 days to remain within biologically relevant values. As the survey period only covers an 80-day period, a 30-day interval avoided estimating shifts referring to these situations in which both seasonal trends are completely separate. Moreover, phenological changes mostly occur within such a time frame. The choice of such narrow intervals (0.1 days) was made to optimize further estimation of the minimal AIC (Akaike 1981). This algorithm looks for the best temporal translation that makes two seasonal abundance trends match, using an iteration on the elementary translation (t) applied to one trend. It then tests whether this elementary translation reduces the difference between both trends: for each t we measured the model's AIC. In this case the AIC is a measure of how two different annual abundance distributions can be fitted under the same model by correcting timing differences using t. As for one comparison all the 301 models corresponding to the 301 different ts (t ranging between −15 and +15 with 0.1 intervals) had the same number of parameters, AIC was equivalent to the negative of the log likelihood so that minimizing AIC was the same as maximizing likelihood in this framework.

(c) Eventually, to estimate the temporal shift (t) corresponding to the minimal AIC we modelled for each species and each year-to-year comparison, the relationship between t and AIC. To do so, we used a quadratic regression: $\text{AIC} \sim t + t^2$. We only applied this model to the ten ts around the minimum AIC that we obtained during the iteration phase because the estimation of a minimum and its standard error are more accurate locally. Using the regression coefficients, the temporal shift between both years was estimated as $-b/2a$, where a is the second-degree coefficient of the quadratic regression and b the first-degree coefficient. We computed the standard estimation error of t as $1/a$, which is equal to the negative inverse of the log likelihood's second derivative. If there was no local minimum AIC within the −15/+15 days interval, the method was considered inefficient for this particular species and this particular year (see Fig. 2 for an illustration of the computation of the shifts). Statistical analyses were performed using the R software (R Development Core Team 2006).

Robustness tests

We compared the phenological shifts with a classical phenological measure. We chose the mean count date because it is widespread in phenological studies (Sparks *et al.* 2005). We computed mean count date shifts by estimating for each year, the mean date weighted by abundance. Mean shifts were then calculated as the difference between this mean and the mean weighted by counts for the reference year (2005). In order to test the relationship between this mean shift and the phenological shifts, we had to subset the dataset into sedentary species, long-distance migrants and short-distance migrants. Indeed, for each of these categories, mean shift sign is not expected to be the same, given the different shapes of the count distributions (see Fig. 1).

We looked at the relationships between the relative standard deviation (rsd) of the phenological shifts and various variables concerning the migratory status of the included species. Rsd was defined as the absolute value of the variation coefficient of the phenological shifts (standard deviation/mean). Migratory index (Migind) was defined as the log-transformed mean distance between breeding and wintering grounds of ringed individuals. This was determined using data from the French ringing database and only considering birds ringed in France between April and July and subsequently recorded anywhere, alive or recently dead, between November and February (Jiguet *et al.* 2006). Migratory status (Mig stat), was defined as a discrete variable (3 for sedentary species (Migind < 300km), 2 for short-distance migrants (300km < Migind < 1500km) and 1 for long-distance migrants (Migind > 3000km). The gap in migration distances between short-distance migrants and long-distance migrants is due to the crossing of the Sahara desert by these species.

It has been reported that long-distance migrants travelling by night are influenced by moon cycles (Pyle *et al.* 1993, James *et al.* 2000). Yet, these cycles do not occur on the same date each year, so the phenological shifts for these species could only reflect the differences between one year's moon cycles and 2005's cycles. Thus, for long-distance migrants we tested the relationship between moon cycles and the estimated phenological shifts (shift). To achieve this, we calculated the temporal delay (Moonshift) lying between April 2005's full moon and the other years' April full moon in order to remain relevant with the way we had estimated the phenological shifts (2005 as the reference year). To test all these relationships we used linear mixed-effects models with species as a random effect. Migind was log-transformed.

RESULTS

Seasonal abundance modelling

We modelled variation in seasonal abundance using GAMS for each species ($n = 93$) and each year ($n = 6$). Abundance was significantly influenced by the counting date in at least one year for 89% of the studied species and in at least three different years for 49% of the species. The percentage of species for which abundance was significantly related to counting date for all six study years dropped to 13% which represented 12 species out of the 93 initially considered in the study. If 2001 (when only 178 sites were monitored) was excluded, the percentage of species that showed a significant effect of

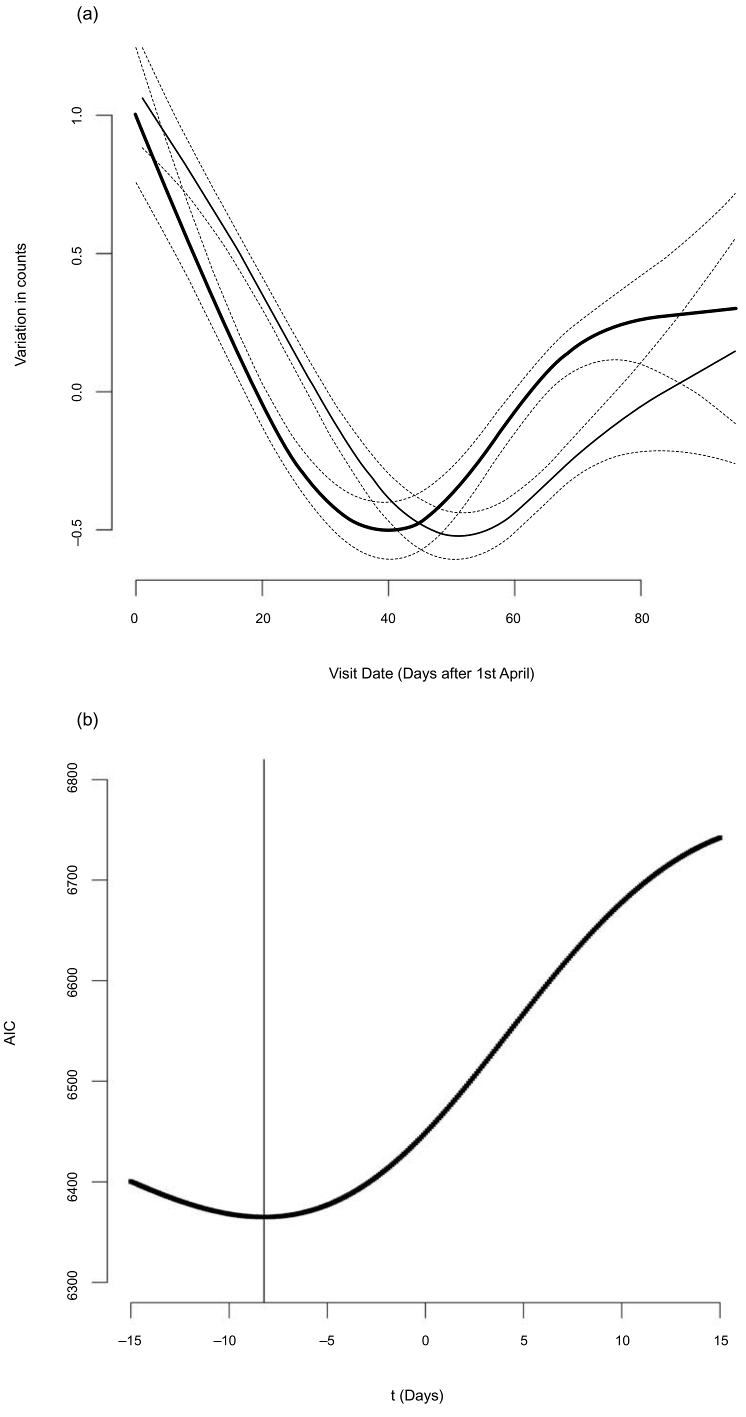


Figure 2. (a) Seasonal abundance distributions for the Wood Nuthatch *Sitta europaea* in 2005 (thick line) and 2006 (slim line). Smoothing was done using a generalized additive model (GAM): Counts~spline function (visit date) with three degrees of freedom assigned to the smoothing term. Ninety-five percent confidence intervals are shown in dotted lines. The figure shows a phenological shift of about 8 days between both curves, 2006 being late compared with 2005. (b) Computed Akaike Information Criterion values for the following GAM: Counts~(Counting site)+spline function (Counting date + t) in relation to t. Three hundred and one different t-values ranging from −15 to +15 days with 0.1 intervals were tested. The relation between AIC and t can be modelled using a quadratic regression: AIC~ $t + t^2$. The phenological shift (vertical line) is estimated by $-b/2a$, where a is the second-degree coefficient of the quadratic regression and b the first-degree coefficient. It is worth −8.32 days in this example. Thus, the phenology of abundance of the Eurasian nuthatch was 8.32 days late in 2006 compared to 2005.

counting date on abundance reached 29%. A plot of abundance against counting date for the species for which abundance was significantly related to counting date for all six study years yielded two clearly different patterns. One type consisted of a decrease, with abundance reaching a minimum and afterwards showing a secondary increase. This pattern was displayed only by sedentary species breeding in France (see Fig. 3a). The other pattern type consisted in an increase in counts at the beginning of the study period followed either by stabilization in counts or a decrease. This type of curve applied mainly to long-distance migrants (see Fig. 3b).

Phenological shift estimation

In all the species for which counting date had a significant effect on abundance for at least five out of the six study years (taking the 2001 issue into account) we observed very similar seasonal abundance year-to-year patterns. Species for which counting date was not important in determining seasonal abundance in more than three study years often displayed various different but non-significant seasonal abundance curves. Examples of such species are Goldcrests *Regulus regulus*, Firecrests *Regulus ignicapillus*, and all the tested Bunting species (*Emberiza schoeniclus*, *E. cirlus*, *E. citrinella*, *E. calandra*). This illustrates heterogeneity in detection through point counts, especially for the Goldcrest and the Firecrest. Their song is difficult to detect which produces heterogeneity in the abundance data. Species like the buntings do not show significant variations of abundance during the season. This feature makes them not suitable for this method.

We applied the method designed for the computation of inter-annual phenological shifts to 46 species (see Table 1). For 34 species, phenological shift computation yielded five relevant estimates (temporal shift estimation lying between −15 and +15 days). This represented 72% of the sedentary species included in the 46 tested species, 77% of the short-distance migrants and 87.5% of the long-distance migrants. The computed phenological shifts have a mean of 0.16 and are distributed around 0. The method's ability to produce a phenological shift varies among species. Thus, more long-distance migrants than sedentary species or short-distance migrants had five annual estimations of the phenological shift. Within these groups failures of the method to compute phenological shifts are most likely due to detectability issues during counts. For species such as European Goldfinches *Carduelis carduelis*, Rooks *Corvus frugilegus* and Grey Partridges *Perdix perdix* the method only yields a single effective estimation. The detection of such species on point counts is highly variable and stochastic depending on the movement of a group. Surprisingly, two very common species of songbirds are unsuited for this method, namely Great Tits *Parus major* and Common Chiffchaffs *Phylloscopus collybita*. When we looked at the values of the shifts in relation to the different years of the study period, we did not find any statistically significant differences. Yet, means of the shifts for the years 2001 and 2003 were positive, unlike the means of the shifts for 2002, 2004 and 2006. This is in accordance with the fact that 2001 and 2003 were among the hottest ever years experienced in France in the past 100 years. Moreover, 2005 was also very hot, so we expected the phenological shifts to be negative for the years 2002, 2004 and 2006 compared with 2005, which was set as the reference year.

Robustness tests

We found a highly significant positive relationship between the phenological shifts computed using the method described in this study and the mean date shift for long-distance migrants (16 species) ($F_{1,92} = 34.67$, $P < 0.001$, species as a random effect; Fig. 4a). A highly significant negative relationship was found between these same variables in sedentary species (18 species) ($F_{1,88} = 16.67$, $P = 0.001$, species as a random effect; Fig. 4b). We observed a weak negative relationship between the phenological shifts and the mean date shifts in short-distance migrants (seven species) ($F_{1,35} = 3.59$, $P = 0.07$) which could also be due to a small sample size. We found no relationship between the shifts' relative standard deviation and the species migratory index ($F_{1,178} = 1.06$, $P = 0.31$). Therefore, migratory status had no significant effect on the phenological shifts' relative standard deviation either ($F_{2,177} = 0.32$, $P = 0.73$). There were no differences between standard deviations of the phenological shifts between sedentary species and short-distance migrants ($P = 0.54$) or between sedentary species and long-distance migrants ($P = 0.49$).

We tested the robustness of the phenological shifts of long-distance migrants to full-moon shifts by looking for a possible relationship between them (difference in abundance timing between one year and 2005) and the moon cycle shifts (difference between April full moon date for one year and April full moon date in 2005). We did not find any significant relationship between both shifts ($F_{1,76} = 0.0002$, $P = 0.99$), thus showing that the phenological shifts clearly do not depend on moon cycles.

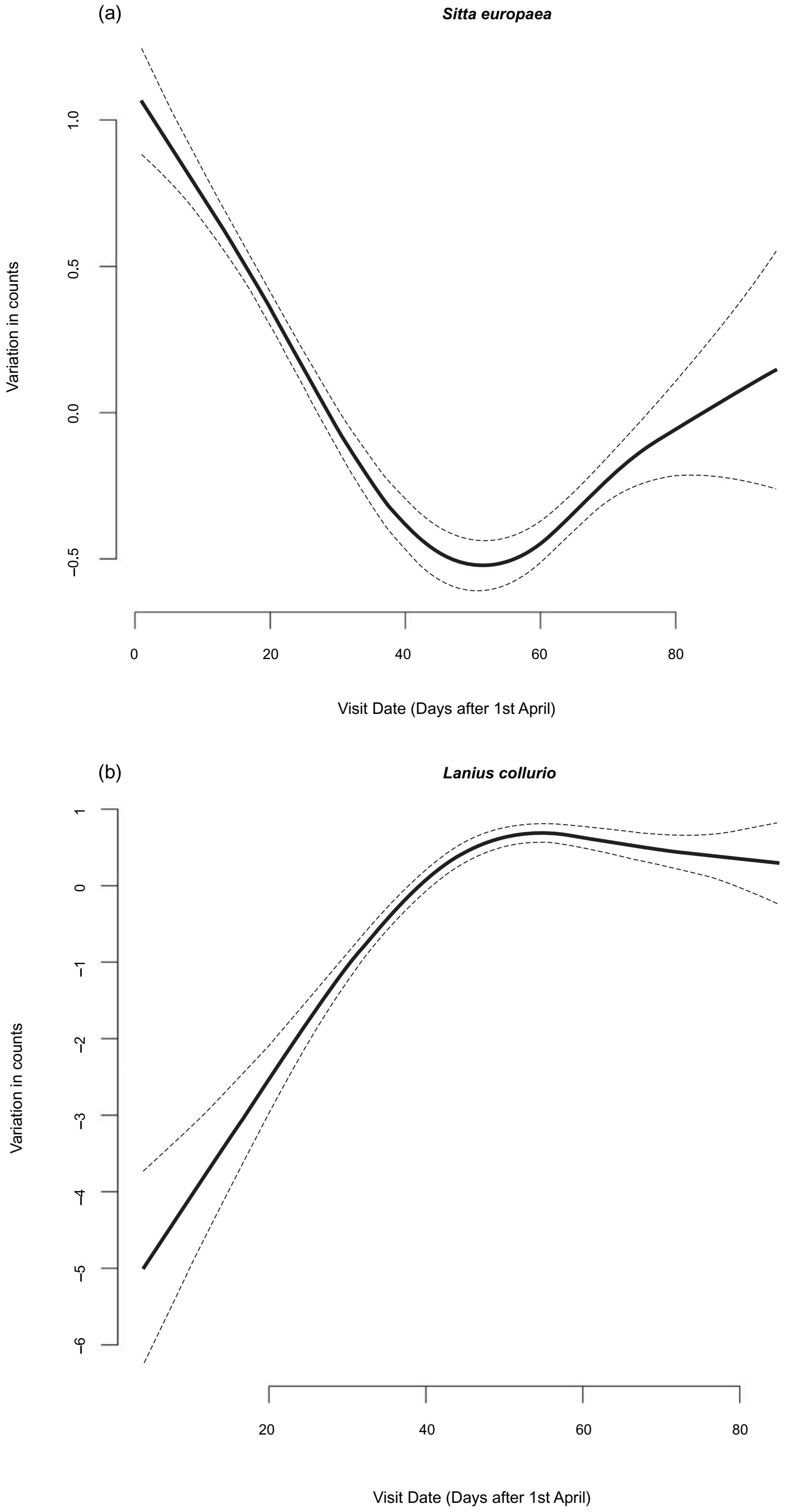
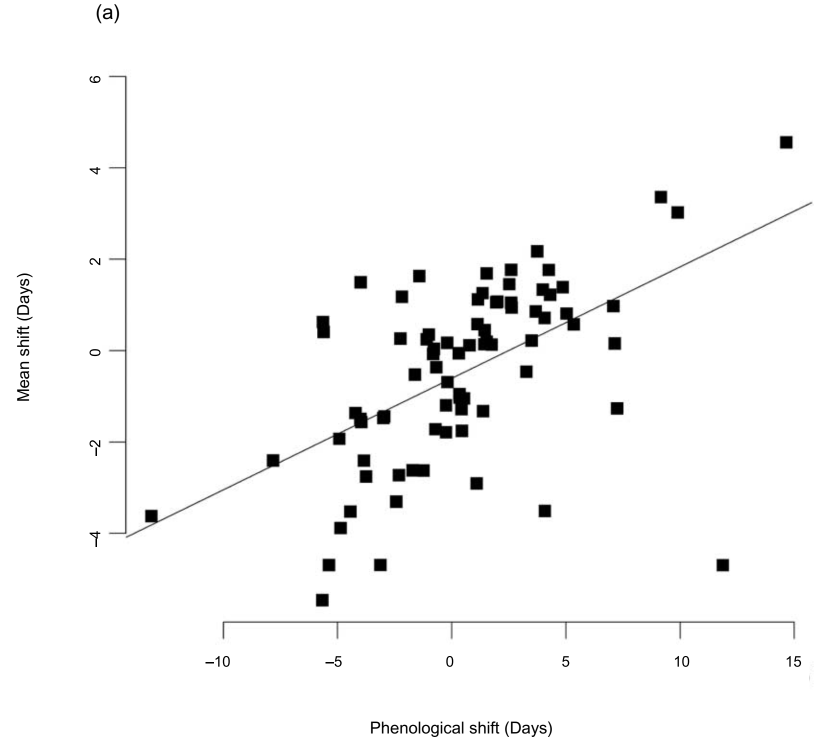


Figure 3. Relationship between abundance and counting date modelled by a generalized additive model with counting date as a smoothing function. (a) example of a sedentary species, Wood Nuthatch; (b) example of a long-distance migrant, Red-backed Shrike. Ninety-five percent confidence intervals are displayed in dotted lines.

Table 1. Phenological shifts estimates computed using the maximum likelihood method. Estimated phenological shifts (in days ± se) between a given year and 2005 for 46 species monitored by the French Breeding Bird Survey. 2005 was chosen as the reference and so is not included in the table because the shift is obviously 0.

Species	2001	2002	2003	2004	2006
Meadow Pipit *Anthus pratensis* (2)	−1.77 ± 3.44	−2.8 ± 1.2	1.03 ± 1.05	−0.48 ± 1.26	2.57 ± 1.27
Common Swift *Apus apus* (1)	−1.42 ± 1.06	0.45 ± 0.62	0.78 ± 0.58	2.6 ± 0.5	−1.61 ± 0.49
Common Buzzard *Buteo buteo* (na)	−9.35 ± 4.55	−0.06 ± 3.66	0.85 ± 2.63	−5.41 ± 3.22	−1.82 ± 2.1
Common Linnet *Carduelis cannabina* (2)	−0.78 ± 4.28	1.9 ± 1.9	−9.48 ± 2.81	−4.68 ± 1.79	4.43 ± 2.2
European Goldfinch *Carduelis carduelis* (2)	11.32 ± 9.71	–	–	–	−8.99 ± 4.66
European Greenfinch *Carduelis chloris* (3)	1.74 ± 3.14	1.43 ± 2.09	1.48 ± 1.93	−1.25 ± 2.19	7.13 ± 2.67
Cetti's Warbler *Cettia cetti* (na)	−4.38 ± 5.89	−1.45 ± 5.13	–	0.52 ± 5.64	−14.44 ± 4.05
Hawfinch *Coccothraustes coccothraustes* (2)	−0.83 ± 4.34	–	−0.79 ± 3.24	−12.11 ± 4.87	−5.49 ± 2.3
Common Wood Pigeon *Columba palumbus* (3)	–	–	–	−4.85 ± 3.73	–
Carrion Crow *Corvus corone* (3)	14.83 ± 3.15	6.72 ± 2.3	4.39 ± 1.5	−1.23 ± 1.23	−3.62 ± 1.63
Rook *Corvus frugilegus* (3)	–	0.89 ± 2.32	–	2.61 ± 2.52	8.96 ± 2.85
Common Cuckoo *Cuculus canorus* (1)	−2.31 ± 1.92	3.68 ± 1.06	4.86 ± 1.04	−4.92 ± 1.23	2.6 ± 1.07
House Martin *Delichon urbicum* Linnaeus (1)	1.75 ± 2.67	−13.15 ± 2.14	−0.81 ± 1.27	14.65 ± 1.87	5.03 ± 1.76
Great Spotted Woodpecker *Dendrocopos major* (3)	1.76 ± 5.07	−4.48 ± 2.37	0.96 ± 1.66	−4.5 ± 1.88	−6.44 ± 1.83
Lesser Spotted Woodpecker *Dendrocopos minor* (na)	1.68 ± 5.7	−4.87 ± 4.05	3.21 ± 2.91	−4.83 ± 2.39	−1.2 ± 3.06
European Robin *Erithacus rubecula* (2)	−11.2 ± 6.32	−3.66 ± 2.48	−1.71 ± 1.68	−2.81 ± 2.05	4.69 ± 2.24
Eurasian Jay *Garrulus glandarius* (3)	–	7.94 ± 2.05	11.2 ± 2.11	−0.96 ± 1.58	−8.83 ± 1.44
Melodious Warbler *Hippolais polyglotta* (1)	−3.12 ± 1.24	−2.43 ± 0.89	−0.71 ± 0.83	−0.67 ± 0.76	1.37 ± 0.78
Barn Swallow *Hirundo rustica* (1)	−1.09 ± 1.38	−4 ± 1.03	−7.82 ± 1.09	1.95 ± 0.66	5.34 ± 0.82
Red-backed Shrike *Lanius collurio* (1)	4.08 ± 2.51	3.27 ± 1.35	1.44 ± 1.04	−0.2 ± 1.36	4.25 ± 1.09
Common Nightingale *Luscinia megarhynchos* (1)	−3.84 ± 1.2	−4.44 ± 0.71	−2.99 ± 0.72	−3.96 ± 0.58	1.15 ± 0.62
Yellow Wagtail *Motacilla flava* (na)	8.87 ± 9.86	4.37 ± 2.27	4.17 ± 2.98	11.58 ± 2.95	5.85 ± 2.35
Eurasian Golden Oriole *Oriolus oriolus* (1)	−3.75 ± 1.08	0.54 ± 0.66	2.52 ± 0.54	1.13 ± 0.54	2.62 ± 0.54
Blue Tit *Cyanistes caeruleus* (3)	−1.12 ± 2.76	0.91 ± 1.65	5.21 ± 1.38	0.78 ± 1.96	−3.72 ± 1.26
Great Tit *Parus major* (3)	–	–	12.94 ± 1.95	–	−3.17 ± 2.05
Marsh Tit *Parus palustris* (3)	13.95 ± 20.9	10.92 ± 5.59	7.37 ± 6.71	−5.99 ± 5.46	5.91 ± 3.61
House Sparrow *Passer domesticus* (3)	−7.81 ± 4.8	−13 ± 4.35	–	0.64 ± 1.66	−1.12 ± 1.61
Grey Partridge *Perdix perdix* (3)	–	–	–	–	9.12 ± 3.02
Black Redstart *Phoenicurus ochruros* (2)	11.41 ± 9.85	7.81 ± 3.42	7.07 ± 4.78	−1.95 ± 5.21	2.48 ± 3.37
Common Redstart *Phoenicurus phoenicurus* (1)	11.87 ± 6.44	−1.71 ± 2.79	−2.95 ± 3.51	−1 ± 2.62	3.74 ± 2.82
Common Chiffchaff *Phylloscopus collybita* (2)	3.51 ± 5.42	–	–	–	–
Wood Warbler *Phylloscopus sibilatrix* (1)	−4.21 ± 4.23	−4.87 ± 2.7	−5.37 ± 5.29	−5.67 ± 3.05	−1.24 ± 2.34
Willow Warbler *Phylloscopus trochilus* (1)	–	−3.99 ± 2.61	0.34 ± 5.15	−0.78 ± 2.85	−2.24 ± 2.55
Black-billed Magpie *Pica pica* (3)	−0.89 ± 1.99	−2.14 ± 2.06	−4.01 ± 2.5	−4.17 ± 1.8	−0.89 ± 1.99
Green Woodpecker *Picus viridis* (3)	10.3 ± 5.79	9.78 ± 2.63	0.56 ± 2.65	−1.11 ± 1.96	−4.38 ± 1.89
Whinchat *Saxicola rubetra* (1)	−5.61 ± 2.58	1.53 ± 1.71	3.5 ± 2.64	–	−2.18 ± 3.3
Stonechat *Saxicola torquatus* (2)	−1.02 ± 4.42	7.97 ± 3.58	11.9 ± 3.26	3.99 ± 3.37	−7.29 ± 4.47
Wood Nuthatch *Sitta europaea* (3)	−8.7 ± 2.58	−1.64 ± 1.31	0.54 ± 1.15	−9.32 ± 1.18	−8.23 ± 0.98
European Turtle Dove Streptopelia turtur (1)	1.53 ± 0.83	−0.25 ± 0.61	0.43 ± 0.58	−0.25 ± 0.57	0.35 ± 0.58
Common Starling *Sturnus vulgaris* (3)	−6.37 ± 2.34	−6.83 ± 2.1	−7.93 ± 1.67	−3.02 ± 1.53	−10.65 ± 1.5
Garden Warbler *Sylvia borin* (1)	0.31 ± 1.72	1.43 ± 1.18	4.31 ± 1.15	2 ± 1.13	3.99 ± 1.23
Common Whitethroat *Sylvia communis* (1)	7.14 ± 2.61	7.08 ± 1.35	4.07 ± 1.22	9.9 ± 1.27	9.16 ± 1.37
Lesser Whitethroat *Sylvia curruca* (1)	−5.64 ± 6.39	1.09 ± 2.93	1.35 ± 2.61	7.24 ± 3.52	−0.19 ± 5.56
Common Blackbird *Turdus merula* (3)	4.58 ± 6.54	−4.34 ± 3.52	−12.43 ± 3.57	−9.1 ± 3.27	−7.35 ± 2.79
Song Thrush *Turdus philomelos* (2)	−0.66 ± 5.11	4.62 ± 2.64	9.39 ± 2.96	2.46 ± 2.35	1.51 ± 2.26
Fieldfare *Turdus pilaris* (na)	2.73 ± 7.02	6.4 ± 3.26	−1.97 ± 2.65	−0.42 ± 3.73	1.15 ± 2.64

The migratory strategy of the species is presented in the species column: 1, long-distance migrant; 2, short-distance migrant; 3, sedentary species; na, information on the mean migration distance not available.



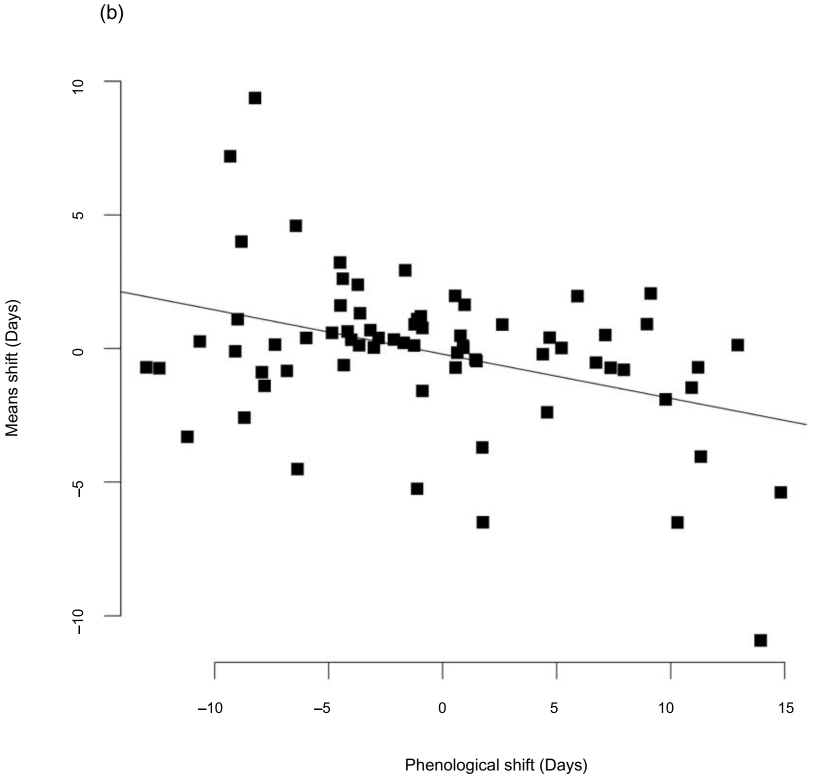


Figure 4. Relationship between the phenological shifts computed using the method described in this study and temporal shifts computed using the mean count date. (a) long-distance migrants; (b) sedentary species.

DISCUSSION

Method novelty and interest in phenological studies

Studies dealing with species phenology are numerous and the field is currently developing rapidly within the context of global climatic change. Proposing a novel approach to these issues would not be very useful if it did not allow new perspectives concerning the data that can be incorporated in phenological studies or the results these studies generate. There are at least two current gaps in the phenological field. First, a gap in the spatial scale. Most works have previously focused on small populations or specific migration monitoring sites. As a consequence, little is known about what happens in the wider countryside. However, the method described here allows very large areas to be studied within the phenological framework. The second gap in our phenological knowledge is due to the particular features of each species, which makes it difficult to include all of them in a single study. Indeed, because species share different life-history traits, the nature of their phenological response is likely to be unclear when combined. Here we have shown that a classical phenological measure, the mean date for a given process, cannot be used on groups of species that include both sedentary species and migrants. Indeed, the same variation in a species' timing results in opposite signs in the behaviour of the measure for these species groups. For this reason such responses could not be combined and included in further studies. The method used in this paper addresses this issue: the shifts in timing are estimated in the same way for all species, which makes them comparable. Nevertheless, as this method should be measuring the same biological process as classical methods, the phenological shifts should somehow relate to the ones yielded by classical measures. One of the most frequently used estimators of a species' phenology is mean date weighted by the intensity of the surveyed biological process (Sparks *et al.* 2005). The issue raised by such estimators is that they do not vary in the same way depending on the shape of the process's distribution across time (Fig. 1). They are relevant only if one is interested in studying a single species or a group of species sharing the same process distributions, but cannot be used in comparisons involving species with different features. We found significant relationships between the phenological shifts and the mean shifts for long-distance migrants and sedentary species breeding in France when taken separately. Moreover, the signs of both relationships were opposite in consistency with the ones predicted by the interaction of the shape of the distribution and the phenological shift (see Fig. 1); i.e. positive for long-distance migrants and negative for sedentary species. This study shows that by estimating the same processes in different ways does not change the predictions about the estimated phenological shifts and it allows larger spatial scales to be studied as well as the combination of more species. However, these advantages rely on several important assumptions which need further discussion.

Interaction between spatial and temporal replicates and method applicability

We used data originating from many different sites surveyed only twice a year and used this to model abundance variations across the whole study area. However, species' seasonal abundance patterns are influenced by time, space and the interaction between them. Migratory species illustrate this point. They first arrive on the monitoring sites located in the south of France and are therefore detected on these point counts before being detected at more northern point counts. Nevertheless, as they colonize the whole study area, the sum of all counts rises, which explains the increasing pattern observed here. Hence it is likely that this pattern reflects the phenology of their return to breeding sites. For sedentary species, this interaction could be a major issue only if maximal song activity (thus detectability) in northern point counts exactly matched minimal activity in southern sites where the breeding season started earlier. This is very unlikely and not in accordance with the clear abundance variation patterns presented here although it might be one explanation for non-significant abundance variation patterns in some species. On the whole, we may conclude that interactions between time and space represent no major bias in the analysis, at least in frequently detected species. Indeed, since roughly the same sites are monitored each year the interaction between time and space remains roughly constant. This allows interannual comparisons to be made. For these, it is possible to consider all the spatial replicates as temporal replicates without altering the biological message that abundance data encompass. More generally, the method may suit datasets where the intensity of a biological phenomenon is monitored either with few temporal replicates for each site but on many sites, or many temporal replicates but on few sites. Indeed, both cases result in a well-described seasonal pattern for the monitored phenomenon as long as the number of observations is large enough to support a smoothing term. Issues resulting from the interaction between time and space would be much smaller in cases where there are many temporal replicates on few sites. We can, therefore, safely assume that in such cases this method would be even more efficient and robust.

Relationship between seasonal abundance trends and breeding phenology

It is assumed that abundance estimated through point counts, transects or other monitoring programmes relates strongly to a species phenology (Best & Petersen 1982, 1985). Taking advantage of this relationship is novel, because the main emphasis has been to get rid of heterogeneous detection probabilities to estimate unbiased abundance at a given site (Boulinier *et al.* 1998, Calladine *et al.* 1999, MacKenzie *et al.* 2002, Selmi & Boulinier 2003, Royle *et al.* 2005). Indeed, the actual number of counted individuals can be split into two components. First, the number of birds that are to be counted in the field (true abundance) and second, the conditional probability, knowing the bird is there and is actually counted (true detectability). True abundance relates to the species' phenology, especially in migratory species. Indeed, there are no birds to count before they arrive back from their wintering grounds. As they arrive, their numbers increase and thus their detectability also increases (Huin & Sparks 2000). This component is probably not as important in sedentary species, although we cannot exclude that fledglings add to the number of birds present at the end of spring. True detectability of a species also relates to its particular phenology. In fact, most birds are detected by their song and it is well established that song activity in males varies across the breeding season in many songbird species (Calladine *et al.* 1999, Hegelbach & Spaar 2000, Poesel *et al.* 2001, Amrhein *et al.* 2002). Relationships have been found between egg-laying by females and song activity in males (Thomas 2002, Amrhein *et al.* 2004, Kunc *et al.* 2005, Amrhein *et al.* 2007, Kunc *et al.* 2007). Moreover, for all bird species, females are far less detectable when incubating, therefore the number of birds susceptible to being counted remains constant but the actual counts decrease.

Therefore, the integration of both true abundance and true detectability into count data originating from large-scale sampling protocols should therefore lead to complex non-linear patterns for estimated abundance across time. We observed such patterns in this study. For nearly half the studied species, these patterns were significant in at least half the number of years. Nevertheless, the ultimate condition to be able to relate such non-linear curves with each species phenology is their repeatability across years. Indeed, phenology, which consists in the succession of different lifecycle stages, remains qualitatively completely constant across years (females always lay eggs after having mated, which, for migratory species, always occurs after having returned to their summering grounds). Therefore, annual patterns should at least also be repeatable qualitatively (in their shape) from one year to another to prove this relationship. Not surprisingly, species that displayed significant seasonal abundance patterns for more than half of the studied years, also showed obvious repeatability in the shape of the curves.

Moreover, we identified two different curve shapes, the first one displayed by sedentary species and the second one by long-distance migrants. As discussed above, these curves are also consistent with a phenological explanation of estimated abundance variations as they were repeatable and quite easy to interpret. On the one hand, sedentary birds start their breeding cycle early in spring (Poesel *et al.* 2001) when males are easy to detect through song activity. This diminishes during the breeding season but may start again if the species are multi-brooded. Detectability could also, for certain species increase, after having gone down to a minimum during incubation, due to chick feeding or activity of fledged families. This scenario could very well explain the estimated abundance pattern we observed in sedentary species (Fig. 3a). On the other hand, long-distance migrants are not present at the beginning of the study period and arrive from the end of April to May and then start breeding. This scenario is consistent with the abundance pattern we observed in migrants with strong increases (Huin & Sparks 2000) and then either stabilization or decrease (Fig. 3b). Although we noticed some variability in the shape of the pattern between species belonging to a given migratory class, these particular features can be related to well-established behavioural features. For example, Common Nightingales *Luscinia megarynchos* displayed a pattern consisting of an increase reaching a peak followed by a strong decrease well matching song activity (Amrhein *et al.* 2002, Kunc *et al.* 2007).

In conclusion, we propose that measuring birds' abundance across the entire monitored area and across the study period (April to June) can be used to address phenological issues as an alternative to studies focusing on particular stages of the breeding lifecycle (e.g. Grieco *et al.* 2002, Both *et al.* 2006, Visser *et al.* 2006).

Method robustness to species heterogeneity

We were able to estimate phenological shifts for 34 species, which represents slightly more than 36% of the total number of species in the study area. The distribution of these species between sedentary, short-distance and long-distance migrants, was roughly homogenous with slightly more long-distance migrants. Hence, since a species' counts are significantly influenced by counting date for at least 3 years, the probability that the method is able to compute phenological shifts is high.

A crucial point is the phenological content of these temporal shifts. As emphasized above, the novelty of this method lies in the phenological estimations it provides, but these should be comparable across species. Possible biases could arise, however. One example is that some long-distance migrants rely, in the timing of their journey, on moon phases (Pyle *et al.* 1993, James *et al.* 2000), which do not occur on the same calendar date each year. Therefore, for long-distance migrants, there could be a bias in the estimated shifts towards the shift of the moon phase of the tested year compared with the reference year. We did not find such a relationship for the 16 long-distance migrant species so that such a bias must remain very small. Phylogenetic autocorrelation was not taken into account in the analysis and could lead to potential bias in the results. Nevertheless, in this case, the effect of moon shifts is so insignificant that taking phylogeny into account would not have changed the results. This shows that the accuracy of the estimated phenological shifts does not vary significantly between species which have very different migration strategies. We made the assumption that the phenological shifts resulted from the match of two almost identical annual abundance patterns. This means that the phenological shifts result only from the difference in the timing of detectability. On such a large scale, it is very likely that such differences are driven by climate. Potential biases, such as inter-annual variations of the sex ratio (Donald 2007), which would lead to more or fewer singing individuals, or of nest predation (leading to males restarting to sing) probably remain limited and are unlikely to influence strongly the seasonal abundance patterns and thus the estimated phenological shifts. Indeed, here it is not only the number of birds that is important but also the moment when they are detectable.

Conclusion

Large-scale abundance monitoring programmes carried out by voluntary observers are a very widespread method to survey common animal and plant populations. These large-scale sampling designs are currently being developed in many countries where there is concern about population trends in response to global change. These data have rarely been used to study phenology, perhaps because the protocol was not designed for this purpose. Nevertheless, the huge amount of dated abundance data collected by programmes such as the BBS has great potential in describing species' phenology and highlighting factors driving their changes. Following Sparks' (2007) wise advice about 'lateral thinking' in the way we should consider data in phenological studies, we demonstrate here that readily accessible data collected in large-scale long-term volunteer monitoring programmes can be used to study phenological shifts on the scale of an entire country. We emphasize that this novel approach can be readily used in other protocols such as constant effort site monitoring in birds to study large-scale variations in the phenology of juvenile captures as a proxy for egg-laying dates or any other taxa as long as the structure of the data meets the one described here i.e. a temporal distribution of counts reflecting phenology. The next step will be to use the computed temporal shifts to create indices which would indicate how species phenology varies across years. It would also be of great interest to test whether phenological plasticity is linked to long-term trends or to the ability of a species to adapt locally to climate change.

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Manuscrit 3

Featuring 10 phenological estimators using simulated data

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Featuring 10 phenological estimators using simulated data

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Summary

1. Studies reporting phenological changes in response to climate change are numerous and concern all groups of living organisms. Phenological changes could cause mismatching in food chains, thus inducing important perturbations in ecosystem functioning. Nevertheless, the relevancy of the conclusions drawn from phenological studies strongly depends on the estimation accuracy of such phenological changes. Many different estimators exist and some have already raised major criticism, although they continue to be used. Therefore, there is a crucial need for an extensive study documenting the behaviour of phenological estimators.

2. Here, we compare the estimation efficiency of 10 phenological estimators: different first appearance dates, mean dates, different percentile dates and a smoothing method based on spline functions using simulated phenological data. Root mean-squared errors and bias of the phenological estimations are calculated in relation to different parameters of the simulated phenological data.

3. Results show that first appearance dates behave as a very inaccurate and biased estimator regarding any phenological data set. Mean dates and estimates calculated using the smoothing method provided in general the most accurate estimates of phenological shifts. They were also the most robust to variation in sample sizes and to imperfect detectability.

4. Our results allow us to warn against the use of first appearance dates in future phenological studies and to recommend using mean dates or smoothing techniques to estimate phenological change of entire distributions. We also provide advice concerning phenological monitoring effort. These recommendations should most importantly apply to studies aiming at comparing phenological variation among sites or among species.

Key-words: bird monitoring, climate change, phenology, shift estimation

Introduction

Together with distribution range shifts, the alteration in animal and plant phenology is an obvious consequence of the current climate change (Walther *et al.* 2002; Parmesan & Yohe 2003). Monitoring of plant flowering (Cleland *et al.* 2007), bird migration (Sparks & Braslavska 2001; Cotton 2003; Jonzen *et al.* 2006), bird breeding dates (Crick *et al.* 1997; Both & te Marvelde 2007) or other seasonal biological events has gathered large amount of phenological data. They should allow us to understand more precisely how living organisms are influenced by long-term climate variations provided that the statistical methods used in the analysis of these data are reliable. Indeed, the major challenge in phenology consists not only in detecting phenological changes but also and above all to measure their magnitude (Visser & Both 2005) as well as their temporal and spatial variations (Primack *et al.* 2009). One of the main issues in phenological studies is to choose the most accurate method to estimate phenological variations in the timing of a biological event. Usually, the phenological data can be described as the seasonal distribution of a biological phenomenon because this phenomenon does not occur at the same time for all the individuals. Yet the properties of this distribution are driven by two major components. The first component relates to the biological features of the monitored event which can be widespread over time or can happen within a short temporal period. Moreover, its seasonal distribution can be symmetrical or skewed towards earliness or lateness depending on the species and the monitored event. The second component influencing the shape of the seasonal distribution relates to the sampling method used to monitor the biological

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event. Sampling effects might greatly influence the phenological message. Indeed, sampling effort might vary along the monitoring period due to bad weather conditions. Moreover, between two different seasons, sampling effort (number of people involved and/or the time they spend in the field) might change (Sparks, Huber, & Tryjanowski 2008). Besides, the amount of available data can vary much between species due to detectability issues (Selmi & Boulinier 2003). Hence, estimating phenological shifts between two seasonal distributions of a biological event is far from being trivial. Numerous methods have been used in the literature to determine phenological shifts: the first occurrence of the event has been frequently used as a proxy for the whole distribution timing (Both, Bijlsma, & Visser 2005; Sparks *et al.* 2005; Donnelly *et al.* 2009; Primack *et al.* 2009). Although it has been criticized for its sensitivity to sampling effort and sample size (Tryjanowski & Sparks 2001; Miller-Rushing, Inouye, & Primack 2008a; Miller-Rushing, Primack, & Stymeist 2008c; van Strien *et al.* 2008), it is continued to be used in recent publications particularly concerning bird migration. Other methods allow the estimation of phenological variation relying on a variable proportion of the total seasonal distribution. These include the estimation of percentile dates (Jonzen *et al.* 2006) or mean dates (Miller-Rushing *et al.* 2008b). The recent development of statistical smoothing techniques has also allowed the use of nonparametric methods (Knudsen *et al.* 2007; Moussus *et al.* 2009). Thus, curve fitting methods using smoothing functions, such as splines, have been developed to estimate phenological variation from standardized monitoring programmes. Last but not the least, Bayesian inference can also be applied to compute phenological shifts, although it is still not frequently used (Schleip *et al.* 2006). Recent work showed that the magnitude of species-estimated response to climate variables was influenced by the choice of the phenological modelling method (Miller-Rushing *et al.* 2008b). However, these differences do not tell which method gets nearest to the true phenological variation. Indeed, they were conducted using real field data from which the true phenological variation remains unknown. In order to address this question properly, the expected estimation output must be known in advance so that the efficiency of the different methods as well as their sensitivity to the parameters controlling the distribution can be evaluated. Thus, there is a true gap in knowledge concerning the methodological choice when analysing phenological data because the behaviour of the existing methods in relation to the quality of the data has not been documented yet. In this study, we compare 10 methods of estimation of phenological shifts using simulated data. We focus on first appearance dates, first 10 and 25 individuals' appearance dates, mean dates, 10, 25, 50, 75, 90 percentile dates and a recently developed curve fitting method using spline functions and maximum likelihood (Moussus *et al.* 2009). Using root mean-squared errors (RMSE), we score the accuracy of these methods in relation to various parameters of the simulated but realistic seasonal distributions. Some of these parameters relate to the properties of the biological event such as symmetry, number of modes, synchrony between different seasons or duration. The other parameters relate to sampling like the difference in the number of individuals between two monitoring seasons and gaps in the distribution due to a lack of sampling as well as imperfect detectability. The aim of this study was to feature clearly the strengths and weaknesses of each type of method regarding these parameters in order to help users make their choice, when possible, so that the estimation of the phenological shifts can be the most accurate and unbiased.

Materials and methods

SIMULATING PHENOLOGICAL DATA

Different types of phenological distributions

The only way to compare the efficiency of phenological estimators is to estimate the difference between the estimates they provide and the 'truth' which therefore has to be known. This prevented us from using data from effective plant or animal monitoring because in such cases phenological changes are precisely the quantity to be estimated and remains obviously unknown. Thus, we simulated phenological data with known phenological changes to compare the efficiency of phenological estimators.

Phenological data take the form of a seasonal distribution of the intensity of a biological event (Knudsen *et al.* 2007). For each parameter combination the data simulated 2 years of monitoring of a biological event. The length of the monitoring season was set to 100 time units (t.u.). A known phenological shift was applied to the second year's phenological distribution (hereafter named the latest distribution) compared with the first distribution (hereafter named the earliest distribution). This phenological shift had then to be estimated by the 10 phenological estimators included in the study.

The first group of simulations was run with symmetrical distributions. The number of individuals monitored during both seasons varied (50, 100, 500, 1000 and 5000). The date at which each individual was contacted was drawn from a normal distribution $N(x, y)$ where x was set to 50 for the first season and (50 + PS) for the second. PS is the actual phenological shift and varies from 0 to 0·5, 1, 2, 5, 10 and 15 t.u. PS is the value that had to be estimated by the estimation methods included in the study (for an example of simulated phenological data set, see Fig. 1a).

A second group of simulations was run with asymmetrical distributions. To model skewness in phenological data, the date at which each individual was contacted was drawn from a β distribution with mean 0·03 and variable variance (0·0005 or 0·001). The variance parameter controlled the skewness of the β distribution. The number of individuals was the same as for a symmetrical distribution (50, 100, 500, 1000 and 5000). As β draws necessarily lie within the [0, 1] interval, the possible temporal range for the biological event had to be defined *a priori* (60, 100 or 150 t.u.). The beginning of the biological event was set at time unit 50 for the earliest distribution. Duration and beginning parameters defined a temporal window for the biological event to occur. Thus, the β draw of each individual (necessarily comprised in the [0, 1] interval) could be converted into a contact date within the defined temporal window. For example, if the β draw of an individual was 0·1 and the temporal window 60 t.u. large and beginning at time unit 50 then the contact date of this individual is 56. As for the symmetrical distribution two data sets were generated. In the second data set, a phenological shift (0, 0·5, 1, 2, 5, 10 and 15 t.u.) was added to the contact date of each individual computed using the β draws and the same temporal window parameters.

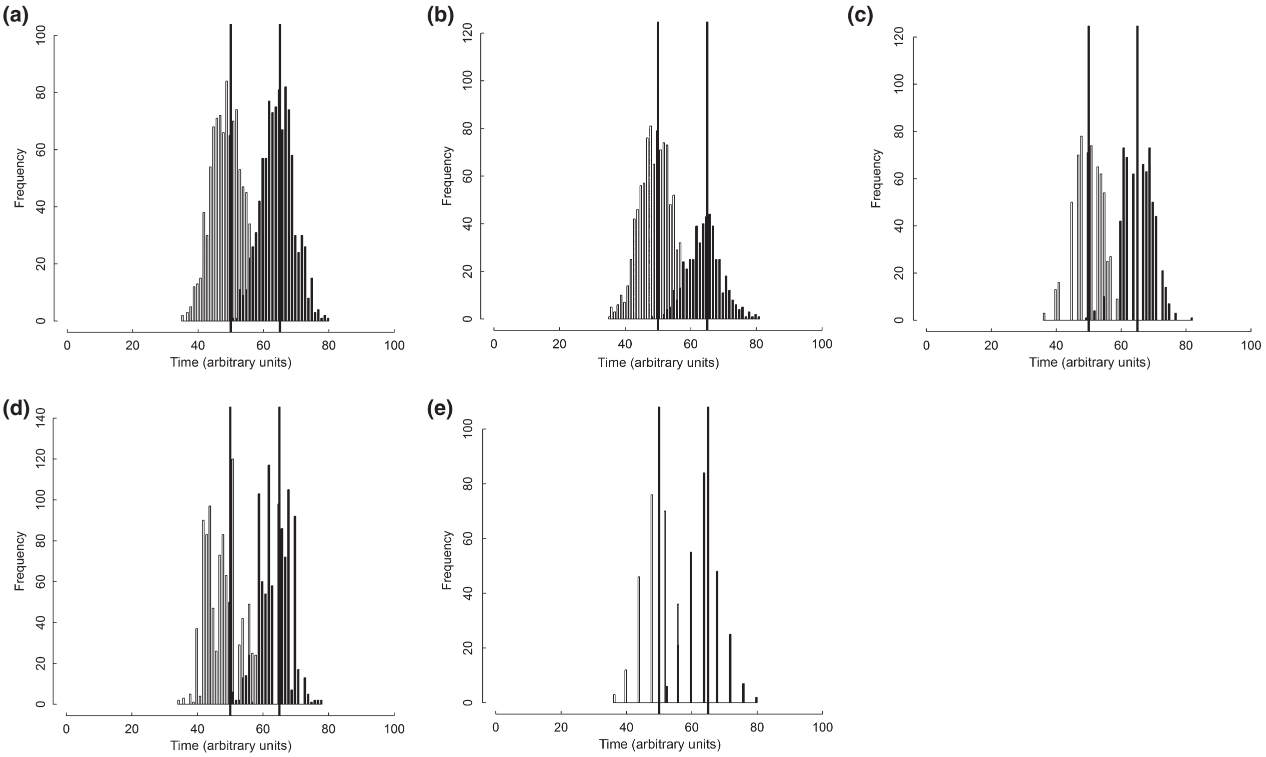

Fig. 1. Examples of simulated phenological data sets. For each simulated data set, a distribution type was chosen (normal shown here, β or bimodal). Two different data sets were generated as if phenological monitoring had been carried out in two different years (white and black bars on the figure). The phenological shift between both years was known (as shown by the vertical thick lines on the figure. These five examples show simulated data sets with normal distributions with mean 50, variance 5 and shifted by 15 time units for 1000 individuals. (a) Same number of individuals drawn in each distribution, (b) 50% less individuals contacted in the latest distribution, (c) random gaps generated in both distributions, (d) variation in detectability: number of contacts at each time unit is multiplied by a vector of values drawn from a normal distribution $N(1, 1)$ and (e) Variation of the sampling effort (here sampling occurs at every 4 time units).

Some biological events show a bimodal temporal distribution. For example, raptors of different sex and age do not migrate together (Kjellen 1992; Yosef *et al.* 2003), but this also applies to some passerines (MacMynowski & Root 2007). Bimodal or multimodal distributions can also well describe nest fledging for multibrooded bird species. To test whether multimodal distributions were better dealt with by some estimation methods, bimodal phenologies were generated by drawing the contact dates of half of the total number of individuals (50, 100, 500, 1000 or 5000) in a normal distribution with mean 50 (mean1) and the other half from another normal distribution whose mean was worth mean1 added to a given shift (10 or 20 t.u.) to create two modes. The variance of the first distribution was set constant at 2, while the variance of the second distribution varied (2, 5, 10 or 15) to model different bimodal distribution patterns. As for the symmetrical and asymmetrical simulation groups a second data set was generated by the addition of a known phenological shift (0, 0·5, 1, 2, 5, 10 and 15 t.u.) to the mean of the normal law from which each contact date was drawn.

Varying sample sizes

Due to sampling stochasticity or biological variation, it is very unlikely that the same number of individuals is sampled during each monitoring season (Knudsen *et al.* 2007). To test the influence of such variations the same sets of parameters for the normal, skewed and bimodal distributions were repeated with each time 25% or 50% less individuals in the latest distribution (for an example, see Fig. 1b).

Accounting for discontinuous sampling

Bad conditions in the field or other sampling shortages often produce gaps in the data set. Thus, days when the monitored biological event occurs but could not be sampled alter the quality of the final data set by changing the shape of the phenology. In order to study the robustness of the tested methods to such lacks of data, data sets comprising missing data were generated (simulations hereafter named gaps). For all types of distributions and parameter combinations, the length of the biological event was measured as the difference between the first and last non-zero contact dates. The number of gaps was set as half this length and the gap dates were randomly drawn within the biological event. The number of contacts at these gap dates was set at 0 (for an example, see Fig. 1c).

Accounting for imperfect detectability

Most phenological studies are confronted with the issue of imperfect detectability of the monitored biological phenomenon. Stochastic events might substantially change the counts and thus alter the phenological distribution. Moreover, when phenological data from multiple sites are pooled together, the imperfections of the detection process add up so that true gaps (zeros) in the resulting phenological distribution are scarce. To compare the behaviour of the phenological estimators in such cases, altered phenological distributions corresponding to all parameter combinations and distribution types were created by multiplying the counts of unaltered phenological distributions by a vector of length 100 (length of the survey period) whose values were drawn from a normal distribution $N(1, x)$ with x either worth 0·5 (weakly altered detection process, simulations hereafter named DetecHalf) or 1 (strongly altered detection process, simulations hereafter named DetecOne). Negative values in the multiplying vector were replaced by zeros (for an example, see Fig. 1d).

Planning sampling effort

An important question when one plans to start phenological monitoring concerns sampling effort. In order to help answering this difficult issue, for all parameter combinations and all unaltered distribution types, phenological distributions were created with regular gaps (zeros). Three different sampling efforts were simulated: the biological phenomenon was surveyed either every 2, 4 or 10 t.u. (simulations hereafter named Effort2, Effort4 and Effort10 respectively). These simulations were only performed with numbers of individuals of 1000 and 5000 for all types of distributions. For normal and bimodal distributions simulations were performed only with variances in (5, 10 and 15). For skewed distributions simulations were performed with variance 0·001 and duration (300, 400 and 500). This prevented the phenological distributions from consisting in only one count when sampling effort was very low (one count in 10 t.u.). As the values and numbers of parameters were different from that of the other groups of simulation, results from sampling effort simulations were treated independently (for an example, see Fig. 1e).

PHENOLOGICAL ESTIMATORS

Phenological shift estimations computed using 10 methods are compared in this study. For all estimators, the estimation of the phenological shift was calculated as the difference between the estimator values for both phenological distributions. The first appearance date (First) was defined as the first date within the 100-t.u. period with a non-zero count. Subsequently, the phenological shift between both simulated data sets was defined as the difference between both first appearance dates. Dates at which the 10 first or 25 first individuals have been contacted were further considered.

Mean dates were calculated as the mean occurrence date weighted by the counts at each date over the entire monitoring period. Percentile dates are frequently used to study phenological data (Jonzen *et al.* 2006). In this study we considered 10%, 25%, 50%, 75% and 90% percentile dates, respectively, hereafter referred to as Q10, Q25, Q50, Q75 and Q90. For a given percentile, the percentile date for one data set was defined as the first date at which this percentile of the population had been contacted.

Curve fitting methods offer interesting opportunities in the study of phenology and have improved in the past few years with the development of smoothing functions. In this study we include a recently published method (Moussus *et al.* 2009) which uses generalized additive models (GAM) and maximum likelihood to estimate phenological shifts between two distributions. The overall rationale of this method is to look for the optimal phenological shift that makes two different phenological distributions match together. If two phenological distributions have exactly the same timing, then a GAM Counts~ spline function (date) would fit the pooled data of both phenological distributions perfectly. If there is a phenological shift between both distributions, the fit will be lower. Thus, the best fit is found when the data of one phenological distribution is temporally translated by the relevant phenological shift before the GAM is fitted. This can be done iteratively with incremental changes in phenological shifts. Details of the method are as follows.

Both simulated data sets are pooled together. To this common data set is fitted the following GAM: number of counts~ spline function, (counting date + t), assuming a Poisson error, where t is worth 0 for data set 1 data (set as the reference) and ranges between −20 and 20 days by 1-day increment for data set 2 data. The number of degrees of freedom for the spline function was set free so that the model could easily fit different types and shapes of distributions (symmetrical, asymmetrical and bimodal). The fit of each model corresponding to each value of t is monitored by its Akaike Information Criterion (AIC) Akaike citation. Thus, for the estimation of one phenological shift 41 AIC values are recorded. As the 41 models have the same number of parameters, minimizing AIC is equivalent to maximizing likelihood. This is achieved by fitting a quadratic regression ($\mathrm{AIC} \sim t + t^2$) using the 10 AIC values around the smallest local minimum of AIC vs. t function. If a is the second-degree coefficient, b the first-degree coefficient and c the intercept of the regression, then the AIC as a function of t is minimized for $t_{\min} = -b/2a$ which is considered as an estimation of the temporal shift between the two breeding seasons. Moreover, the variance of this estimator is given by the second derivative of the log-likelihood and is worth $1/a$.

Number of simulations

Each parameter combination was simulated 1000 times. Lastly, the smoothing method rarely fails to converge towards an estimate of phenological shifts. The number of failures varied between 0% and 5·35% of the total number of simulations according to the type of distribution and the degree of alteration in the data sets (for details, see Supporting Information).

STATISTICAL ANALYSES

The efficiency of the methods to estimate the phenological shifts was evaluated using the trade-off between estimation variance and estimation bias. Indeed unbiased but variable estimators might not be as interesting as slightly biased but much less variable estimators. Thus, for each method, each type of distribution (normal, skewed and bimodal), each type of data set alteration and each parameter combination, the RMSE of the shift estimation was calculated:

$$\mathrm{RMSE} = \sqrt{\left[\frac{1}{1000}\sum_{i=1}^{1000}(x_i - \mu)^2\right] + (\mu - \mathrm{k})^2}$$

where x_i is ith estimation of the phenological shift for a given parameter combination, μ the average phenological shift estimation for this given parameter combination and k the actual phenological shift set to simulate the data set. RMSE measures (in time units) the absolute value of the average difference between the actual shift and the estimated shift. RMSE was treated as the score of the method for a given parameter combination. Differences between method scores in relation to a parameter were investigated by averaging RMSEs over the other parameters.

Bias alone (in time units) was also included in the study and defined as:

$$B = \mu - k$$

whereμ is the average phenological shift estimation for a given parameter combination and k the actual phenological shift set to simulate the data set. Simulations and analysis of the results were performed using the R software (R Development Core Team, 2008).

Results

DISTRIBUTION TYPES

Normal distributions

When considering normal distributions, the most accurate estimates were produced by mean dates (RMSE 2·31) or by GAMs (GAM method, RMSE 2·71). The efficiency of the percentile dates reached a maximum for the median date (RMSE 4·81). First appearance dates performed very badly (RMSE 23·28), while First10 and First25 appearance dates were more accurate (RMSE 6·65 and 8·39, respectively, see Table 1). Concerning the sensitivity to the parameters of the normal distributions, accuracy increased when the number of individuals counted increased (average RMSE ratio 2·74, see Fig. 2a), although this increase was most pronounced when sample size increased from 50 to 500 individuals (average RMSE ratio 2·05). Except for first appearance dates, the phenological estimators were not sensitive to the actual size of the phenological shift they were supposed to estimate (see Fig. 2b). Lastly, increasing the variance of the distribution caused the estimation accuracy of all methods to decrease linearly (average RMSE ratio between variance 2 and variance 15 = 4·51). Mean dates and GAM estimates remained the most accurate at maximum variance.

Bias was not a major issue when considering normal distributions as only one estimator produced positively biased estimates by more than 1 t.u., namely the First25 appearance dates (see Table 2).

Skewed distributions

All the methods seemed to cope well with skewness. Mean dates and GAM estimates were the most accurate estimators of the phenological shift (RMSE 0·92 and 0·92 respectively), but 75th percentile dates performed almost as well (RMSE 1·07) (see Table 1). Unlike normal distributions, the estimations were much less sensitive to sample size (average RMSE ratio between 50 and 5000 individuals = 1·39). The sensitivity was higher when the percentile date increased (RMSE ratio between 50 and 5000 individuals for Q10, Q25, Q50, Q75 and Q90, respectively, 1·01, 1·06, 1·07, 1·68 and 2·08). The gain in accuracy mainly occurred when sample size increased from 50 to 500 individuals as RMSEs stabilized beyond. As for the normal distributions the size of the actual phenological shift did not influence the estimation accuracy. There was no evident general pattern of the influence of skewness on the accuracy of phenological shift estimations (average RMSE ratio between skewness 0·0005 and 0·001 = 1·16). The sensitivity to skewness seemed to increase with the percentile dates (RMSE ratio between 50 and 5000 individuals for Q10, Q25, Q50, Q75 and Q90, respectively, 1·02, 0·98, 1·17, 1·35 and 1·49, see Fig. 2d). No estimator produced biased estimates by more than 1 t.u. (see Table 2).

Bimodal distributions

Generalized additive model estimates were by far the most accurate when dealing with bimodal phenological distributions (RMSE 0·64), while low percentile dates (10th and 25th) also performed well (RMSE 1·13, and 1·16, respectively, see Table 1). On the contrary, median dates behaved as very inaccurate phenological shift estimators for bimodal distributions (RMSE 2·93). The worst estimator remained first appearance dates (RMSE 4·20) (see Table 1). As for the normal distributions, the estimation accuracy increased, while the sample size increased from 50 to 5000 individuals. The accuracy of the GAM estimates was the most influenced by sample size (average RMSE ratio between 50 and 5000 individuals = 2·23). The estimation accuracy did not vary in relation to the size of the actual phenological shift nor did it with the shift between both modes of each phenological distribution (see Fig. 2e). Lastly, RMSE increased linearly when the variance around the latest mode of each distribution increased. No estimator produced biased estimates by more than 1 t.u. (see Table 2).

SAMPLE SIZE VARIATION

Reducing the sample size of the latest phenological distribution affected the performance of all 10 estimators. When sample sizes were reduced by 50% in normal distributions RMSE were multiplied on average by 1·5 (ranging between 1·12 and 2·41). The least sensitive estimators were the First and First10 appearance dates (RMSE ratio, respectively, 1·12 and 1·21), but these estimators still performed very poorly with unequal sample sizes. Mean dates and GAM estimates, although they were sensitive to such variation in sample size (RMSE ratios, respectively, 1·50 and 1·54) still yielded the most accurate estimates (see Table 3). Most estimators were not sensitive to sample size variation when the phenological distribution was skewed as RMSE ratios averaged 1·17 (ranging between 0·86 and 2·22). Surprisingly, the First25 date was very sensitive (RMSE ratio 2·22). The most performing estimators were mean dates and 75th percentile dates. For bimodal distributions, the most performing estimators when sample size was reduced by 50% were GAM estimates, 25th percentile dates and mean dates (RMSE 0·39, 0·66 and 0·72 respectively). The

Table 1. Average root mean-squared error (RMSE) values of each type of distribution and total average RMSE of 10 phenological estimators

Distribution	Type	First	First10	First25	Mean	Q10	Q25	Q50	Q75	Q90	GAM
Normal	Average	23·28	6·65	8·39	2·31	6·82	5·11	4·81	5·12	6·65	2·71
Skewed	Average	1·14	1·14	1·59	0·92	1·16	1·24	1·28	1·07	1·46	0·92
Bimodal	Average	4·20	1·73	3·11	1·47	1·13	1·16	2·93	2·87	2·52	0·64
Total average		9·54	3·17	4·36	1·56	3·04	2·50	3·01	3·02	3·54	1·42

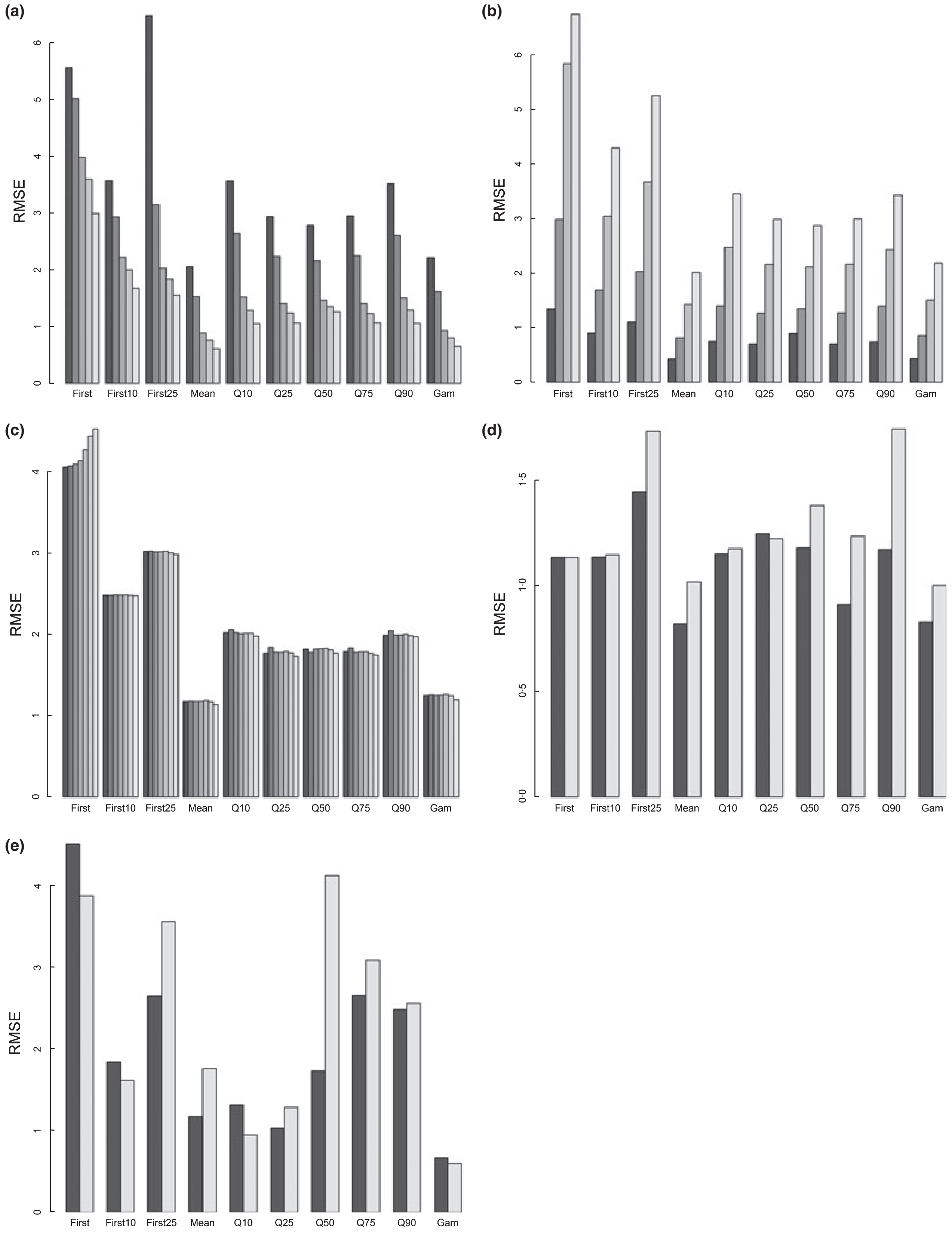

Fig. 2. Root mean-squared error (RMSE) of the estimations of known phenological shifts in relation to different simulation parameters. (a) Sample size (normal distributions, from dark to light bars 50, 100, 500, 1000, 5000 individuals), (b) Event duration simulated using different variances (normal distributions, from dark to light bars variance is worth 2, 5, 10, 15), (c) Actual phenological shift (normal distributions, from dark to light bars variance is worth 0, 0·5, 1, 2, 5, 10, 15 time units), (d) Skewness (β distributions, with variance worth 0·0005 or 0·001 in dark and light bars respectively) and (e) Temporal latency between the two modes of a bimodal distribution (10 and 20 time units in dark and light bars respectively).

Table 2. Average bias values (in time units) for each type of distribution and each type of data set alteration in 10 phenological estimators

Distribution	Type	First	First10	First25	Mean	Q10	Q25	Q50	Q75	Q90	GAM
Normal	Unaltered	−0·28	−0·04	−0·02	−0·03	−0·01	0·01	−0·01	−0·04	−0·02	0·03
	Sample25	0·40	1·08	1·68	−0·03	0·09	0·05	0·04	−0·03	0·13	0·03
	Sample50	1·40	2·81	5·68	−0·04	0·03	0·07	−0·01	−0·09	−0·04	0·03
	Gaps	−0·27	−0·03	< 0·01	−0·05	−0·03	−0·02	−0·04	−0·04	−0·05	< 0·01
	DetecHalf	−0·23	−0·04	−0·02	−0·04	−0·02	−0·03	−0·03	−0·03	−0·04	0·01
	DetecOne	−0·22	−0·06	−0·05	−0·05	−0·04	−0·04	−0·04	−0·04	−0·06	< 0·01
	Average	0·13	0·62	1·21	−0·04	0·00	0·01	−0·02	−0·05	−0·01	0·02
Skewed	Unaltered	−0·98	−0·98	−0·98	−0·62	−0·96	−0·99	−0·99	< 0·01	−0·01	−0·68
	Sample25	−0·97	−0·89	−0·65	−0·62	−0·95	−0·98	−0·97	0·01	0·10	−0·73
	Sample50	−0·96	−0·70	0·92	−0·62	−0·94	−0·97	−0·98	−0·01	< 0·01	−0·79
	Gaps	−1·01	−1·00	−0·84	−0·63	−1·01	−1·00	−0·79	−0·20	−0·07	−0·68
	DetecHalf	−1·02	−1·01	−0·96	−0·63	−1·00	−1·00	−0·87	−0·12	−0·02	−0·68
	DetecOne	−1·02	−1·00	−0·94	−0·62	−1·00	−0·97	−0·78	−0·21	−0·04	−0·66
	Average	−0·99	−0·93	−0·58	−0·62	−0·98	−0·99	−0·90	−0·09	−0·01	−0·70
Bimodal	Unaltered	−0·02	< 0·01	< 0·01	−0·12	−0·02	0·01	−0·04	−0·17	−0·23	0·02
	Sample25	0·65	0·71	2·48	−0·12	0·02	< 0·01	−0·10	−0·21	−0·14	0·02
	Sample50	1·56	1·47	3·90	−0·12	−0·02	−0·01	−0·20	−0·26	−0·30	0·02
	Gaps	−0·01	0·00	−0·03	−0·13	−0·01	−0·02	−0·07	−0·18	−0·26	0·01
	DetecHalf	0·03	−0·03	0·05	−0·26	0·45	0·27	0·04	−0·22	−0·43	−0·01
	DetecOne	0·21	0·12	−0·58	−0·21	−0·21	1·58	−0·35	0·31	0·09	0·10
	Average	0·40	0·38	0·97	−0·16	0·03	0·30	−0·12	−0·12	−0·21	0·03
Total average		−0·15	0·02	0·53	−0·27	−0·31	−0·23	−0·34	−0·08	−0·08	−0·22

Table 3. Average root mean-squared errors (RMSE) of 10 phenological estimators for each type of distribution when sample sizes vary between the phenological distributions

Distribution	Type	First	First10	First25	Mean	Q10	Q25	Q50	Q75	Q90	GAM
Normal	Unaltered	19·81	4·00	2·65	1·14	3·61	2·23	2·09	2·26	3·33	1·25
	Sample25	20·89	4·32	2·97	1·34	4·21	2·61	2·40	2·60	4·01	1·48
	Sample50	22·14	4·83	6·39	1·71	5·17	3·26	2·96	3·28	4·95	1·93
Skewed	Unaltered	0·98	1·01	1·03	0·69	0·98	1·03	1·09	0·53	0·85	0·71
	Sample25	0·98	0·95	0·93	0·70	0·98	1·03	1·08	0·56	0·93	0·76
	Sample50	0·97	0·87	2·29	0·72	0·97	1·03	1·10	0·62	1·01	0·83
Bimodal	Unaltered	3·97	1·15	0·86	0·60	0·67	0·58	0·80	1·57	1·64	0·32
	Sample25	4·07	1·34	2·84	0·65	0·71	0·61	0·84	1·67	1·77	0·34
	Sample50	4·33	1·86	4·12	0·72	0·81	0·66	0·92	1·84	1·96	0·39

average loss of accuracy given by the RMSE ratio was 1·58 (see Table 3).

Reduction in sample sizes caused positive bias (too large phenological shift estimates) in the first appearance dates (First, First10 and First25) for normal and bimodal distributions. This bias increased when sample size differences increased and was worth more than a time unit when sample size reduction reached 50% (normal: First = 1·40 t.u., First10 = 2·81 t.u., First25 = 5·68 t.u.; bimodal: First = 1·56 t.u., First10 = 1·47 t.u., First25 = 2·48 t.u., see Table 2).

DETECTABILITY VARIATION

Detectability variation either due to sampling shortages (gaps in the phenological distribution) or to the stochasticity of the counts themselves caused an important decrease in the estimation accuracy of the phenological estimators. For normal distributions, randomly drawn gaps in the data resulted in a threefold increase in RMSE (average RMSE ratio 3·17), while imperfect detectability (DecOne simulations) had an even greater effect (average RMSE ratio 3·48). The most sensitive estimators were the First25 appearance dates and the median date, while the least sensitive were the First and First10 appearance dates. Nevertheless, the best performing estimators remained by far the mean date and the GAM estimates, although their sensitivity was high (see Table 4). Altering the detection process in skewed distributions increased RMSE by around twofold (average RMSE ratio for: gaps 2·00, imperfect detectability 1·74). The most sensitive estimators in this case were high percentile dates (75th and 90th percentile dates) and the best performing estimators remained mean dates and GAM estimates. Lastly, for bimodal distributions detectability markedly influenced the phenological shift estimation accuracy (average RMSE ratio for: gaps 3·40, imperfect detectability 3·24). Mean dates were particularly sensitive to such alterations

Table 4. Average root mean-squared error (RMSE) of 10 phenological estimators for each type of distribution with different alterations in the detection process

Distribution	Type	First	First10	First25	Mean	Q10	Q25	Q50	Q75	Q90	GAM
Normal	Unaltered	19·81	4·00	2·65	1·14	3·61	2·23	2·09	2·26	3·33	1·25
	DetecHalf	24·31	7·11	10·09	2·43	7·18	5·47	5·04	5·47	7·06	2·83
	DetecOne	25·77	11·10	13·93	3·82	10·87	9·01	8·60	9·00	10·78	4·66
	Gaps	26·79	8·54	14·33	3·39	9·86	8·09	7·78	8·12	9·80	4·12
Skewed	Unaltered	0·98	1·01	1·03	0·69	0·98	1·03	1·09	0·53	0·85	0·71
	DetecHalf	1·06	1·14	1·37	0·88	1·14	1·25	1·24	1·15	1·50	0·84
	DetecOne	1·22	1·33	1·72	1·17	1·33	1·47	1·53	1·71	2·15	1·07
	Gaps	1·59	1·56	2·19	1·37	1·58	1·61	1·66	1·88	2·31	1·29
Bimodal	Unaltered	3·97	1·15	0·86	0·60	0·67	0·58	0·80	1·57	1·64	0·32
	DetecHalf	4·08	1·51	2·90	1·69	1·12	1·05	4·07	3·12	2·72	0·62
	DetecOne	4·28	2·22	3·78	2·56	1·65	1·93	5·40	4·65	3·60	1·01
	Gaps	4·45	2·30	4·14	2·57	1·83	2·12	5·54	4·38	3·44	1·14

in the phenological signal (RMSE ratio 6·72 for imperfect detectability and 6·88 when random gaps were present). The best performing estimator was by far the GAM estimates for this type of distribution (see Table 4). There was no change in bias between unaltered distributions and distributions where the detection process had been altered either with random gaps or imperfect detectability (see Table 2).

SAMPLING EFFORT

When sampling effort decreased from an every time unit monitoring to an every 10-t.u. monitoring, RMSE increased markedly for all methods. For normal and bimodal distributions though, RMSE increased most when switching from monitoring every 4 t.u. to monitoring every 10 times units. Mean dates were very robust to such a decrease in sampling effort when estimating shifts from normal distributions, while this robustness was lost when dealing with bimodal distributions (see Fig. 3a and c). The pattern was quite different for skewed distributions where the increase in RMSE as a result of the decrease in sampling effort occurred as soon as sampling effort was reduced (monitoring every 2 t.u., see Fig. 3b). Quantile dates displayed a very high sensitivity to reduced sampling effort regardless of distribution type. The performance of first appearance dates (First, First10 and First25 individuals) were also affected by the reduction in sampling effort except for skewed distributions (see Fig. 3a–c). Bias remained almost always negligible (lower than 1 t.u.) except for the least sampling effort (monitoring every 10 t.u.) in case of bimodal phenological distributions where most estimators produce significantly positively biased (too large) phenological shift estimates (Bias: mean dates = 2·13 t.u, Q25 = 1·61 t.u, Q50 = 3·77 t.u, Q75 = 3·50 t.u, Q90 = 1·70 t.u).

Discussion

BACK TO FIRST APPEARANCE DATES

As results concerning phenological changes accumulate in the literature, little is known of how close these estimated phenological changes are from the true biological shifts. Simulated data where the true phenological shift is known are an invaluable tool to assess the efficiency of the existing phenological estimators. The estimations are discussed here using two main criteria namely RMSE and bias. The results apply to the estimation of a phenological shift between 2 years' phenological data. Nevertheless, these results should also remain true for the estimation of phenological trends. Indeed, the detection of phenological trends relies on the estimation accuracy of individual phenological shifts or anomalies. The same conclusions can be drawn for the estimations of nonlinear phenological shifts over long time periods. As long as individual interannual phenological shifts are accurately estimated, the detection of such nonlinear phenological shifts should not be an issue.

First, although first appearance dates are still frequently used to model phenological variation, especially with bird migration data (Biadun, Kitowski, & Filipiuk 2009; Primack *et al.* 2009; Saino *et al.* 2009), our findings suggest once more that this measure is the worst possible. Indeed RMSEs of first appearance dates were almost always the largest with all methods. High RMSEs suggest that this estimator is highly variable and/or biased. First appearance dates appeared to be notably biased when sample sizes varied among the compared distributions. This is expected as when less individuals are counted, the probability of seeing the first individual at a given date decreases. As a consequence phenological shifts are overestimated just because less individuals are counted as sampling effort remains constant. Previous studies had already shown relationships between the phenological estimates produced by first appearance dates and sample sizes (Tryjanowski & Sparks 2001; Miller-Rushing *et al.* 2008a). Here, additional negative features of this modelling method are highlighted: first appearance date also was the only phenological measure that was sensitive to the size of the true phenological shift it was supposed to estimate. Thus, although sometimes it is the only measure applicable to the data set (especially long-term data sets when the entire distribution of the biological event was not recorded) we recommend not using the very first appearance date to model phenological data (Miller-Rushing *et al.* 2008b). The first 10 or 25 individuals' appearance dates showed in general

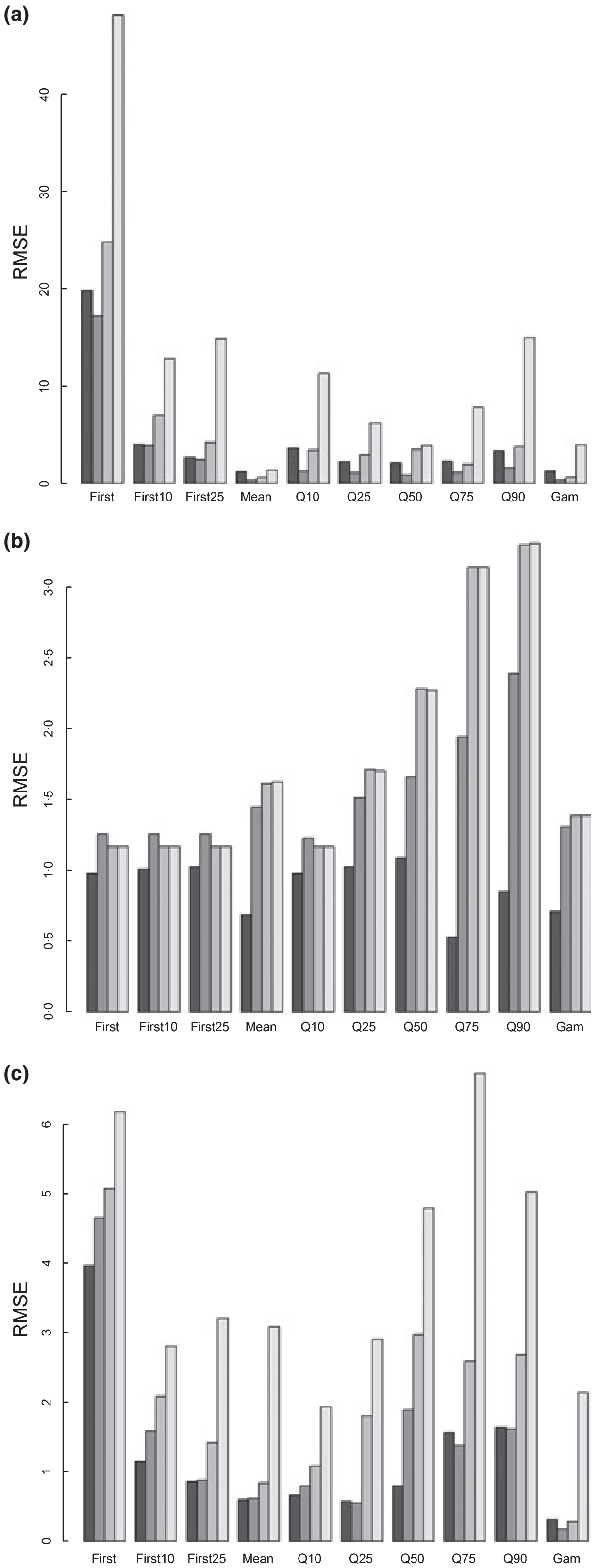

Fig. 3. Root mean-squared error (RMSE) in relation to sampling effort. For each type of distribution (a) normal, (b) β and (c) bimodal, RMSE are shown for four different sampling efforts (from dark to light bars respectively: sampling occurs at every time unit and at every 2, 4 and 10 time units).

much lower RMSEs, but they assume that at least part of the phenological distribution has been recorded. An alternative to overcome this issue would be to consider the first 10% or 25% of all first appearance dates of closely related sites, although such estimators can yield biased phenological shift estimates when sample sizes vary from one year to another (van Strien *et al.* 2008). This measure was not included in this study because data were simulated as if coming from the monitoring of a single site or represented data pooled from different sites.

ESTIMATOR SENSITIVITY TO PHENOLOGICAL DATA ALTERATION

Apart from first appearance dates (First, First10 and First25) when sample size between years varied, none of the included estimators yielded significantly biased phenological estimates. Thus, determining the best performing method depends only on the method efficiency, in other words its estimation variance. Estimation accuracy was highly sensitive to data set alteration either due to differences in sample sizes or to an imperfect detection process. Estimators were not equally sensitive to such alterations. This can raise concern about previous analyses where phenological trends have not been detected or substantial variations between the phenological trends have been reported. The present simulations have been performed only between 2 years and results already show important errors (on average more than 1 t.u. when RMSE > 1). However, phenological data sets comprise many years so that estimation errors sum up. This can noise the estimation of phenological trend which might then not be detected, or yield a significant trend somewhat different from the actual trend. This can potentially produce to artefactual variation between trends from different data sets. Effort should thus be carried out to relate phenological trend variation to meaningful factors such as latitude or species life-history traits as it has recently been the case.

ADVICE TO PRACTITIONERS

The main goal of this study was to provide guidelines for researchers who wish to analyse phenological data or start phenological monitoring using the scores of the present simulations. First, it is important to remember that all estimators do not have the same ecological meaning. Therefore, to answer specific phenological questions regarding specific portions of the phenological distribution (e.g. phenology of the earliest individuals), some estimators such as 10th or 25th percentile dates are irreplaceable (Jonzen *et al.* 2006). Nevertheless, in most phenological studies the general purpose is the estimation of the phenological change of the entire distribution. Before providing some advice for practitioners, it is important to note that this study suffers from some shortcomings, the most important being that phenological shifts between different distribution types (skewed, not skewed, for example) were not considered. As this study relies on simulated data where the actual phenological shift is known, it was not possible to perform these combinations. Indeed because the shapes of the distributions would vary, the definition of the phenological shift would not be straightforward. Such changes in the distribution type might occur in the real world, for example, in butterflies' emerging dates (Roy & Sparks 2000; Stefanescu, Penuelas, & Filella 2003; van Strien *et al.* 2008) and could favour percentile dates instead or mean dates or GAM estimates. Nevertheless, for most parameter combinations, our findings suggest that two estimators truly outcompete the eight others on the basis of the performed simulations: mean dates and GAM estimates. In case of unimodal symmetrical or unimodal skewed distributions, the use of mean dates allows accurate estimations of the phenological shift. In case of bimodal distributions, however, mean dates are undoubtedly less performing than GAM estimates. Based on the present results, these recommendations apply regardless of how the phenological distributions are altered. Indeed although the sensitivity of both methods to variations in sample sizes and alteration in the detection process was in some cases higher than the sensitivity of other methods, their estimations remained clearly the most accurate. Last point concerning the choice of a phenological estimator: GAM estimates are associated with an estimation error which can be interesting in further statistical analysis involving phenological estimates. Indeed, further regressions on the phenological shift can be weighted by the inverse of the squared standard estimation error.

The present simulations also allow us to provide some piece of advice for those desiring to start phenological monitoring. Running monitoring programmes is very costly so that it is very important to know whether monitoring effort can be saved especially when the programme relies on volunteering. Our findings suggest that is it not necessary to monitor the biological phenomenon every time unit to accurately estimate phenological shifts (RMSE <1). Indeed, at least for normal and bimodal distributions, the drop in estimation accuracy occurs when the phenology is monitored below once every 10 t.u. Although this result should be taken with caution because simulations were performed using unaltered phenological distributions (equal sample sizes, no alteration in the detection process), it should provide interesting monitoring opportunities. Estimation variance was highly sensitive to the phenological distribution parameters. An interesting feature is the sensitivity of the estimation efficiency to sample size. Our simulations show that maximum efficiency is reached when a few hundreds of individuals are monitored. Beyond this threshold, the gain is negligible. This feature was true even when the phenological distributions were altered in the detection process or when sample size varied. RMSE increased linearly with event duration (simulated using distribution variance). Thus, this feature should be taken into account when starting a monitoring programme or analysing the data. Indeed less intense and temporally widespread phenological events should require more intensive monitoring so that subsequent phenological estimations can be relatively accurate. Last but not the least point to mention concerning phenological monitoring programmes is that the entire period when the biological event of interest occurs should be monitored even at moderate resolution. This option is by far preferable to only recording the first or first few individuals.

To conclude, we show that one of the most widely applied phenological estimation first appearance, dates produce very poor quality estimates of phenological changes. As they have been so widely used in phenological studies, it is possible that part of the considerable variation previously reported in phenological responses emerged from the poor reliability of this estimator. Considering most distribution types and most data set configurations, mean dates and estimates provided by a smoothing technique based on GAMs are closest to the true phenological shifts defined by the simulation parameters. Therefore, we recommend the use of such modelling methods for the estimation of phenological shifts between entire distributions using data from long-term and large-scale monitoring schemes. The choice of most efficient methods to model phenological changes is of major importance as one of the current challenges in phenological science is to investigate whether phenological chains differ within food webs and whether mismatches occur between different trophic levels.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. RMSE values in relation to the number of individuals used in the simulations.

Table S2. RMSE values in relation to the true phenological shift as defined by simulation parameterization.

Table S3. RMSE in relation to biological event duration.

Table S4. Number of failures of the smoothing method based on generalized additive models.

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Advanced departure dates in long-distance migratory raptors

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ORIGINAL ARTICLE

Advanced departure dates in long-distance migratory raptors

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Abstract Evidences for phenological changes in response to climate change are now numerous. One of the most documented changes has been the advance of spring arrival dates in migratory birds. However, the effects of climate change on subsequent events of the annual cycle remain poorly studied and understood. Moreover, the rare studies on autumn migration have mainly concerned passerines. Here, we investigated whether raptor species have changed their autumn migratory phenology during the past 30 years at one of the most important convergent points of western European migration routes in France, the Organbidexka pass, in the Western Pyrenees. Eight out of the 14 studied raptor species showed significant phenological shifts during 1981–2008. Long-distance migrants displayed stronger phenological responses than short-distance migrants, and advanced their mean passage dates significantly. As only some short-distance migrants were found to delay their autumn migration and as their trends in breeding and migrating numbers were not significantly negative, we were not able to show any possible settling process of raptor populations. Negative trends in numbers of migrating raptors were found to be related to weaker phenological responses. Further studies using data from other migration sites are necessary to investigate eventual changes in migration routes and possible settling process.

Keywords Climate change · Migrating birds · Trans-Saharan · Mean passage dates · Phenology

Introduction

Living organisms displayed various responses to 30 years of climate warming at the end of the twentieth century (Walther et al. 2002). Among the most documented responses are temporal shifts in species phenology, witnessed thanks to long-term monitoring datasets. Many studies reported advances in the seasonal start of breeding or growth in numerous animal and plant species. Among them, the ones on migratory birds' spring arrival dates in Europe have been particularly noteworthy (Sokolov et al. 1998; Lehikoinen et al. 2004; Sparks et al. 2005; Jonzén et al. 2006; Zalakevicius et al. 2006). However, the effects of climate change on subsequent events of the annual cycle, like autumn migration, remain poorly studied and understood (but see Jenni and Kéry 2003; Tøttrup et al. 2006; Thorup et al. 2007). Evidence for a delayed or advanced autumn migration was equivocal in numerous studies with some species departing earlier and others later (Gatter 1992; Bairlein and Winkel 2001; Gilyazov and Sparks 2002; Lehikoinen et al. 2004). In fact, the phenological response often depends on specific life history traits (Lehikoinen et al. 2004). Indeed, Jenni and Kéry (2003) showed for 65 passerine species that the temporal trend in peak passage date depended on several specific life history traits like the migration strategy, the number of broods or the main food type.

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As most studies have been undertaken on passerines, taking advantage of the numerous migration observatories, raptor migration phenology—as well as its phenological changes according to specific life-history traits—remains poorly investigated.

Here, we chose to study these possible phenological shifts using migration counts of visually-detected migrants at one of the most important convergent points of major western European migration routes in France, the Organbidexka pass, Western Pyrenees. To achieve this, we computed mean passage dates weighted by species abundance for 14 raptor species over a 28-year period (1981–2008), and looked for long-term trends in these mean dates. We further tested whether among-species variations in these long-term trends depended on several traits. Firstly, migration strategy: we predicted long-distance migrants to advance their migration dates in autumn. Indeed, there are several advantages to departing earlier. Their survival could increase if they are able to track ecological changes due to climate change en route as well as on the wintering grounds (i.e. the onset of the dry season in the Sahel from September onwards) (Jenni and Kéry 2003). They could also find better winter territories if arriving earlier than other non-nomadic wintering species thus resulting in better body condition in preparation for spring migration (Alerstam 1990; Newton 2008). Some evidence also shows that raptors are able to advance their breeding phenology due to increased spring temperature which enables them to depart earlier (Lehikoinen 2009; Lehikoinen et al. 2009). In contrast, we predicted short-distance migrants to delay their departure dates. Indeed, as they winter in areas offering better conditions resulting from global warming, they may delay autumn migration or even winter in the breeding grounds (Berthold 1990). They could thus achieve higher survival rates and/or obtain higher quality breeding territories by arriving earlier in spring (Berthold 1990; Jenni and Kéry 2003; Newton 2008). Secondly, moult strategy: arrival and departure dates could be linked to moult timing. Moulting some flight feathers is necessary each year in raptors but cannot occur simultaneously with migration because it reduces their gliding ability. Species replacing large flight feathers (wings and tail) before migration could be more constrained and depart later than the others. And thirdly, generation time: if selection for a changing phenology in response to a changing climate is occurring, it could occur more rapidly in species with a shorter generation time.

Next, we looked at the relationship between population trends (as available for European breeding populations) and our estimated temporal trends in species phenology of migration in the 14 raptor species considered. In European birds (Møller et al. 2008), most declining species could be those displaying the least phenological responses to climate change. We made this prediction with trends related to breeding populations. As trends of migrating species could both signify a settling process (reduction of the migratory behaviour within a constant population size) or a decline in population size, we also found it of interest to test this relationship with trends of migrating raptors at Organbidexka.

Methods

Study site

The Western Pyrenees and their passes constitute one of a few convergent points along the most important western European migration flyways. The main pass there for raptor migration is the Organbidexka pass (43°02′19.06″N, 1°00′21.68″W). It is located in the Basque Country, in the department of Pyrénées-Atlantiques (south-west France), lying 1,283 m above sea level. It is one of the most important migration sites in Western Europe together with Falsterbo (Sweden) and the Strait of Gibraltar (Spain), particularly for the observation of raptors, storks, cranes and pigeons.

Data on bird migration

At the pass, annual autumn surveys are conducted from 15 July to 15 November from dawn to dusk by varying numbers of observers among which permanent skilled ones are present throughout the period. Annual counts of raptors average ~40,000. We used a dataset comprising 28 years of migration counts, from 1981 to 2008, with the same data recording methodology used during the whole period (Devisse and Urcun 1994). Daily numbers of birds flying south were used for analyses.

Tested traits were taken from different sources: generation time and migration strategy from (Birdlife International 2004), moult strategies from Cramp et al. (1977–1984). Trends for European breeding populations were taken from Birdlife International (2004) and transformed using a 6-level scale (as in Møller et al. 2008), ranging from large decline to moderate increase (mentioned as "TrendEU" hereafter), while local trends in numbers migrating at Organbidexka were calculated as slopes of total annual counts by species as a function of years (hereafter "TrendOrg") (Table 1). Two categories designed migration strategy: short-distance migrants which winter in Europe and North Africa, and long-distance migrants which winter south of the Sahara. The Marsh Harrier (*Circus aeruginosus*) was classified as a long-distance migrant because birds passing the Pyrénées originate from northern European breeding populations, which winter mainly in sub-Saharan Africa (Strandberg et al. 2008).

Table 1 Species traits tested on the temporal trend in the mean passage date during 28 years at Organbidexka pass for 14 raptor species

Species	Mean-counts (Min–max)	Temporal trend	Migration	Moult	Generation time	TrendEU	TrendOrg	Slope (days/year) ± SE	Difference (days/28 years)	*P* value
Circus aeruginosus	217.82 (74–408)	−0.36	Long	BM	6	2	0.02	−0.36 ± 0.08	−9.73	<0.001
Accipiter nisus	274.46 (129–599)	−0.33	Short	BM	4	1	0.04	−0.33 ± 0.10	−8.80	0.00
Milvus migrans	12,478.28 (1,406–33,304)	−0.21	Long	BAM	6	−3	0.08	−0.21 ± 0.06	−5.55	0.00
Pandion haliaetus	104.96 (45–198)	−0.17	Long	BAM	9	2	0.04	−0.17 ± 0.07	−4.67	0.02
Aquila pennata	66.78 (37–108)	−0.14	Long	BM	11	0	0.01	−0.14 ± 0.08	−3.78	0.08
Pernis apivorus	10,811.82 (6,481–21,504)	−0.13	Long	BAM	9	0	−0.01	−0.13 ± 0.04	−3.39	0.00
Circus pygargus	87.85 (47–145)	−0.12	Long	BAM	6	2	0.00	−0.12 ± 0.06	−3.30	0.06
Circaetus gallicus	107.00 (41–176)	−0.03	Long	BM	13	−1	0.04	−0.03 ± 0.07	−0.79	0.69
Falco subbuteo	49.39 (22–86)	−0.02	Long	BAM	5	0	0.00	−0.02 ± 0.08	−0.50	0.82
Milvus milvus	3,080.50 (1,521–4,529)	−0.01	Short	BM	6	−2	−0.02	−0.01 ± 0.08	−0.25	0.91
Falco columbarius	25.25 (11–41)	−0.01	Short	BM	3	NA	0.01	−0.01 ± 0.08	−0.15	0.94
Circus cyaneus	85.53 (40–158)	0.30	Short	BM	6	NA	0.00	0.30 ± 0.14	8.15	0.05
Buteo buteo	191.64 (34–378)	0.32	Short	BM	8	1	−0.06	0.32 ± 0.13	8.55	0.02
Falco tinnunculus	120.89 (29–252)	0.32	Short	BM	3	−2	−0.01	0.32 ± 0.14	8.63	0.03

Mean counts Mean annual numbers of each raptor species with minimum and maximum numbers, *Temporal trend* the slope between the mean passage date and years ($n = 14$), *Migration* migration strategy (short or long-distance migrant), *Generation time* mean age of breeding females, *Moult* moult strategy (*BM* before migration, *BAM* before and after migration), *TrendEU* population trends on a 6-point scale from large decline to moderate increase, *TrendOrg* slopes of raptor numbers at Organidexka in function of years, *Slope* phenological shift (slope of the mean passage date in function of years at Organbidexka pass ± SE) and *P* values for each of the 14 raptor species

Statistical analyses

Various phenological modelling methods designed to compute phenological shifts exist in the literature. These include first appearance dates (Sparks et al. 2005; reviewed in Lehikoinen et al. 2004), mean or median dates (Sokolov et al. 1998; Vähätalo et al. 2004; Sparks et al. 2005), different percentiles (Jonzén et al. 2006) or smoothing techniques (Knudsen et al. 2007). Although the accuracies of these methods have still not been extensively compared, first appearance dates and other methods relying on a small portion of the total phenological distribution have aroused major criticism (Tryjanowski and Sparks 2001; Miller-Rushing et al. 2008). The issue is even more crucial with raptor migration phenology as some species display a bimodal phenological distribution due to different passage dates between males and females or between adults and juveniles. Moreover, there was an important variation in sample size between years in our data, with up to 50% variations between the annual counts. To deal with these issues, the two most robust methods are the mean passage dates and the smoothing techniques which both take the entire phenological distribution into account and compute sensible estimates for bimodal phenological distributions (Moussus et al., unpublished results). The results which are presented here relate to the estimates computed using the mean passage dates, while the results we obtained with phenological shift estimates from the smoothing method are very similar. Indeed, there is a strong correlation between estimations of the phenological shifts between the two methods which range between $r = 0.55$, $n = 28$, $P = 0.002$ for the Merlin (*Falco columbarius*), and $r = 0$ 0.98, $n = 28$, $P < 0.001$ for the European Sparrowhawk (*Accipiter nisus*) with a mean Pearson's coefficient $r = 0.90 \pm 0.11$ for the 14 species. Methodological details of the smoothing method are available in Moussus et al. (2009).

The temporal trend of mean passage dates was modelled using linear models and tested using analyses of variance (ANOVAs). Adjusted effects of moult date, migration strategy and generation time on the temporal trend in mean passage dates were tested using linear models and ANOVAs. Relationships between the temporal trend of mean passage dates and species population trends were modelled using linear models and statistical significance of trends tested with ANOVAs. Population trends effect was first adjusted to migration and moult strategies as well as to generation time. We computed the contribution of each explanatory term to the variation in the responses after fitting all other terms in the models.

To avoid considering too imprecise data, Vähätalo et al. (2004) omitted from their analysis the species data for years when less than 20 individuals were counted. In our case, this restriction would apply only for the Merlin. If we restrict the species-specific dataset to years with at least 20 individuals detected, 8 years have to be deleted. Considering only the remaining years with more than 20 birds changed the temporal trend of mean migration dates from -0.01 ± 0.08 to -0.09 ± 0.09, but did not affect the outputs of the other analyses.

All analyses were conducted using the R statistical software (R Development Core Team 2006).

Results

Phenological shifts during the last 28 years were significant for 8 out of the 14 species. They ranged from an advance of 10 days for the Marsh Harrier to a delay of 9 days for the Common Kestrel (*Falco tinnunculus*) (Table 1). In addition, two species, Booted Eagle (*Aquila pennata*) and Montagu's Harrier (*Circus pygargus*), had P values lower than 0.10 (Table 1).

Relationship to life history traits

Migration strategy was found to explain significantly the changes in phenology ($F_{1,10} = 5.83$, $P = 0.03$) when adjusted for moult strategy ($F_{1,10} = 0.84$, $P = 0.37$) and generation time ($F_{1,10} = 1.72$, $P = 0.21$). The model with migration strategy as a single predictor explained 33% of the total variance ($F_{1,12} = 5.92$, $P = 0.03$). Other traits did not relate to the temporal trend in mean passage dates when tested separately. Long-distance migrants showed a significant negative slope in their temporal trend in mean passage dates (mean ± SE: -0.14 ± 0.06, $P = 0.04$) whereas short-distance migrants showed a non-significant positive slope (mean ± SE: 0.09 ± 0.07, $P = 0.23$; Fig. 1).

None of the studied long-distance migrants (8 species) delayed its autumn migration during the last 30 years, while 3 out of the 6 short-distance migrants delayed their passage dates significantly (e.g. Fig. 2; Table 1).

Within the same genus, comparisons between species are noted. For example, Montagu's and Hen Harriers (*Circus cyaneus*) display very different responses to climate change. The first is a long-distance migrant and has advanced its migration date, while the second winters in Europe and North Africa and has delayed its migration. Among the genus *Falco*, responses are also contrasted. Only the Common Kestrel which can be classified as a short-distance migrant, displayed a strong response (as a delay) in mean passage dates temporal trends whereas the Merlin did not respond at all. As a long-distance migrant, the Eurasian Hobby (*Falco subbuteo*) did not show significant earlier migration dates.

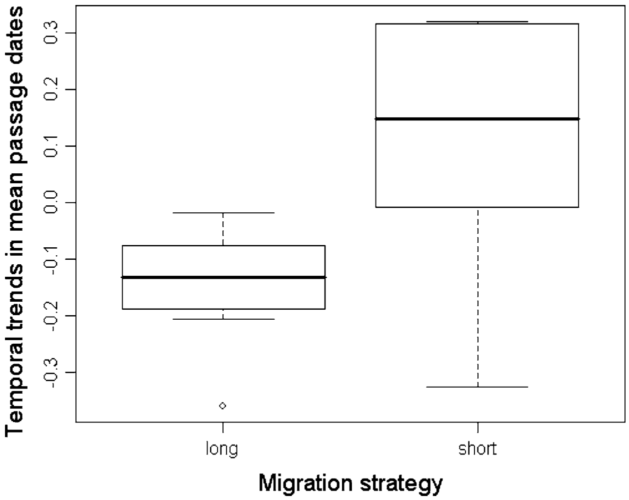

Fig. 1 The temporal trends in mean passage dates as a function of the migration strategy (short- or long-distance) for 14 raptor species migrating at the Organbidexka pass, Western Pyrenees in southern France

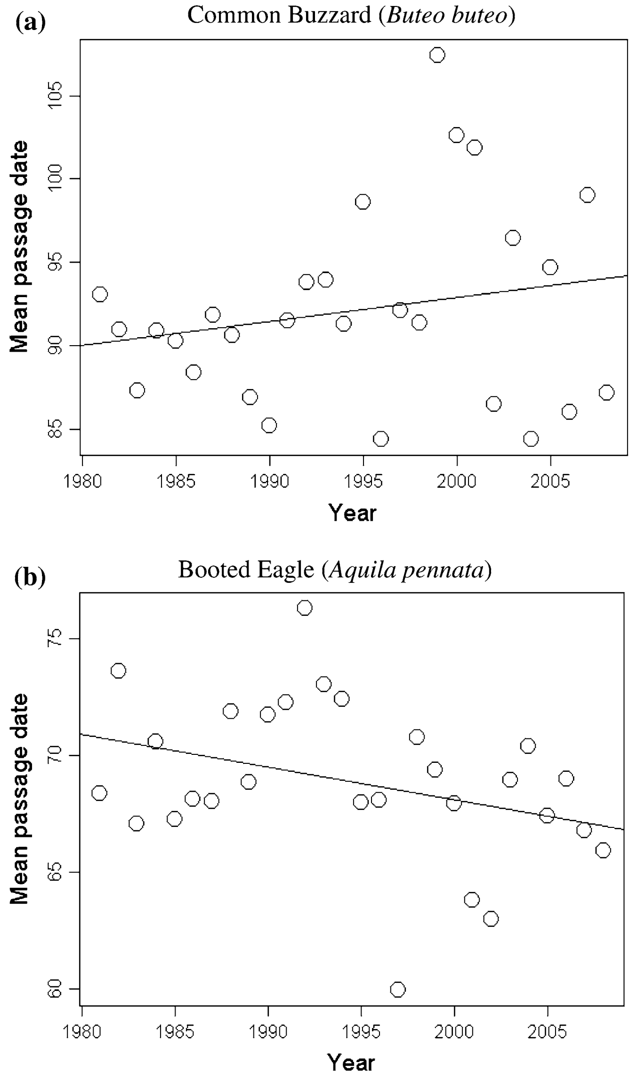

Fig. 2 Examples of changes in the migratory phenology during 28 years by **a** a short-distance migrant, the Common Buzzard (*Buteo buteo*) and **b** a long-distance migrant, the Booted Eagle (*Aquila pennata*). Mean dates are given in number of days, day 1 being 12 July

Relationship to population trends

We failed to find a significant negative relationship between the trends in European breeding populations (TrendEU) and the temporal trends in mean passage dates ($F_{1,10} = 1.17$, $R^2 = 10.5\%$, $P = 0.30$), whereas the trends in migrant numbers at Organbidexka (TrendOrg) and the temporal trends of mean passage dates were found to be negatively and significantly correlated ($F_{1,12} = 8.73$, $R^2 = 42\%$, $P = 0.01$) (Fig. 3). When adjusted for the effect of migration and moult strategies and of generation time, the relationship between breeding populations trends and trends in phenology remained non-significant, while the one between migrating numbers trends and temporal trends in mean passage dates become non-significant (TrendEU: $F_{1,7} = 0.48$, $P = 0.50$; TrendOrg: $F_{1,9} = 2.98$, $P = 0.11$).

We found a significant difference in trends of migrating raptor numbers according to the migration strategy ($F_{1,376} = 41.15$, $P < 0.001$).

Migrating and breeding trends were not correlated when considering all species ($F_{1,10} = 0.32$, $R^2 = 0.03$, $P = 0.57$). There was no difference in this relationship between migration strategies (TrendEU × migration strategy: $F_{1,8} = 0.58$, $P = 0.46$).

Discussion

Phenological trends

The main result is that long-distance migrants advanced their autumn migration during this 28-year period, while some, though not all, short-distance migrants delayed their passage. Apparently, raptors display the same dichotomic response as passerines according to their migration strategy (Jenni and Kéry 2003) which is in favour of a common pattern of the response among birds to global climate change, the same constraints driving the same adaptations even for bird species with very different demographic traits.

However, some exceptions remain within short-distance migrants suggesting that other traits could be responsible for the change in migratory phenology. For example, the Eurasian Sparrowhawk showed a great advance in its mean passage dates whereas it is classified as short-distance migrant. It could be possible that an important part of individuals passing at Organbidexka are long-distance

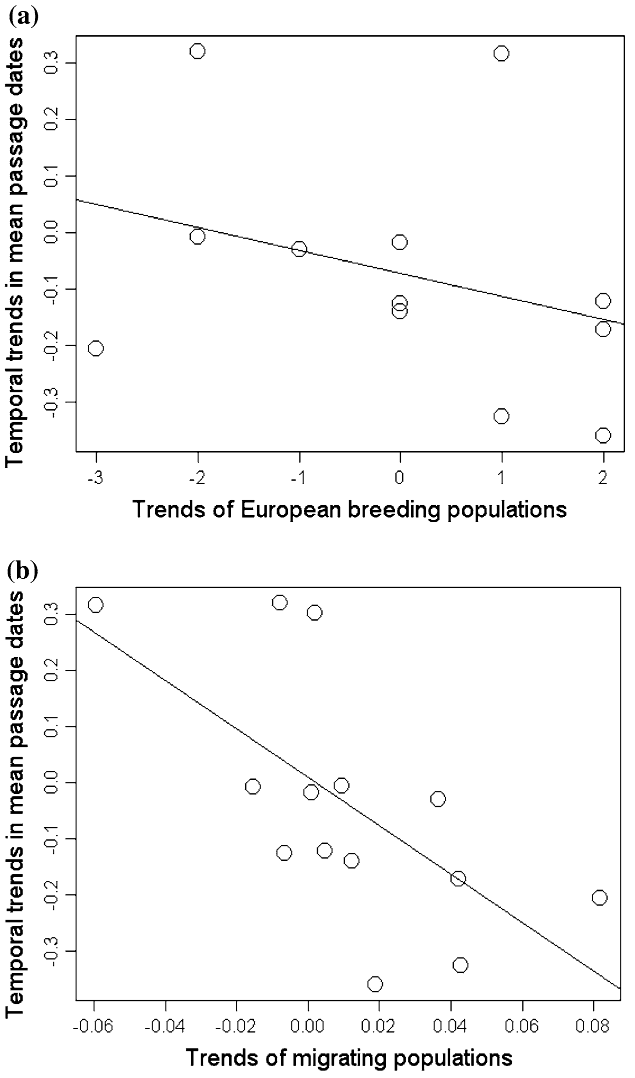

Fig. 3 Relationship between the temporal trends in mean passage dates and **a** trends of European breeding populations and **b** trends of migrants counted at Organbidexka

migrants. Another explanation could be that the Sparrowhawk is a predator specialized on passerines, in contrast to the other short-distance delaying species (Hen Harrier, Common Kestrel and Common Buzzard) which feed on small mammals. Small mammals do not migrate but occur all over the Europe year round while passerines are mainly migratory. Sparrowhawks are possibly trying to migrate with the passerines whereas mammal eaters do not need to do so (Lehikoinen 2009).

Lehikoinen (2009) found the same advance of autumn migration in Sparrowhawks. The advance was in accordance with an earlier breeding schedule. The author found differences between early migrating young that have advanced their autumn migration and late-phase migrants, mainly representing adults, which have not advanced their autumn schedule. As we here referred to mean migration dates, it is possible that our pattern of advanced migration is explained mainly by juvenile Sparrowhawks which would be more numerous than adults (Thorup et al. 2007). Two hypotheses have been proposed regarding the effects of climate change on the autumn phenology of migratory birds. Jenni and Kéry (2003) suggested that single-brooded short-distance migrants, such as Sparrowhawks, should show delayed rather than advanced autumn phenology despite advancing spring arrival (Lehikoinen 2009). Because of the warming climate, it would be beneficial for those species to winter as close to breeding areas as possible with respect to earlier arrival and territory establishment (Jenni and Kéry 2003; Newton 2008). On the other hand, Tøttrup et al. (2006) have documented advancing autumn migration times in many northern European short- and long-distance migrating passerines. These authors hypothesized that the time spent by the species on their breeding areas is constant, and thus earlier spring arrival and breeding would lead to an earlier autumn migration of both adult and young birds (Thorup et al. 2007). Taken as a whole, our migration data on Sparrowhawks would provide support for the hypotheses of Thorup et al. (2007) as we found an advance of autumn migration for this species despite it being a short-distance migrant (Cramp et al. 1977–1994; Birdlife International 2004). However, a closer look at the differential migration between ages or sexes could highlight that different groups of the same species may respond differently to climate change, making it possible to test both hypotheses (Lehikoinen 2009).

We did not find any significant response in temporal trends of mean passage dates of one short-distance species, the Merlin, and of one long-distance migrant, the Eurasian Hobby which did not show significant earlier migration dates. Organbidexka is possibly not the best migration site to study phenological trends of these two falcons, as these species present the smallest mean annual counts out of our 14 species (Table 1) and therefore significant phenological shifts could be harder to detect. This could prevent us from finding any temporal trend in mean passage dates.

Relationship between phenological shifts and population trends

No relationship was found between breeding population trends and temporal trends in mean passage dates. We could have expected species whose breeding populations are increasing to display the strongest advances in autumn migration, as found by Møller et al. (2008) for 100 European species using breeding population trends and spring arrival timing. As autumn migration timing is often related to the timing of spring events (Sokolov 2006), we suggest that species which advanced their spring migration would have also advanced their autumn migration. Consequently, those species which have advanced their autumn migration would be expected to have better population trends.

It is possible either that our sample size is not large enough to give evidence of such effects or that there is no such relationship in raptors.

Conversely, species-specific decreases in migrating numbers tend to be associated with the latest mean passage dates. However, if a decrease in counted numbers on the breeding grounds can be interpreted as a decline of breeding population numbers, this does not apply to migration counts. A decrease in migrating numbers can also ensue from a disappearance of the migratory behaviour even if the global population size is stable, a case of some putative ongoing settling process. We here have no proof of such possible ongoing settling process for "European" migrant raptors as only some short-distance migrants delayed their migration and as this species group did not show significant negative trends in migration counts.

Further investigations on the link between recapture distances taken from ringing database for those species suspected to have begun a settling process (Common Buzzard, Common Kestrel) would be necessary to highlight this possible phenomenon. We can add that evidence of a shortening of the distance between breeding and wintering sites has been recently shown for 24 bird species and that it has been proposed as a possible explanation for the stronger advancement of arrival date found in several short-distance species relative to long-distance migrants (Visser et al. 2009). Among them, Hen Harrier, Common Kestrel and Common Buzzard showed significant decreases in their winter recapture distances—and delayed their mean passage date at Organbidexka—while Sparrowhawk and Marsh Harrier did not show such significant decreases—both migrate earlier at Organbidexka. Comparisons between trends detected at other migration sites like Gibraltar and Falsterbo would also be worthwhile.

Zusammenfassung

Verfrühte Herbstzugtermine bei langstreckenziehenden Greifvögeln

Hinweise für phänologische Veränderungen als Antwort auf den Klimawandel sind inzwischen zahlreich. Eine der am häufigsten dokumentierten Veränderungen sind die früheren Ankunftsdaten der Zugvögel im Frühjahr. Jedoch bleibt bis jetzt der Einfluss von Klimaveränderungen auf aufeinanderfolgende Ereignisse des Jahreslaufes schlecht untersucht und verstanden. Darüber hinaus beschäftigten sich die wenigen Studien zum Herbstzug hauptsächlich mit Singvögeln. In dieser Studie untersuchten wir, ob es in den letzten 30 Jahren im Herbstzug von Greifvögeln eine phänologische Veränderung an einem der wichtigsten Durchzugspunkte der westeuropäischen Zugrouten in Frankreich, dem Organbidexka Pass der westlichen Pyrenäen, gab. Acht der vierzehn untersuchten Greifvogelarten zeigten phänologische Verschiebungen während der Jahre 1981-2008. Langstreckenzieher zeigten deutlichere phänologische Reaktionen als Kurzstreckenzieher und verfrühten ihren mittleren Durchzugstermin signifikant. Da nur einige Kurzstreckenzieher ihren Herbstzug verspäteten und da ihr Trend in Brut- und Zugzahlen nicht signifikant negativ war, konnten wir keine möglichen Veränderungen ihrer Zugbereitschaft nachweisen. Rückgänge in den Zahlen durchziehender Greifvögel korrelierten mit schwächeren phänologischen Reaktionen. Weitere Studien mit Daten anderer Durchzugsgebiete sind notwendig, um mögliche Änderungen in Zugrouten und Zugbereitschaft zu untersuchen.

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Manuscrit 5

A similar advance of autumn migration in Common Crane along Western Pyrenees

Soumis à *Journal of Ornithology*

A similar advance of autumn migration in Common Crane along Western Pyrenees

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A similar advance of autumn migration in Common Crane along Western Pyrenees

Abstract

In migratory birds, differences in response to climate change in terms of phenology have been widely studied and particularly concerning the timing of spring migration compared to the timing of autumn migration. Moreover, most avian studies have dealt with small-sized passerines even though larger species may have a poorer ability to respond to environmental changes than smaller species. Here we analysed the fall migration phenology of a large-bodied migrating bird, the Common Crane *Grus grus*, at one of the most important convergent points of western European migration routes, the Western Pyrenees in France. Phenological shifts were computed separately for three mountain passes, Organbidexka, Lindux and Lizarietta, where daily counts of Common Cranes were collected for 29, 23 and 22 years, respectively. To do this, we used a recent method based on Generalised Additive Models. We analysed trends in phenological shifts during each period and tested the influence of local and large-scale meteorological variables both in Pyrenees and on Cranes' breeding areas at Northern latitudes on autumn migration dates. Owing to the possible increase in the spring temperatures at northern latitudes during the last 30 years as well as to changes in frequency and strength of local winds in the western Pyrenees throughout the period, Common Cranes have advanced their autumn migration timing of 20 days/30years in Pyrenees. This study gives evidence that also large-bodied species are capable of responding quickly to a warming climate.

Keywords: Climate change; Waterbirds; Autumn migration; Phenology; Grus grus

Introduction

In migratory birds, differences in the responses to climate change in terms of phenology have been widely studied and particularly concerning the timing of spring migration compared to the timing of autumn migration (Jenni and Kéry 2003; Lehikoinen et al. 2004). Moreover, despite the growing knowledge of the effects of climate change, most avian studies have dealt with small-sized passerines (Ahola et al. 2004; Dunn 2004; Laaksonen et al. 2006; but see: Lehikoinen et al. 2009), even though larger species may have a poorer ability to respond to environmental changes than smaller species (Stevenson and Bryant 2000, Perry et al. 2005). Consequently, more information about species responses is still needed to unravel the various ways in which different taxa react to changing climate conditions. For example, investigations on phenological responses of species to climate change could help to explain breeding population fluctuations due to eventual trophic mismatches.

Using long-term monitoring data on the Common Crane autumn migration, we analyse the phenologial response of this large species to climate change. The Common Crane (*Grus grus*) is a migratory palearctic species with a wide distribution (Hagemeijer and Blair 1997). Cranes that use the western migratory route breed in northern latitudes and mainly winter in North Africa, the Iberian Peninsula and France (Hagemeijer and Blair 1997). Their breeding period lasts from April to September while migration occurs between February and May and August and late November. It is provisionally evaluated as Depleted (Birdlife International, 2008).

Very few studies tried to investigate causal factors of such declines as well as the possible impact of climate change on its phenology. However, some authors like Lundgren et al. (2003), which studied a Swedish breeding population noted that over a 10 years period (1992-2002), Common Cranes arrived on their breeding grounds one week earlier and began their reproduction accordingly. This could directly relate to early spring warming during 1979-

2004 period at those latitudes which led to same consequences in the Common Buzzard (Lehikoinen et al. 2009).

In order to study the possible phenological shift in Common Crane's autumn passage, we used migration counts of visually-detected cranes at one of the most important convergent points of western European migration routes in France, the Western Pyrenees. To achieve this, we computed phenological shifts for the three most important passes for Common Cranes' migration, Organbidexka, Lindux and Lizarrieta over a 29, 23 and 22 years period (1981-2009; 1987-2009; 1988-2009), respectively, and looked for long-term trends in these phenological shifts.

We compared the phenological trends between the 3 monitoring sites to assess how robust the migration phenological trends were. Trends in migrating phenology were also estimated while taking local meteorological variables (e.g. wind) into account. We further tested whether such shifts were dependent on large scale or local meteorological variables like the North Atlantic Oscillation or temperature from the departure grounds in Sweden and Germany or en route in Northern France. Temporal trends were then re-estimated taking account of parameters identified as correlated to the shift.

Methods

Common cranes counts

We used hourly counts of visible migrating common cranes during autumn migration (September–November) at three passes Organbidexka (43°02'19.06"N, 1°00'21.68"W), Lindux and Lizarrieta situated at 1283, 1221, 441 m, respectively above sea level, to compute phenological shifts. Migration counts have been conducted at Organbidexka, Lindux and

Lizarietta since 1981, 1987 and 1988, respectively. Lindux lies at 28 km from Organbidexka and Lizarrieta at 33 km from Lindux and 61 km from Organidexka.

At all three sites, data were collected following the same "Transpyr" protocol (Devisse and Urcun 1994) and counts were conducted by trained volunteers and staff, with primary responsibility given to one or two people for each observation season. Observations at Lindux and Lizarrieta were typically recorded from September 15th to November 15th and from dawn to dusk, while it lasted from July 15th to November 15th at Organbidexka. The same period was considered for the three passes (September 15th to November 15th). As the Common cranes never pass before September 15th, the entire distribution was kept. Annual counts of Common Cranes averaged ~10,600 at Organbidexka, ~12,900 at Lindux and ~5,100 at Lizarrieta.

Meteorological variables

NAO in winter is a large-scale hemispheric oscillation redistributing atmospheric mass from the Arctic to the subtropical Atlantic and has consequences for regional climate in both Europe and Africa (Hurrell et al. 2001). It has been shown to influence migration timing of species (Forchhammer et al. 2002; Hüppop and Hüppop 2003; Vähätalo et al. 2004; Sokolov 2006). We used the NAO index for winter (December-March) of the same year than the migration year, further labelled "NAOW", available at http://www.cgd.ucar.edu/~jhurrell/nao.html.

Autumn passage dates in Pyrenees are likely to be influenced by reproduction onset and end at Northern latitudes which could directly depend on temperatures in spring and at the end of summer. We used mean spring temperatures (March, April) near two main places of cranes concentration in Sweden and Germany in order to test this relationship, the lake

Hornborga and the Bock-Rügen-area, respectively. Mean temperatures were taken from the website of the European Climate Assessment & Dataset (ECA&D) (http://eca.knmi.nl/). ECA&D is receiving data from 55 participants for 62 countries and the ECA dataset contains 12058 series of observations at 3089 meteorological stations throughout Europe and the Mediterranean. We chose the nearest meteorological station from Lake Hornborga (58°19’05.26’’N, 13°32’45.81’’) and the Bock-Rügen-area (54°22’14.22’’N, 13°19’51.86’’E), which were Linköping (58°27’12.00’’N, 15°36’26.84’’E), 121km from Lake Hornborga, and Greiswald (54°05’53.48’’N, 13°23’18.06’’E) 37 km from Rügen (Fig.1). On their way to South, lot of Common cranes winter at the Champagne lakes like the Der Lake (North of France) or stop over there. It is also possible that temperatures at these stopover sites influence passage dates in the Pyrenees. Thus we tested the influence of the mean temperatures of this period (September, October) at the nearest meteorological station from Der Lake (48°34’15.88’’N, 4°45’9.49E), Langres (47°51’46.71’’N, 5°20’02.80’’E) at 86.77km Southeast from the Der lake (Fig.1).

Wind speed and direction are believed to be the weather variables that most directly affect the concentration of raptors near migration watchsites (Kerlinger 1989). It is then also likely to influence large birds like Cranes. We used winds’ frequency (number of days when winds occur within the observation season reported to the number of days of observation), and winds’ strength measured each hour in Beaufort speed by observers at Organbidexka pass for the three passes as control variables when testing long-term temporal trends in phenological shift.

Modelling the phenology

The phenological shift was calculated using the method of Moussus et al. (2009). It presents advantages compared to first appearance dates and other methods relying on a small portion of the total phenological distribution which have aroused major criticism (Tryjanowski and Sparks 2001; Miller-Rushing et al. 2008). Moreover, there was an important variation in sample size (Crane counts) between years in our dataset which can influence each method's effectiveness in computing phenological shift (Moussus et al. submitted). To deal with these issues the two most robust methods are the mean passage dates and the smoothing techniques which both take the entire phenological distribution into account (Moussus et al. submitted). We chose the smoothing technique developed by Moussus et al. (2009) because in addition to estimating phenological shifts, it also computes an estimation error of the phenological shift. Thus further linear regressions on the estimated shifts can be weighted by the inverse squared standard error of the phenological shifts. Anyway the results we obtained with the mean passage dates were very similar. Indeed, there is a good correlation between estimations of the phenological shifts between the two methods (with a Pearson's coefficient $r = 0.59$, $P<0.001$ for the three passes).

Phenological shifts were estimated separately for the three passes over a 29, 23 and 22 year period (1981-2009; 1987-2009; 1988-2009). The method is based on maximum likelihood: the main picture being to compare the timing of two smoothed seasonal abundance trends by setting one as a reference and by shifting the other one temporally until it best matches the first one. The algorithm consists in the following steps:

a) Both the tested year's and the reference year's abundance data were pooled into a common dataset comprising dated abundance data.

b) Onto this dataset we fitted the following GAM: Counts~ spline function (Counting date +t) with a Poisson error, where t was equal to 0 for all the data gathered during the reference year (for which abundance data remains temporally fixed) and ranged from –30 to +30 days with 1 day intervals for the tested year (the trend that is translated temporally until it matches the reference trend). This algorithm looks for the best temporal translation that makes two seasonal abundance trends match, using an iteration on the elementary translation (t) applied to one trend. It then tests whether this elementary translation reduces the difference between both trends: for each t we measured the model's AIC.

c) Finally, to estimate the temporal shift (t) corresponding to the minimal AIC we modeled for each species and each year to year comparison, the relation between (t) and AIC. To do so, we used a quadratic regression: AIC~ t + t2. We only applied this model to the 10 t around the minimum AIC that we obtained during the iteration phase because the estimation of a minimum and its standard error are more accurate locally. Using the regression coefficients, the temporal shift between both years was estimated as –b/2a where (a) is the second degree coefficient of the quadratic regression and (b) the first degree coefficient. We computed the standard estimation error of (t) as 1/a, which is worth the negative inverse of the log likelihood's second derivative. If there was no local minimum AIC within the -30/+30 days interval, the method was considered inefficient for this particular year to year comparison. The phenological distribution of migrating Crane counts of each year was compared to all the other years (each time set as the reference year). For example at Organbidexka pass where monitoring occurred between 1981 and 2009, the phenology of each year was compared to the 28 others.

Whenever one year to year comparison could not be estimated directly, it was reconstructed using the average linear combinations between the other available shifts. For example if the phenological shift between 2001 and 1995 could not be estimated but the shifts 2001-2004 and 2004-1995 were available, then the shift 2001-1995 was worth shift (2001-2004) + shift (2004-1995). Averaging all possible two way combinations thus allowed a robust estimation of missing shifts.

The phenological anomaly of each year across the entire monitoring period was defined as the average of all phenological shifts between this year and all the other years. This anomaly was then used as the phenological indice to compute phenological trends.

Statistical analysis

Significance of phenological shifts was tested using weighted linear regressions. The inverse squared standard deviations associated to the estimates of the phenological shifts were used as weights.

The relationships between migration time of common cranes and NAOW were tested using linear models. Temporal trends in NAOW, winds' frequency and strength and mean temperatures in Sweden, Germany and France as well as the correlation (Pearson's coefficient) between those factors were also investigated over the studied period.

Statistical analyses were performed using the R software (Development Core Team 2008).

Results

Trend analysis

A significant temporal trend in phenological shifts was found for the three passes (Fig.2, Organidexka: -0.74 ± 0.14, $P<0.001$; Lindux: -0.73 ± 0.19, $P=0.001$; Lizarrieta: -0.62 ± 0.16, $P=0.001$) leading to an advance of -20.72 days/29years, -20.44 days/29years, and -17.36 days/29years for Oranbidexka, Lindux and Lizarrieta, respectively, when extrapolation to the same 29 years period for the two last passes. Consequently, Common Crane has advanced its passage through the Pyrenees by approximately 20 days (19.50) during the last 30 years when considering these slopes. No difference in mean passage dates and temporal trends in the phenological response were detected between sites when site effect, time and the interaction between time and sites was tested (site: $F_{2,68} = 0.10$; P = 0.90; site x year: $F_{2,68} = 0.10$; P = 0.90). Slope of the temporal trend for the three sites together was highly negative and significant (-0.73 ± 0.16, P<0.001).

Trends and correlations in meteorological variables

No significant trend in WNAO was found during the study period (P = 0.31) while a significant increase in April temperature in Germany and Sweden were found (-0.39 ± 0.13, P=0.35; 0.20 ± 0.11, P=0.08). Mean spring temperature was found to increase marginally (Table 1). An increase in the frequency of S winds was found at Organbidexka during the period (0.05 ± 0.02, P=0.02) while a decrease in S and E winds' strength was noted (-0.03 ± 0.01, P=0.01; -0.01 ± 0.003, P=0.002, respectively). No significant trend in the frequency of E winds was found (P = 0.74). Strength of S and E winds were found to be correlated (r = 0.66, P < 0.001)).

Impact of meteorological variables on phenology

WNAO was not found to have any effect on the migration timing of cranes in Pyrenees (Organidexka: 0.07 ± 0.95, P=0.94; Lindux: 0.78 ± 1.02, P=0.45; Lizarrieta: 0.82 ± 0.92, P=0.38).

The frequency of S winds at Organbidexka was found to affect marginally the migration timing of Cranes at Organbidexka (-2.73 ± 1.42, P=0.06) while its strength affected it significantly (5.65 ± 2.14, P=0.01) meaning that cranes' passage was delayed by strong S winds. No significant effect was detected on phenological shift at Lindux (S wind frequency: P= 0.89; S wind strength: P=0.93) and Lizarrieta (S wind frequency: P= 0.90; S wind strength: P=0.77). The frequency of E winds at Organbidexka was found to advance the cranes' passage at Lindux (-11.11 ± 3.87, P=0.009) and Lizarrieta (-9.72 ± 3.46, P=0.01) while it has no significant effect at Organbidexka (-4.81 ± 4.72, P=0.31). Conversely, the strongest the E wind blows at Organbidexka, the later is the passage at this pass (24.38 ± 8.28, P=0.006).

Increasing mean spring temperature in Germany entailed a significant delayed passage at Organidexka while no significant trend can be noted for Lizarrieta and Lindux (Table 1). We did not find any significant relationship between the migration timing of Common Cranes and the mean spring temperatures in Sweden (Table 1). No effect of October and September temperatures in the Champagne lake region (France) was found to affect the Crane phenology in Pyrenees (Table 1).

Trend analysis accounting for meteorological variables

When taking account of local meteorological variables identified as being correlated to phenological shift (frequency and strength of E winds, frequency of S winds), we still found a negative and significant slope (-0.64 ± 0.13, $F_{1,64} = 25.79$; P<0.001). The advance of the Common Crane could be evaluated to ~ 18 days/29years.

When controlling for all other significant meteorological parameters (with P<0.10), we found a negative and significant slope (-0.65 ± 0.13, $F_{1,63} = 26.01$; P < 0.001). The advance of the Common Crane, independently of meteorological influences and changes, could be then evaluated to ~ 18 days/29years.

Discussion

Temporal trend in the phenological shift

The main result of this study is the coherent and quite similar advance in the autumn migration of the Common Crane through the three western Pyrenean passes. Indeed, they allowed a similar and thus robust estimation of the phenological response of the Common Crane and this despite local variations in meteorological parameters. It was not easily predictable to have such a robust result because of possible effects of local meteorological variables which could influence the count distribution differently at each pass.

It is also possible that such a constancy in phenological trends between passes is methodological. Indeed, it is likely that birds of the same migrating ‘population’ cross the three passes and even that individuals can cross Pyrenees at one pass one year and at another next year. This could mean that for this species, it seems unnecessary to monitor its phenology at the three passes in order to obtain its phenological response. The pass with most cranes could be sampled alone and considered representative of the ensemble.

Moreover, our results suggest a common response of the Common Crane to climate change, despite the fact that we did not find any effect of the WNAO on phenology. It also emphasized the importance of local meteorological variables. For example, the higher correlation of estimated phenological shifts between the nearest passes reveals that similarities in local meteorological conditions entail more similar responses (e.g. Pearsons’correlation between phenological shifts: Organidexka/ Lindux: $r = 0.72$, $P<0.01$; Organidexka/ Lizarrieta: $r = 0.61$, $P = 0.002$; Lindux/ Lizarrieta: $r = 0.86$, $P <0.001$). Indeed, the most distinct geographical and meteorological conditions are between Organbidexka and Lizarrieta and this is also the weakest correlation in the estimated phenological shifts. However, it is important to note that phenological shifts were not estimated on the same time period for the three passes meaning that other sources of difference can exist.

Finally, compared to the findings of Lundgren et al. (2003) which found an advance in spring arrival of one week over a 10-year period (1992-2002) at Swedish marshlands, we found quite similar advance in autumn passage when calculated on a 10-year period according to slopes obtained for Lizarrieta and Lindux - which shared the most similar period (1988-2009 and 1987-2009) with the one of Lundgren's study: we obtained an advance in fall migration by 6 to 7 days/10years (-5.58 and -6.57/10years).

Impact of meteorological variables

Correlation between nesting dates and autumn migration dates have been shown in literature (Sokolov 2006) as well as between spring temperature, breeding timing and autumn migration (Sokolov et al. 1998; Péron et al. 2007; Lehikonen et al. 2009). We found that temperature at northern latitudes could influence Cranes' autumn passage in the Pyrenees. In particular, spring temperature in the selected location in Germany was found to have a negative effect on migration dates. It means that the higher those temperatures were, the earliest was the autumn passage.

As we found a significant trend in April temperature both at selected stations in Sweden and Germany during those last 30 years, it is possible that such increase is the cause of the advance in the Cranes' autumn migration. Moreover, we also found a tendency of spring temperatures to advance through the period. This increase in spring temperatures could entail a better and faster reproduction and, thus, an earlier departure. Indeed, this has been shown by the Finnish Common Buzzard whose hatching dates were earlier when April and March temperatures were higher (Lehikoinen et al. 2009). Those birds also advanced the onset of breeding with approximately 11 days in less than 30 years (Lehikoinen et al. 2009).

More locally we also found significant trends in winds' frequencies and strength which could explain such advance since the last 30 years. Indeed, S wind frequency was found to increase at Organbidexka on the period and to have a negative effect on Cranes' passage dates. It means that the higher frequencies of S wind on the period could be responsible of the earlier passage of Cranes at least at Organbidexka. Moreover, we also found a decrease of the strength of S and E winds on the period which could be responsible of this advanced passage as well. Indeed, the stronger these strengths were, the later was the passage at Organbidexka. Interestingly, we also found a possible complementarity between passes. Indeed, as suspected, Lindux and Lizarrieta with their lower elevation could represent a possible retreat for birds when E winds blows strongly at Organbidexka. We indeed, found that the higher was the frequency of E winds at Organbidexka, the earlier the Cranes passed at Lindux and Lizarrieta.

Conclusion

We here found a strong phenological shift in Common Cranes, which was independent of monitoring and detection processes. Owing to the possible increase in the spring temperatures at northern latitudes during the last 30 years as well as to changes in frequency and strength of local winds in the western Pyrenees throughout the period, Common Cranes have advanced their autumn migration timing of 20 days in Pyrenees. Such an advance in phenology has rarely been recorded, even by large-bodied species like raptors (Filippi-Codaccioni et al. in press). Similar responses in the timing of migration and breeding (Dunn 2004, Nielsen and Møller 2006) have until now mainly been reported in shorter-lived passerines (but see

Lehikoinen et al. 2009). Thus, also larger-bodied species are capable of responding quickly to a warming climate and this study brings another evidence to the small but growing number of studies which showed such a response. It also demonstrates that not only long-distance migrants can show an advance in their phenology in response to climate change as it has been suggested (Jenni and Kéry 2003; Filippi-Codaccioni et al. in press). Further studies on the advance in the timing of breeding of Common Cranes at northern latitudes could help in better understanding its influence on the subsequent events of their life annual cycle.

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Table 1. Effect of mean spring and autumn temperature in Sweden, Germany and France.

Country	Mean temperature	Organbidexka	Lindux	Lizarrieta	Trend
Sweden	Spring (Mar-Apr)	-0.16 ± 0.10 (P = 0.11)	-0.07 ± 0.10 (P = 0.52)	-0.07 ± 0.09 (P = 0.39)	+
Germany	Spring (Mar-Apr)	**-0.27 ± 0.12 (P = 0.04)**	0.15 ± 0.14 (P = 0.28)	0.15 ± 0.13 (P = 0.25)	+.
France	Autumn (Sep-Oct)	-0.15 ± 0.13 (P = 0.30)	-0.11 ± 0.14 (P = 0.43)	-0.08 ± 0.12 (P = 0.51)	+

Slopes ± SE of the relation between phenological shifts and mean season temperature. Regressions were weighted by the inverse of the variance associated to the estimates of the phenological shifts. In bold, P-value < 0.05. Trend = trends of mean season temperature from 1981 to 2009 (**.** for P = 0.10).

Figure captions

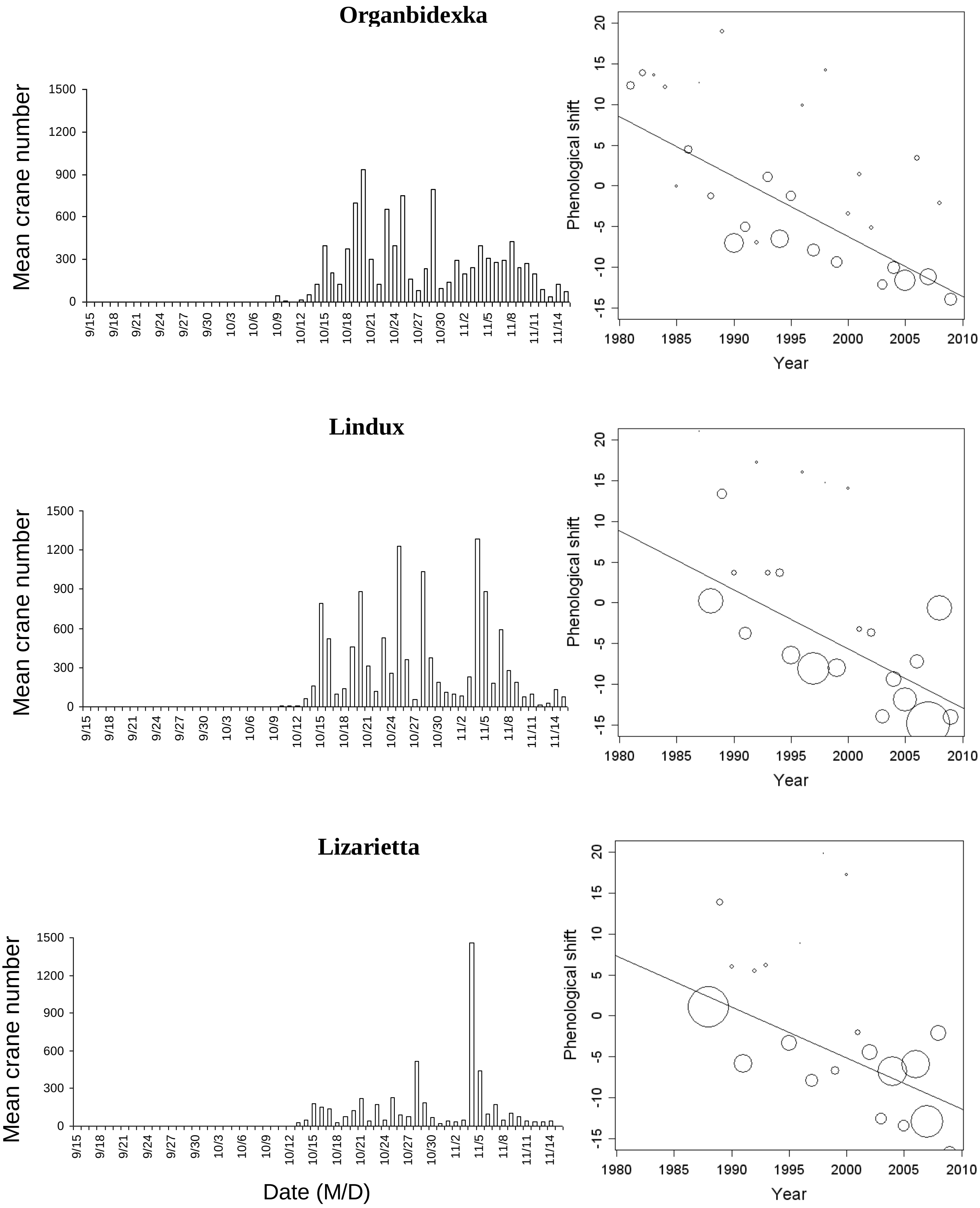
Fig.1 Representation of the 3 chosen sites for studying temperature influence on phenological shifts: Lake Hornborga, Sweden; the Bock-Rügen-area, Germany and Der Lake, France. Nearest meteorological stations are represented (Linköping, Greiswald and Langres).

Fig.2 Phenological distribution and trend in phenology for the three passes in the Common Crane. Histograms represent mean daily number of Common Cranes over the study period. Size of points is proportional to the inverse squared standard deviations associated to the estimates of the phenological shifts used as weights in the regressions.

Fig.1


Linköping
Lake
Hornborga
Rügen
Greiswald
Der Lake
Langres
Lizarrieta
Lindux
Organbidexka

Fig.2


Organbidexka
Mean crane number
1500
1200
900
600
300
0
9/15
9/18
9/21
9/24
9/27
9/30
10/3
10/6
10/9
10/12
10/15
10/18
10/21
10/24
10/27
10/30
11/2
11/5
11/8
11/11
11/14
Phenological shift
20
15
10
5
0
-5
-10
-15
1980
1985
1990
1995
2000
2005
2010
Year
Lindux
Mean crane number
1500
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10/18
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10/24
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11/5
11/8
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10/21
10/24
10/27
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11/8
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11/14
Date (M/D)
Phenological shift
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-5
-10
-15
1980
1985
1990
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2010
Year

Manuscrit 6

Flexible phenology better than gradual phenological advancement to cope with ongoing climate change in European passerines

En preparation

Flexible phenology better than gradual phenological advancement to cope with ongoing climate change in European passerines

Running title: Advantage of flexible phenology in passerines

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Abstract

The alteration in the timing of seasonal events in ecosystems is an important consequence of the recent and rapid climate change. For birds, a lack of response in timing of reproduction may cause population declines. Phenological responses to climate warming comprise two components: a short term flexible response to temperature and a long term temporal trend towards earlier breeding. Whether the first or the second component is most important in driving current population trends remains unknown.

We use data from a national Constant Effort Site ringing program (1989-2008 representing more than 130000 captured individuals) to estimate the timing of the realized breeding season of 20 common passerine species and examine whether it is correlated with annual variation in temperature or presents a linear relationship over time. The relative influence of the response of the breeding time to temperature and its temporal trend on large scale population growth rates is then assessed.

There is a homogenous trend across species towards earlier breeding over the study period whereas the response of the breeding time to temperature differs significantly among species. Species long-term population growth rates (1990-2005) estimated for Europe with an independent dataset, are strongly correlated to species short-term flexible breeding phenological response to temperature, but not to the long term trend in breeding phenology.

These results imply that climate change should mostly impact species with poor short term adjustment capacities and raises concern about the limits of such flexibility in birds as climate variability is predicted to increase in the future.

Key-words: Bird, temperature, population trends, Constant Effort Site, Breeding success.

Introduction

How current climatic changes impact bird populations has been investigated now in a number of studies during last decade (Parmesan and Yohe, 2003; Visser, 2008 Gregory et al., 2009). Yet climatic variation is complex and can be divided into at least two major components. First it is generally accepted that a trend towards warmer temperatures exists at global, regional and local scales even if there are spatial variations in its intensity (IPCC, 2007). Secondly, year to year fluctuations in climate cause departure from the linear increasing trend. This climate variance is predicted to increase during the next century and so constitutes an important component of ongoing climate change (IPCC, 2007). The mismatch between the breeding events and climate has been shown to play a crucial part in the breeding outputs in birds (Stenseth and Mysterud, 2002; Visser, Holleman and Gienapp, 2006; Drever and Clark, 2007). Indeed, the amount of available resources does not remain constant over time and peaks briefly during spring (Visser and Both, 2005; van Asch and Visser, 2007). In temperate ecosystems, the chick rearing period is constrained by this peak in food abundance (Nager and Vannoordwijk, 1995). Thus, laying date must occur within a short temporal window. Yet the timing of this peak in food varies each year according to both the temporal trend in temperature and the anomalies to this trend. In response to climate change, gradual temporal advancement of bird phenology is already known for migration dates (Cotton, 2003; Jenni and Kery, 2003; Both, Bijlsma and Visser, 2005; Jonzen et al., 2006; Both and te Marvelde, 2007; Van Buskirk, Mulvihill and Leberman, 2009). Similar evidence exists for the temporal advancement in the bird's breeding season (Brown, Li and Bhagabati, 1999) and is mainly based on monitoring laying dates in various European experimental forests especially on a few species like tits (Parus major and Cyanistes caeruleus) and the Pied flycatcher (Ficedula hypoleuca) (Both et al., 2004) although "nest record cards" for a wider suite of species have shown a similar relationship (Crick et al., 1997 Crick, 2004). Short term adjustment to climate anomalies are also known for migration and breeding (Saino et al., 2004; Saino et al., 2007; Visser, Holleman and Caro, 2009). Thus the phenology of the breeding season reacts to annual climate fluctuations. However, not all bird species are able to adjust their breeding phenology to climate variation (Both et al., 2009). Because of the resulting reduction in breeding success, this may have consequences on the overall population dynamics. Consistent with these predictions, Møller et al. (2008) show that the temporal trend of phenological change in migration dates relates to species population status at the European scale. Hence, species not able to adjust their phenology to increasing temperatures are decreasing at a national (Both et al., 2006) or a continental scale (Møller et al, 2008). Yet the linear trend in phenological change is a mixture of species long term phenological response and their short term adjustment to increasing temperature. Potential mechanisms underlying these two types of responses might not be the same and could lead to very different future changes in bird populations. Indeed, in the case of a long term phenological response shown as gradual advancement in timing of breeding, in terms of the population dynamics it is the overall rate of phenological change that matters, thus the speed at which a population is able to shift its timing of breeding in a given direction. Alternatively, if short term phenological response of the timing of breeding has the greatest influence on population growth rates, it is the ability of a population to shift its time of breeding according to annual temperature that matters, thus the flexibility of the population. In this study we specifically address the relative importance of species long-term and short-term phenological responses and their relationship with population growth rates. With this aim, we use data from the French Constant Effort Site ringing scheme for the period 1989-2008 and involving more than 130 000 individual birds captured at 216 sites distributed across France. We first estimated the temporal shift in the seasonal distribution of juveniles within total captures between different years. Based on these estimates we calculated an annual breeding time index for 20 species. The linear temporal trend of the breeding time index was then estimated while controlling for annual temperature fluctuations which constitutes species long-term phenological response (LTR), whereas species short-term phenological response (STR) is estimated as the response of the breeding time index to temperature while controlling for the linear temporal trend. Both types of response are then related to species population growth rates estimated for Europe using independent data from national Breeding Bird Surveys.

Materials and methods

Bird ringing data

Data originate from the French Constant Effort Site Program (CES) (Julliard, Jiguet and Couvet, 2004). CES are standardized bird ringing schemes using mist nets during the breeding period. Standardization on CES relies on a fixed position and number of nets used per site (between 10 and 50), and on a fixed number and similar dates of capture sessions per site (usually between three and five, depending on the site, with dates ranging from the beginning of May to the end of July, and covering at least two months for a given site). The scheme started in 1989. The data used in this study cover the 1989-2008 period.

In the field, each bird captured is individually ringed to avoid double counting, and the species and age (breeding adults or young of the year) are determined unambiguously from plumage by experienced volunteer bird ringers. All data for which there was uncertainty as to the age of birds were excluded (<1%). Over the 20-year period the data were collected from 216 CES sites representing 1012 site-years. Species for which adults and juveniles were captured each year throughout the study period were included in the study. Thus 20 species were considered [*Acrocephalus scirpaceus (*n=11715), *Aegithalos caudatus* (n=3926*), Certhia brachydactyla* (n=926) , *Erithacus rubecula* (n=10904)*, Fringilla coelebs* (n=2522)*, Hippolais polyglotta* (n=2967)*, Luscinia megarhynchos* (n=4741)*, Cyanistes caeruleus* (n=5707), *Parus major* (n=12493), *Parus montanus* (n=1298), *Parus palustris* (n=1298)*, Phylloscopus collybita* (n=12672)*, Phylloscopus trochilus* (n=2937)*, Prunella modularis* (n=5167)*, Sylvia atricapilla* (n=24969)*, Sylvia borin* (n=4035), *Sylvia communis* (n=5044), *Troglodytes troglodytes* (n=2976)*, Turdus merula* (n=12149) and *Turdus philomelos* (n=3147)].

Estimating a Breeding Time Index

For each species and each year, a Breeding Time Index (BTI) was estimated using a curve fitting method (Moussus et al., 2009). The main features of this method will be described here but for further details concerning the algorithm and model justification please refer to Moussus et al. (2009). It is assumed that seasonal distribution in the proportion of juveniles within total captures reaches an inflexion point and that the shape of this distribution remains constant for different years (See Fig. 1a for an example). Under these assumptions seasonal distributions in the proportion of juveniles within total captures for two different years only differ in their timing (i.e. they match if a certain temporal translation is applied to one of them). This method aims to estimate a temporal shift necessary to make two different year's distributions match using an iterative algorithm. To achieve this, numbers of captures of juveniles and total captures were summed over all CES sites per species per year and per day (in days after 1st April). We will illustrate the functioning of the method with an example, the estimation of the temporal shift in timing of breeding of Great tit (*Parus major*) in 2006 and 2007. In this case 2007 is set as the reference year and 2006 will be the year for which data is iteratively temporally shifted until it fits the data for 2007. This is done by fitting the following Generalized Additive Mixed effects Model (GAMM) to the capture data of both years (2006 and 2007 for example): *(Number of juveniles, Number of Adults)~ spline function (Date + t)* with a Binomial error and where *t* is worth 0 for the 2007 data (set as the reference) and ranges between -30 and 30 days by 1-day increment for the 2006 data. To account for between years variations of the overall productivity, year was considered as a random categorical variable in the GAMM. The fit of each model corresponding to each value of *t* is monitored by its Akaike Information Criterion (AIC) (Akaike, 1981). Thus for one comparison 61 AIC values are recorded. As the 61 models have the same number of parameters, minimizing AIC is equivalent to maximizing likelihood (See Fig. 1b for an example). This is achieved by fitting a quadratic regression (AIC~$t + t^2$) using the 10 AIC values around the smallest local minimum of AIC versus *t* function. If *a* is the second degree coefficient, *b* the first degree coefficient and *c* the intercept of the regression, then the AIC as a function of *t* is minimized for $tmin = -b/2a$ which is considered as an estimation of the temporal shift between the two breeding seasons. Moreover, the standard error of this estimation is given by the second derivative of the log-likelihood and is worth $1/a$. For each year, temporal shifts were estimated for all the other years.

Rarely, the GAMM fails to converge and the estimation of the phenological shift between the two compared years cannot be produced directly (167 out of 7600 estimations). These gaps were filled by recalculating the shifts using linear combinations of other available shifts. For example, if the temporal shift between year 2005 and 2004 could not be estimated for one species but the shifts between 2005-2003 and 2003-2004 were available, then the shift between 2005 and 2004 was calculated as the sum of shifts 2005-2003 and 2003-2004. All possible linear combinations involving two shifts were used and the reconstructed value was treated as the average of the sums. Eventually for each species and each year, the Breeding Time Index (BTI) was defined as the average temporal shift between one year and the others. Thus it is the relative anomaly in timing of breeding across the 1989-2008 period.

Defining species short term and long term phenological responses

Species response to climate change could be driven by long term temporal trends or short term flexibility related to annual climate fluctuations. In order to disentangle these mechanisms, to each species we fitted a simple multiple linear regression between the species Breeding Time Index (BTI), temperature (over the selected period) and year as a continuous variable. Because all the phenological shifts were not estimated with the same accuracy, the inverse squared standard estimation errors of the BTI were used as weights in the regressions. The regression coefficients of temperature and year were defined as respectively the Short Term flexible phenological Response (STR) and the Long Term phenological trend Response (LTR) of species to climate change over the 1989-2008 period. We also fitted a linear regression between the BTI and time (years) without including temperature in the model. The regression coefficient of time in these regressions was defined as species' Undistinguished Phenological Response (UPR).

Climatic data

Temperature data were obtained from the website of the European Climate Assessment & Dataset (ECA&D) (http://eca.knmi.nl/). The monthly mean daily temperature data of 57 meteorological stations located across the entire country were averaged to produce the climate variable (*Temp*) used in the study. Temp was defined as the average mean daily temperature from January to May. The choice of this period is justified by the fact that early breeders are predicted to be more sensitive to late winter temperatures to set their phenology while late breeders rely on early spring temperatures. Considering a unique climatic temporal window also allows an easier interpretation of the results as the climatic parameter is constant.

Average population growth rates

Average population growth rates and their standard errors over the 1990-2005 period were obtained from the website of the European Bird Census Council (EBCC), which reports results from the Pan-European Common Bird Monitoring scheme (PECBMs; http://www.ebcc.info/index.php?ID=358). This period was almost the same as the one concerning the phenological analyses. Moreover, this dataset was completely independent from the one we used to estimate the Breeding Time Index.

Explanatory variables

Explanatory variables for species population growth rates included species UPR, STR and LTR which are the variables of interest. Because bird population trends are influenced by numerous factors, we included variables that have previously been found to predict bird population growth rates (Gregory et al., 2007; Jiguet et al., 2007). These included thermal maximum, average number of broods per year, diet, as insectivorous or omnivorous following Gregory et al. (2007), species migratory index as the average distance between breeding and wintering grounds of the French breeding population (see Jiguet et al. 2007), log-body weight and species habitat specialization index as a coefficient of variation in the abundance of a species in 18 different habitat classes in France, using counts data from 2001 to 2004 (Julliard et al., 2006). The latter was not available for the wetland species included in the analysis (*Acrocephalus scirpaceus*).

Statistical analyses

We first examined the temporal trend and the effect of temperature on the BTI for all species. To do this, we fitted a generalized linear model to the BTI including year (continuous variable) and spring temperature. In order to test the for differences between species phenological trends and responses to temperatures we fitted a GLM including species, continuous year, spring temperature, species x temperature and species x continuous year interactions. The effects were test adjusted to each other using an analysis of variance (ANOVA). The inverse squared standard estimation errors of the BTI were used as weights in the regressions. The non linearity of the temporal trend and temperature effect on the BTI were investigated using Generalized Additive Models (GAM).

In the second part of the analysis we focused on species population growth rates and tested the effects of the type of phenological responses shown by species. Treating species as independent replicates would not be correct given their phylogenetical relatedness (Harvey et al., 1991). Thus it is possible that some explanatory variables might be very similar between closely related species. Moreover, species population growth rates themselves can be correlated (Thomas, 2008). To take phylogenetical relatedness into account in our dataset, we used the generalised least squares phylogenetic comparative method. Practically, we used package “ape” of the R software (R Development Core Team 2008) to run the GLSs assuming a Grafen correlation structure (Grafen, 1989) for the model dependence because branch lengths were not available (and therefore all set to 1). The phylogeny used to build the tree was taken from Jonsson et al (2006) (Online Resource 1).

The effects of UPR, STR and LTR on species population trends were tested alone in the GLS models. To ensure that potential effects of these phenological responses were not confounded with the other previously published predictors, we included those that were significantly related to species population growth rates in the GLSs namely diet and log-body weight. The inverse squared standard estimation errors of the population trends were used as weights in the regressions.

Lastly, there is a distinction between finding the best model to describe the data and drawing inferences about the likely causality of variables, and dealing with multicollinearity is difficult in single-model approaches. A possible solution is hierarchical partitioning, which uses all models in a regression hierarchy to distinguish those variables that have high independent correlations with the dependent variable (Chevan and Sutherland 1991). We therefore also analyzed our data with hierarchical partitioning (Mac Nally, 2002) using package "hier.part" of the R software. The probabilities of independent contribution of the predictors (STR or LTR) to species population growth rates were assessed with z-scores obtained using 1000 randomization (and R^2 as the goodness of fit measure).

Results

Phenological responses across species

For all species analysed and using GLMs, we found a significant temporal trend in the Breeding Time Index towards earlier breeding adjusted to temperature and this trend is homogenous across species (year: $F_{1,397}$ =40.1, P<0.0001; year:species interaction: $F_{19,340}$ =0.78, P=0.73) (See Table 1). Adjusted to the temporal trend, birds tended to breed earlier when temperature was higher between January and May and this pattern was common to all species although the strength of the interaction between species was stronger than the interaction between year and species (Temperature (Jan-Apr): $F_{1,397}$ =15.03, P=0.0001; Temperature:species interaction: $F_{19,340}$ =1.23, P=0.23) (See Table 1).

The relation between spring temperatures and breeding phenology was significantly non linear (GAM smoothed temperature effect: $F_{1,393}$=8.71, P<0.0001) while the non linearity of the temporal trend was only marginally significant (GAM smoothed year effect: $F_{1,393}$=3.15, P=0.025). The effect of temperature on species breeding phenology seemed to be non linear. Indeed, the breeding time index seemed to be much more sensitive to spring temperatures above 8 Celsius degrees (See figure 2a). The temporal trend in the breeding time index appeared linear across the entire period (See figure 2b). For each species we estimated the partial R^2 of both the year and the temperature effects on the breeding phenological indices. Averaged for the 30 species, the partial R^2 was higher for the linear year effect than for the temperature effect (year mean R^2=0.12 ranging between 3E-06 and 0.51; temperature (Jan-Apr) mean R^2=0.07 ranging between 3E-05 and 0.38, see Table 2). These results show that the long term phenological response (LTR) is quantitatively more intense than the short term flexible response (STR) but they do not give information about what matters in terms of species population growth rates.

UPR, STR and LTR in relation to large scale population growth rates

In order to address this question we estimated for each species the Undistinguished Phenological Response (UPR), LTR and STR using multiple regressions including year and temperature effects. These coefficients were then tested against species European growth rates using GLSs enabling us to account for phylogenetic relatedness between species and weighting the regressions by the accuracy of the estimations of population growth rates. We did not find any relation between species Undistinguished Phenological Response (time effect on the breeding phenological index not adjusted for temperature) and species population growth rates (UPR: $F_{1,18}$=1.67, P=0.21) (See Table 3). Species which show the greatest short term flexibility in relation to climate shown the least declines (STR: $F_{1,18}$=11.7, P=0.003) (see Table 3 and Fig. 3a). Population growth rates were positively correlated with long term trend in the breeding phenology (LTR: $F_{1,18}$ =3.53, P=0.08]) (See Table 2 and Fig.3b). As many factors are currently influencing bird population growth rates we investigated whether some of these predictors could be confounding with our phenological variables (STR and LTR). Potentially confounding variables included were: thermal maximum, diet, nest location, number of broods and habitat specialization, body weight and log-mean migration distance. Probably because the set of species included in this study represents a subset of the species that these predictors have been shown to influence, only three of them were marginally significantly correlated to species European population growth rates namely the thermal maximum, the mean annual number of broods and the degree of habitat specialization (thermal maximum: $F_{1,18}$=5.09, P=0.04; Brood number: $F_{1,18}$=5.11, P=0.04; Diet: $F_{1,18}$=1.57, P=0.23; Body weight: $F_{1,18}$=2.86, P=0.11; log-migration distance: $F_{1,18}$=2.01, P=0.17; Habitat specialization: $F_{1,17}$=7.63, P=0.01). The effect of STR on European population growth rates significant when the three significant predictors (namely thermal maximum, mean annual number of broods and degree of habitat specialization) were included in the GLS models whereas the effect of LTR remained as a tendency adjusted to these two potentially confounding predictors (STR: $F_{1,14}$=6.42, P=0.02; LTR: $F_{1,16}$=4.49, P=0.05, see Table 3).

When the significant population trend predictors were tested in Hierarchical partitioning of variance analyses, thermal maximum was the most important factor influencing population trends (R^2=0.26, Z-score=3.74, P<0.0001). STR had no significant independent contribution to the population growth rates (R^2=0.13, Z-score= 1.22, P=0.11). LTR had no significant contribution to bird population trends either (LTR, R^2=0.15, Z-score=1.4, P=0.08).

Discussion

The Breeding Time Index used in this study was calculated using a novel method which allows the use of data from large abundance monitoring programmes such as Constant Effort Site or Breeding Bird Surveys (Moussus et al., 2009). The information given by the BTI is somewhat different from the classical phenological measures used to study bird phenology like the exact laying dates derived from intensive nest monitoring. Indeed, here as the sampling of juveniles occurs at the end of the breeding season, the results found here apply to the phenology of successful breeding attempts. Those successful attempts are the ones that count most in terms of population growth rates which justifies their use in this study.

The Breeding Time Index was highly sensitive to climate within a period ranging from January to April. This is not surprising since for many species, laying occurs at the beginning of spring when the timing of the environment is already determined. Indeed information gathering by breeding birds must occur during a period preceding the laying period (Bourgault, Caro and Perret, 2006; Visser et al., 2006). Yet the temperature index used here includes temperatures of early spring. First, long-distance migrants could be more influenced by early spring temperatures because they only arrive on their breeding grounds by April (Both et al., 2004; Both et al., 2007; Sanz, 2003). The migratory return phenology has also been shown to react to temperatures “en route” which could be correlated to temperatures on the breeding grounds (Gordo and Sanz, 2008; Tottrup et al., 2008). Second, previous work has shown that minor phenological adjustments can occur between egg laying and chick fledging. Such small shifts could also account for this tendency (Cresswell and McCleery, 2003). Eventually in case of breeding failures occurring with the first clutch, replacement clutches could be more sensitive to spring climate conditions.

The most important phenological shift predicting species population declines is their flexible short term response to climate. Species able to cope with annual temperature anomalies through a short-term phenological response are currently suffering smaller population declines. There is a difference between trying to understand which of the two mechanisms (short term flexible response to temperature STR or long term phenological trend response LTR) is currently most frequently happening in bird populations in response to climate change and identifying which of these have the greatest influence on populations dynamics in the long term. Whereas the first aspect is currently widely debated (Reale et al., 2003; Pulido and Berthold, 2004; Charmantier et al., 2008; Gienapp et al., 2008;), to our knowledge few studies have related species phenological changes and their population trends in the long term (but see Both et al. 2006; Visser et al. 2006; Møller et al. 2008). Moreover, in none of these studies has it been possible to distinguish between LTR and STR to climate because changes in phenology have not been quantitatively adjusted to each other. Here, as the regression slopes of the annual phenological indices are extracted from additive models incorporating the temporal trend and temperature, their additive effects are measured.

There was no clear contribution of species LTR to their population trends although we cannot exclude a positive relationship with population trends. This would mean that species having less advanced their phenology over the study period would suffer the least declines. Such gradual temporal changes are observed when natural selection is acting on bird populations towards progressively earlier breeding (Berthold et al., 1992; Jonzen et al., 2006). Nevertheless our data do not allow us to associate unambiguously LTR with natural selection because we cannot show that earlier breeding is genetically based. Natural selection can only be considered as a possible but non exclusive process lying behind LTR. LTR might generally not occur fast enough in order to have consequences on bird population trends (Burger and Lynch, 1995; Bradshaw and Holzapfel, 2006; Gienapp, Postma and Visser, 2006; Gienapp et al., 2008). Another hypothesis to account for this result is that LTR does not vary much between species which is consistent with our results (see table 2). Indeed LTR supported by this study as the LTR were all comprised within a narrow range suggesting that among these 20 common species they are no major differences between the breeding time long term trends. Thus it cannot clearly drive species population growth rates.

Species STR is strongly correlated to large scale demography. As for LTR, the nature of our data does not allow us to associate STR with phenotypic plasticity (and there is no such attempt in this study) because these data do not provide information about individual behaviour. Indeed, as we measure the phenology of the realized breeding season, we do not know if it represents phenological adjustment of the majority of the individuals in the population (in that case phenotypic plasticity). This ambiguity justifies the term of flexibility (of the total population) instead of plasticity. Species are not equally flexible and cannot face climate short term variability in the same way they face gradual warming (Torti and Dunn, 2005). Indeed, flexibility involves complex information gathering systems (Dall and Cuthill, 1997) so that a species is able to track annually fluctuating environments. Such complex cognitive systems are unlikely to be evenly distributed among species and could account for the relationship between short-term phenological plasticity and ongoing long-term population trends (Shultz et al., 2005) and the wide range of STR found in this study. Recent experimental work suggests a causal role of temperature in determining the egg laying date in Great Tits Parus major (Visser et al., 2009). It is also very unlikely that such sensitivity to temperature is evenly distributed across avian species which could account for the results found here. Theoretical discussions on the reasons how phenological change could drive demographic changes in plant and animal populations are numerous (Visser et al., 2005). It has been mainly suggested that climatic changes are causing alterations in the synchronization of different organisms at different trophic levels, because different species use different clues to adjust to changing temperature. Birds have to adjust the timing of their breeding events such as the maximum food requirements for the offspring match the peak in resource abundance (Visser et al., 2005; Jonzén, Hedenström and Lundberg, 2007). These results suggest species long term population trends are driven by the sum of species annual adjustments to spring or late winter temperatures. Thus they provide some support for the Match-Mismatch hypotheses at a large spatial scale and for many common species.

Among various life history traits predicting species population declines (Sanderson et al., 2006, Gregory et al., 2007; Jiguet et al., 2007; Jiguet et al., 2009), three of them, namely thermal maximum diet and degree of habitat specialization, were significantly related to bird population trends. The 20 species included in the analyses represent a subset of the species on which all predictors included in the study have been tested previously. For obvious methodological reasons they are the most detectable species within ringing schemes, which mostly sample birds within bushy areas. Here, the effect of STR on large scale bird population growth rates remained significant adjusted to the three significant potentially confounding predictors. This stresses the importance of phenological adjustment during the current climate change. Although STR was negatively correlated to population trends, hierarchical partitioning did not show any independent contribution of STR to species large-scale population trends. This is not surprising since phenological adjustment abilities are a consequence of species life-history traits so that STR might be correlated to these traits. STR could thus be an important mechanism explaining how these traits can drive population changes but the estimated independent contribution of this variable remains low.

To conclude, this study identifies species short term phenological flexibility as the most important phenological mechanism in driving bird population trends facing climate change during the past two decades. We did not identify any relationship between species long term temporal phenological change and their population trends. Species short term flexible response to temperature appears to be a major predictor of bird population trends adjusted to other predictors of large scale bird population growth rates although it probably depends on species life-history traits. Thus this study should raise major concern for species displaying low phenological flexibility. Moreover these results are worrying as we do not know to the extent and for how long species flexibility will allow birds to adjust their phenology to expected temperature change, and as climate variability increases beyond the range of variation to which species are currently adapted.

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Tables

Table 1. Breeding phenological index of 20 common European passerine species related to temperature and time. The table shows the additive effects on the Breeding phenological index, of temperature (January-May), time and the interactions between temperature and species and time and species modelled using Generalized Linear Models. Significance and effects magnitude was tested using Analysis of Variance.

Variables	*F*	df	*P*	Estimate (SE)
		Phenological indice		
Temperature	15.03	1,397	0.0001	-1.28 (0.33)
Temperature:species	1.23	19,340	0.23	
Year	40.1	1,397	<0.0001	-0.26 (0.04)
Year:species	0.78	19,340	0.73	

Table. 2. Phenological responses of 20 common passerines to temperature (average January-May). Partial R² of temperature and linear year for the Breeding Time Index, as well as Short Term phenological responses to temperature and temporal trends in species breeding phenology are reported.

Species	**R^2 Year**	**R^2 Temperature**	**STR (SE)**	**LTR (SE)**
Acrocephalus scirpaceus	0.06	<0.01	1.26 (1.83)	-0.4 (0.2)
Aegithalos caudatus	0.03	0.38	-6.6 (1.8)	-0.32 (0.23)
Certhia brachydactyla	0.01	0.01	-2.58 (2.2)	-0.77 (0.18)
Erithacus rubecula	<0.01	0.04	-1.3 (1.15)	-0.27 (0.15)
Fringilla coelebs	0.08	0.04	-1.58 (2.69)	-0.31 (0.16)
Hippolais polyglotta	0.22	0.03	1.37 (1.47)	-0.12 (0.17)
Luscinia megarhynchos	0.31	0.05	1.15 (0.8)	-0.32 (0.13)
Cyanistes caeruleus	<0.01	0.06	-2.34 (1.95)	-0.35 (0.21)
Parus major	0.14	0.15	-2.68 (1.05)	-0.21 (0.35)
Parus montanus	0.01	0.02	-1.99 (3.07)	-0.29 (0.3)
Parus palustris	0.05	<0.01	-0.76 (2.25)	-0.04 (0.25)
Phylloscopus collybita	0.01	0.12	-2.06 (1.45)	-0.24 (0.13)
Phylloscopus trochilus	0.19	0.02	0.87 (1.07)	-0.09 (0.22)
Prunella modularis	0.29	0.02	-2.42 (1.58)	0.06 (0.28)
Sylbvia atricapilla	0.12	0.05	-1.36 (1.2)	-0.67 (0.19)
Sylvia borin	0.51	<0.01	0.25 (1.37)	-0.26 (0.38)
Sylvia communis	0.13	<0.01	-0.49 (1.34)	-0.34 (0.26)
Troglodytes troglodytes	0.01	0.29	-5.24 (1.71)	-0.04 (0.34)
Turdus merula	0.1	0.01	-1.13 (2.13)	-0.03 (0.15)
Turdus philomelos	0.03	0.02	-2.83 (2.94)	-0.31 (0.09)
Average	**0.115**	**0.067**		

Table. 3. Relation between species phenological UPR, STR, LTR and population growth rates for 20 common European passerines. The table shows the effects of species undistinguished phenological response (year effect on Breeding phenological index not adjusted for temperature), short term flexible phenological response (STR, temperature (January to May) effect on the breeding phenological index adjusted to linear year) and species long term phenological trend response (LTR, year effect on the breeding phenological index adjusted to temperature) on species population growth rates (1990-2005) calculated for Europe. The estimations were made using Generalized Least Square models accounting for phylogenetic relatedness between species. Principal effects were tested alone and adjusted to the significant potential confounding variables (thermal maximum, diet and degree of habitat specialization).

Variables		*F*	df	*P*	Estimate (SE)
		Population trend during 1989-2005			
UPR	alone	1.67	1,18	0.21	0.02 (0.01)
	adjusted	3.3	1,14	0.10	0.02 (0.01)
STR	alone	11.7	1,18	0.003	-0.004 (0.001)
	adjusted	6.42	1,14	0.02	-0.004 (0.001)
LTR	alone	3.53	1,18	0.08	0.02 (0.01)
	adjusted	4.49	1,14	0.05	0.02 (0.01)

Figure legends

Fig. 1. Estimation of the phenological shift of the breeding season for the Great Tit (*Parus major*) between 2006 and 2007. (a) Anomaly of the Proportion of Juveniles in Total Captures (PJTC) throughout the sampling season modelled using a Generalized Additive Model (GAM). In bold the PJTC in 2007 set in this example as the reference year. The normal line is the PJTC in 2006. 95 % confidence limits are shown in dotted lines. The breeding phenology of 2006 seems to be late compared to 2007. (b) AIC of the 61 GAMs applied to the data of 2006 and 2007 in relation to the temporal shift applied to the data of 2006 (2007 is set as the reference year). Minimal AIC is obtained by shifting the data of 2006 by -8 days (vertical line). Thus the 2006 breeding season is estimated to be -8.0 ± SE days late on the 2007 breeding season. The Breeding Time Index for one year and one species is calculated as the mean of the phenological shifts between this year and all the other years.

Fig. 2. Effects of temperature and linear year on the breeding phenology of 20 common passerine species. (a) Effect of temperature (Average daily temperature from January to May) on the Breeding Time Index (BTI) of 20 common passerine species as modelled by a Generalized Additive Model (GAM) *BTI~spline(Temperature)* . 95 % confidence intervals are shown in dotted lines. Note the effect seems not to be linear. (b) Temporal trend in the BTI for 20 common passerine species as modelled by a GAM *BTI~spline (Year)*. 95 % confidence intervals are shown in dotted lines. Note that the trend seems to be linear across the study period (1989-2008).

Fig. 3. Long-term population growth rates related to flexible phenological responses (STR) and phenological trends (LTR). The figure shows the relation between species additive population growth rates over the 1990-2005 period calculated for Europe and (a) the short term flexible phenological

response to temperature (averaged over January to May) adjusted to the temporal trend of the phenological response, and (b) the temporal trend of species phenology over the 1989-2008 period (LTR) (adjusted to the phenological response to temperature). The solid regression line indicates the effect was significant ($P<0.05$) from the Generalized Least Square model accounting for phylogenetic relatedness between species and weighted by the squared inverse of the standard estimation of the population growth rates.

Figures

Figure 1.

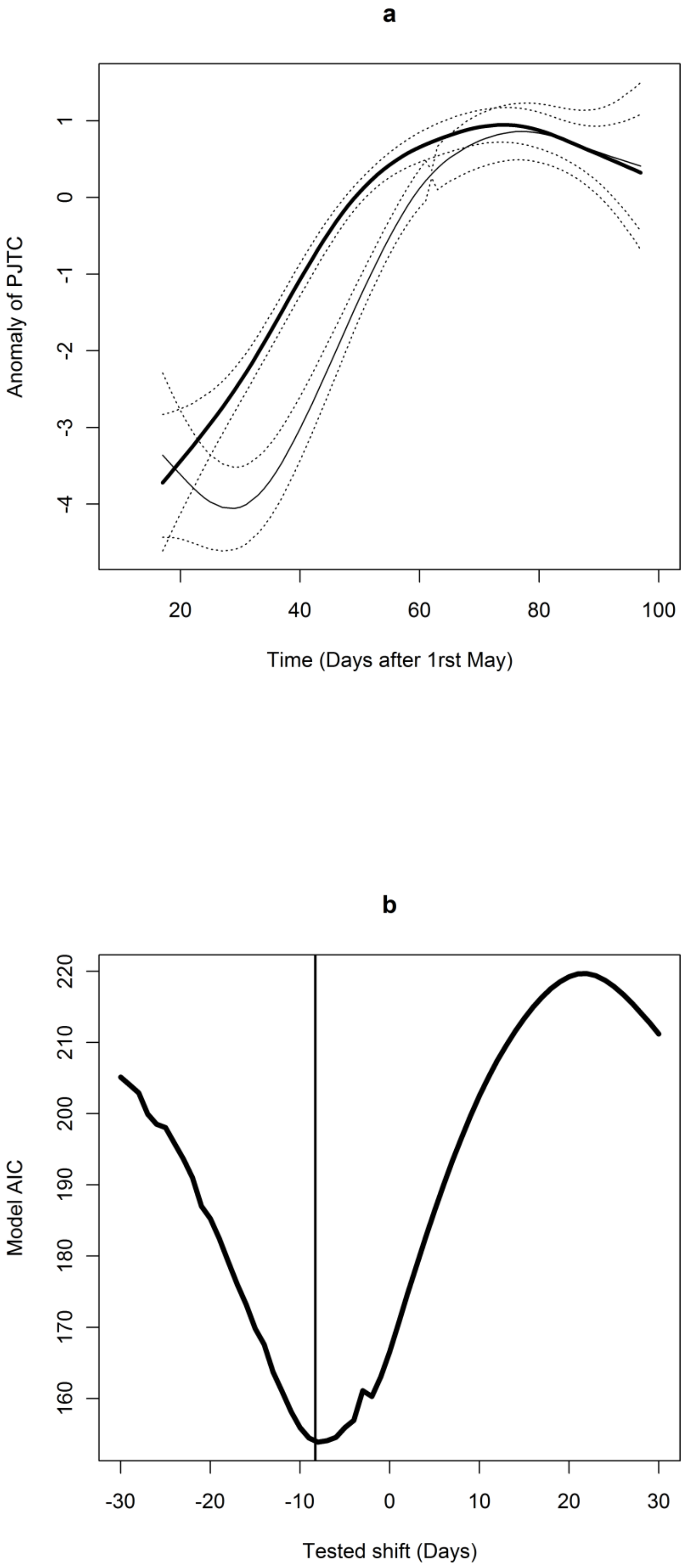


Figure 2.

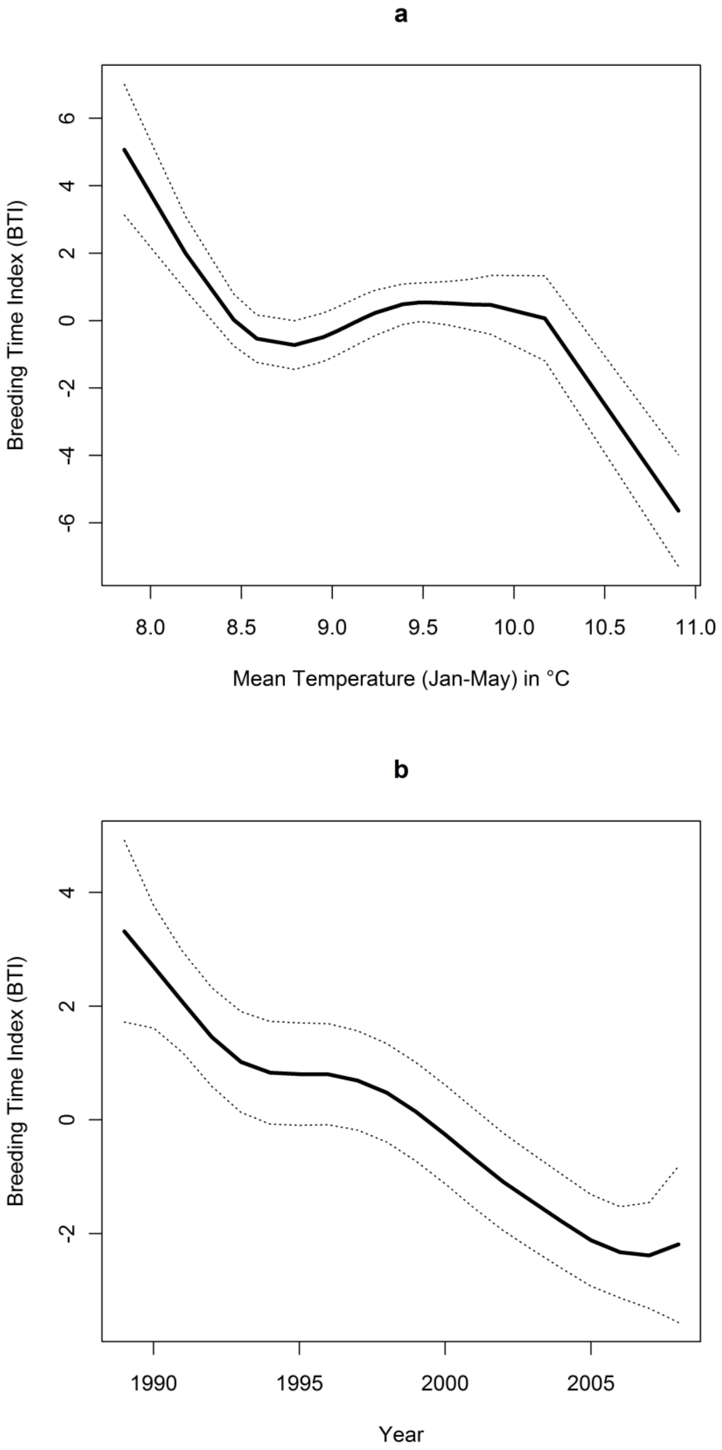
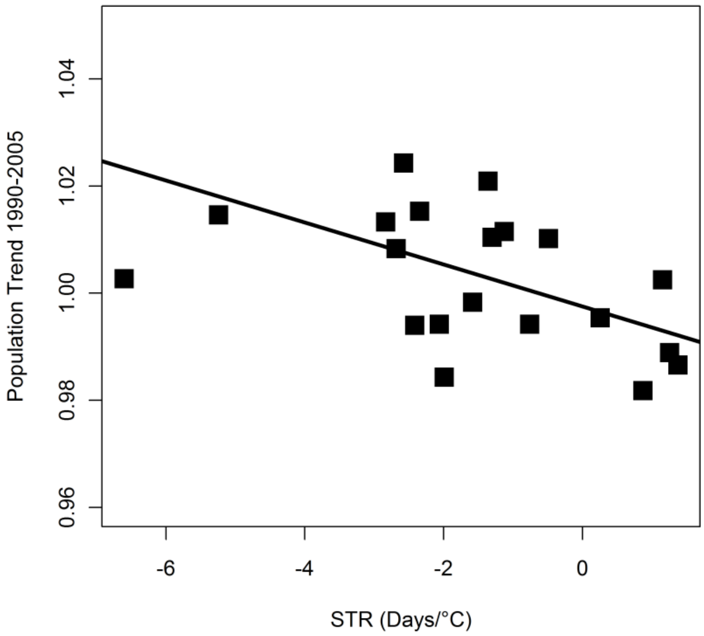
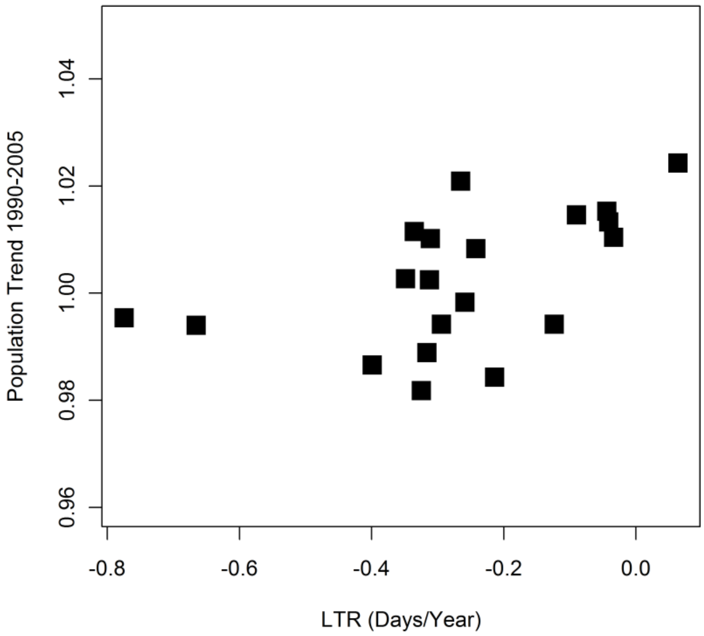

a
Breeding Time Index (BTI)
6
4
2
0
-2
-4
-6
8.0
8.5
9.0
9.5
10.0
10.5
11.0
Mean Temperature (Jan-May) in °C
b
Breeding Time Index (BTI)
4
2
0
-2
1990
1995
2000
2005
Year

Figure 3.


Population Trend 1990-2005
0.96
0.98
1.00
1.02
1.04
-6
-4
-2
0
STR (Days/°C)


Population Trend 1990-2005
0.96
0.98
1.00
1.02
1.04
-0.8
-0.6
-0.4
-0.2
0.0
LTR (Days/Year)

Manuscrit 7

Which are the phenologically flexible species? a case study with common passerine birds.

Soumis à *Oikos*

Which are the phenologically flexible species? a case study with common passerine birds.

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Abstract

One of the most consensual ecological effects of the current climate warming is the alteration of the environmental timing of ecosystems. Phenological shifts at different levels of food webs are predicted to have major effects on species assemblages. Indeed it is unlikely that all species should be able to respond to the phenological shifts of their environment evenly. Yet questions remain about the specific traits that predict the ability of a species to track the temporal fluctuations of their environment. In this study, we use data from the French Constant Effort Site ringing program over a 20 year period (1989-2008) to estimate the ability of 20 common passerine species to adjust their breeding phenology to spring temperature variations. We show that the sensitivity of species breeding phenology to climate relates to species mean migration distance, species thermal and habitat niche breadth and brain mass. Species with the broadest ecological and thermal niches, the shortest mean migration distances and the largest brains were most able to adjust their breeding phenology to temperature variations. Our results thus identify long distance migrants and ecological specialists as the species that could most suffer from the future climate changes and suggests phenological adjustment as one possible mechanism underlying the replacement of specialist species by more generalist ones, the so called functional biotic homogenization.

Introduction

Among important changes caused by the current global warming, changes in the timing of biological events, thus phenological changes, have received particular attention during the last two decades (Walther et al. 2002; Parmesan and Yohe 2003; Visser 2008). Indeed, in terrestrial ecosystems, numerous studies show among others, phenological shifts in the timing of budburst (Wielgolaski 1999; Korner and Basler 2010), flowering (Menzel et al. 2006), caterpillar emergence (van Asch and Visser 2007), avian spring migration (Cotton 2003; Sparks et al. 2005; Jonzen et al. 2006) or avian breeding (Crick and Sparks 1999; Both et al. 2004). Because species interact within complex food webs, different phenological changes in different species can lead to resource mismatch between different trophic levels (Durant et al. 2005; Durant et al. 2007; Both et al. 2009). Differences in the phenological responses to climate changes between organisms can relate to the physiological mechanisms by which a species responds to climatic fluctuations. In plants, budburst or flowering times are controlled by day length and temperature (Korner and Basler 2010). Insects spending winter in resistance forms also have time emergence dates based on temperature (van Asch and Visser 2007). In such organisms, phenological responses result from the influence of climatic parameters on physiology without important decision making processes (Both et al. 2009). On the contrary, bird breeding times are thought to be the result of decision making involving environmental information gathering (Both et al. 2009; Thomas et al. 2010). Indeed, laying dates should occur so that maximal resource requirements of the offspring match the resource abundance peak (Visser et al. 2006). Although temperature (Visser et al. 2009) and even solar activity (Visser and Sanz 2009) have been shown to directly influence laying dates in the Great Tit (Parus major) , more complex environmental cues particularly involving vegetation development, have also been studied

(Bourgault et al. 2006; Bourgault et al. 2009; Thomas et al. 2010). There is now accumulating evidence for birds, that a lack of phenological response is detrimental for populations. The resource match/mismatch hypothesis (Cushing 1990) offers an interesting framework to study the mechanisms underlying this relation because replaces species within food webs and stresses the importance of inter specific relations. The absence of phenological trends has indeed been related to steeper population declines in migratory species (Both et al. 2006; Moller et al. 2008) while weaker phenological responses of the breeding time to spring temperatures are also correlated to lower population growth rates in a subset of 20 common passerine species (Moussus et al. submitted). The purpoise of the present study is to look for potential correlates of a species ability to track climate fluctuations efficiently in order to identify groups of species susceptible of suffering most from the current climatic changes, which are predicted to amplify during the next decades (IPCC 2007). Because the predicted climatic changes not only consist in a linear increase in mean temperatures but also in an increase in climate variability (IPCC 2007), the timing of resource abundance peaks could become lesser predictable in the future. Two different types of constraints could limit species efficiency in tracking phenological changes in their environment. First, a number of life-history traits relate directly to the organization of species lifecycles and set constraints on the breeding phenology. Among these traits, species migration strategy could account for species variable phenological adjustment capacities (Jones and Cresswell 2010). Indeed, if the timing of the breeding environments become increasingly variable and the tracking of such variability involves sensitivity to local cues, it can be expected that migrant species, especially transsaharan migrants should be less able to time their breeding phenology in relation with meaningful variables such as spring temperature on their breeding grounds (Gwinner 1996; Both 2010). Moreover, previous work has shown that migration strategy has a strong phylogenetical inertia (Bohning-Gaese and Oberrath 1999). Besides migration strategy, the number of brood a species raises during one breeding season could also be related to species ability to track climate fluctuations, as the reproductive output of multi brooded species could be less dependent on the match between offspring requirements and the abundance peak of a single group of resources (Jiguet et al. 2007). The second type of constraints on phenological adjustment emerges the ecological niche history. Gathering information concerning the timing of the breeding environment should require important cognitive abilities. Yet such complex information gathering systems are unlikely to be uniformly distributed among species because of evolutionary contingence (Dall and Cuthill 1997). Species which evolved a broad ecological niche (Hutchinson 1957), the so called generalist species, tend to have more developed information tracking systems given the variety of resources they can exploit (Dall and Cuthill 1997). Such species have been shown to cope better with environmental changes than specialist species with narrower ecological niches (Fischer and Stocklin 1997; Kotze and O'Hara 2003; Julliard et al. 2004; Munday 2004). Niche width could thus correlate positively with species ability to adjust their breeding phenology to annual climatic fluctuations. In this study, we estimate the phenological adjustment capacity (PAC) of the breeding time of 20 common passerine species to late winter and spring temperature averages. We use the data originating from the French Constant Effort Site ringing scheme (CES) to compute the phenology of the relative proportion of juveniles in total capture over the 1989-2008 period. We then use the estimated PAC to look for correlations with species ecological and physiological features namely species migration distance, average annual brood numbers, diet, brain size and ecological niche breadth.

Materials and methods

Bird ringing data

Data originate from the French Constant Effort Site Program (CES) (Julliard, Jiguet and Couvet, 2004). CES are standardized bird ringing schemes using mist nets during the breeding period. Standardization on CES relies on a fixed position and number of nets used per site (between 10 and 50), and on a fixed number and similar dates of capture sessions per site (usually between three and five, depending on the site, with dates ranging from the beginning of May to the end of July, and covering at least two months for a given site). The scheme started in 1989 and the data used in this study cover the period 1989-2008.

In the field, each captured bird is individually ringed to avoid double counting, and the species and age (breeding adults or young of the year) are determined unambiguously from plumage (including pattern of wear) by experienced volunteer bird ringers. All data for which there was uncertainty as to the age of birds were excluded (<1%). Over the 20-year period the data were collected from 216 CES sites representing 1012 site-years. Species for which adults and juveniles were captured each year throughout the study period were included in the study. Thus 20 species were considered for a total of 131588 captured birds [Acrocephalus scirpaceus (n=11715), Aegithalos caudatus (n=3926), Certhia brachydactyla (n=926) , Erithacus rubecula (n=10904), Fringilla coelebs (n=2522), Hippolais polyglotta (n=2967), Luscinia megarhynchos (n=4741), Cyanistes caeruleus (n=5707), Parus major (n=12493), Poecile montanus (n=1298), Poecile palustris (n=1293), Phylloscopus collybita (n=12672), Phylloscopus trochilus (n=2937), Prunella modularis (n=5167), Sylvia atricapilla (n=24969), Sylvia borin (n=4035), Sylvia communis (n=5044), Troglodytes troglodytes (n=2976), Turdus merula (n=12149) and Turdus philomelos (n=3147)].

Estimating a Breeding Time Index

For each species and each year, a Breeding Time Index (BTI) was estimated using a curve fitting method (Moussus et al. 2009). The main features of this method will be described here but for further details concerning the algorithm and model justification please refer to (Moussus et al. 2010). It is assumed that seasonal distribution in the proportion of juveniles within total captures reaches an inflexion point and that the shape of this distribution remains constant for different years. Under these assumptions seasonal distributions in the proportion of juveniles within total captures for two different years only differ in their timing (i.e. they match if a certain temporal translation is applied to one of them). This method aims to estimate a temporal shift necessary to make two different year's distributions match using an iterative algorithm. To achieve this, numbers of captures of juveniles and total captures were summed over all CES sites per species per year and per day (in days after 1st April). We will illustrate the functioning of the method with an example, the estimation of the temporal shift in timing of breeding of the Great tit (Parus major) in 2006 and 2007. In this case 2007 is set as the reference year and 2006 will be the year for which data are iteratively temporally shifted until they match the data of 2007. This is done by fitting the following Generalized Additive Mixed effects Model (GAMM) to the capture data of both years (2006 and 2007 for example): (Number of juveniles, Number of Adults)~ spline function (Date + t) with a Binomial error and where t is worth 0 for the 2007 data (set as the reference) and ranges between -30 and 30 days by 1-day increment for the 2006 data. To account for between years variations of the overall productivity, year was considered as a random categorical variable in the GAMM. The fit of each model corresponding to each value of t is monitored by its Akaike Information Criterion (AIC) (Akaike 1981). Thus for one comparison 61 AIC values are recorded. As the 61 models have the same number of parameters, minimizing AIC is equivalent to maximizing likelihood. This is achieved by fitting a quadratic regression ($AIC \sim t + t^2$) using the 10 AIC values around the smallest local minimum of AIC versus t function. If a is the second degree coefficient, b the first degree coefficient and c the intercept of the regression, then the AIC as a function of t is minimized for $t_{min} = -b/2a$ which is considered as an estimation of the temporal shift between the two breeding seasons. Moreover, the standard error of this estimation is given by the second derivative of the log-likelihood and is worth 1/a. For each year, temporal shifts were estimated with all the other years. Rarely, the GAMM fails to converge and the estimation of the phenological shift between the two compared years cannot be produced directly (167 out of 7600 estimations). These gaps were filled by recalculating the shifts using linear combinations of other available shifts. For example, if the temporal shift between year 2006 and 2007 could not be estimated for one species but the shifts between 2006-2003 and 2003-2007 were available, then the shift between 2006 and 2007 was calculated as the sum of shifts 2006-2003 and 2003-2007. All possible linear combinations involving two shifts were used and the reconstructed value was treated as the average of the sums. Eventually for each species and each year, the Breeding Time Index (BTI) was defined as the average temporal shift between one year and the others. Thus it is the relative anomaly in timing of breeding across the 1989-2008 period.

Estimating species phenological adjustment to temperature

For each species the Phenological Adjustment Capacity (PAC) to climate was defined as the slope of the temperature effect in a Generalized Linear Model (GLM) relating the BTI with temperature and linear year. Because all the phenological shifts were not estimated with the same accuracy, the inverse squared standard estimation errors of the BTI were used as weights in the regressions.

Climatic data

Temperature data were obtained from the website of the European Climate Assessment and Dataset (ECAandD) (http://eca.knmi.nl/). The monthly mean daily temperature data of 57 meteorological stations located across the entire country were averaged to produce the climate variable (Temp) used in the study. Temp was defined as the average mean daily temperature from January to May. A large temporal window for the temperature averages was chosen deliberately in order to limit the number of tests. Indeed, the breeding times of a majority of species seem to occur earlier when late winter or early spring temperatures are higher. This result was expected since numerous previous studies bring evidence that laying dates are related to climatic variables within this time period (Crick and Sparks 1999; Both and Visser 2001; Visser et al. 2006; Both and te Marvelde 2007). The focus of this study was not to identify precisely the best fitting temporal window for each species but to find ecological correlates to the ability of these species to adjust their breeding phenology. In this respect, the climatic temporal window was defined broadly so that it could comprise the relevant information for all species. Moreover, if the study had been performed with the best fitting temporal window for each species, the interpretation of the results would not have been straightforward. We assume that this large temporal climatic window encompasses information regarding the timing of all the considered species.

Defining explanatory variables

We assumed that the potential drivers for species PAC belonged to two very different categories. The first category of potential predictors for species PAC relates to the life-history traits which are directly involved in species lifecycle, particularly those which directly influence the timing of breeding. Thus the mean annual number of broods was considered (Brood) and taken from Jiguet et al. (2007). Species migratory strategy (MigrDist) was included in the study as the average log-distance between breeding and wintering grounds of the French breeding population based the French ringing database (Jiguet et al. 2007).

The second category comprises features the relations between species and their environment. Thus we tested the relations between the PAC and various continuous specialisation indices: first a habitat specialisation index (SSI) calculated as the variation coefficient (standard deviation/average) of a species densities among 18 habitat classes (Julliard et al. 2006) using the French Breeding Bird Survey (BBS) counts. This habitat specialization index has been shown to predict large scale population trends of common bird species in France (Julliard et al. 2004). This index represents a broad measure of species realized ecological niche at the scale of a country.

Species thermal range which represents a Thermal Specialisation Index (TSI) as it measures a species thermal niche width, as the difference between the thermal maximum and thermal minimum (mean spring/summer temperature of 5 percent hottest/coldest atlas breeding cells in Europe; (Hagemeijer WJM 1997; Jiguet et al. 2006).

Species diet could also influence PAC. Indeed, it is possible that species relying on multiple resources like omnivorous species have better PACs than species relying on fewer resource types. Thus diet (as insectivorous or omnivorous, Diet) was also included in the set of explanatory variables and was taken from Gregory et al. (2007).

Lastly, several studies suggest that phenological adjustment in birds is based on the gathering of environmental cues providing information on the timing of the species resources. It is likely that such information gathering systems relate to species cognitive abilities (Bourgault et al. 2009; Thomas et al. 2010). To account for such effects, the residuals of brain mass against body weight, both variables available from Sol et al. (2010), were extracted and considered as a proxy for species cognitive abilities (BrainMass). Brain mass was not available for two species in the dataset, the Melodious Warbler (Hippolais polyglotta) and the Short-toed Treecreeper (Certhia brachydactyla).

Statistical analyses

Treating species as independent replicates would not be correct given their phylogenetic relatedness (Harvey et al. 1991). Thus it is possible that some explanatory variables might be very similar between closely related species. To take phylogenetic relatedness into account in our dataset, we used the generalised least squares phylogenetic comparative method. We used package “ape” of the R software (R Development Core Team 2008) to run the GLSs assuming a Grafen correlation structure (Grafen 1989) for the model dependence because branch lengths were not available (and therefore all set to 1). The phylogeny used to build the tree was taken from (Jonsson and Fjeldsa 2006), see appendix 1 for the phylogenetic tree used in this study). First, explanatory variables were tested alone in the GLSs. The effects of those variables with significant contributions to species PAC were then tested adjusted to each other. The inverse squared standard estimation errors of the PACs were used as weights in the GLSs. The relationships between the different explanatory variables were investigated using the same approach.

Lastly, there is a distinction between finding the best model to describe the data and drawing inferences about the likely causality of variables, and dealing with multicollinearity is difficult in single-model approaches. A possible solution is hierarchical partitioning, which uses all models in a regression hierarchy to distinguish those variables that have high independent correlations with the dependent variable (Chevan and Sutherland 1991). We therefore also analyzed our data with hierarchical partitioning (Mac Nally 2002) using the package “hier.part” of the R software (R Development Core Team 2008). The probabilities of independent contribution of the predictors shown to have a significant effect on PAC in the GLS approach were assessed with z-scores obtained using 1000 randomization (and R^2 as the goodness of fit measure).

Results

For 15 species out of the 20 included in the study, the Breeding Time Index was negatively correlated with average temperatures from January to May although this relation was significant for only 3 species namely the Long-tailed Tit ($F_{1,17}$=13.41, P=0.002), the Great Tit ($F_{1,17}$=6.50, P=0.02) and the Winter Wren ($F_{1,17}$=9.39, P=0.007), see table 1. There were significant relations between the potential predictors considered for species PAC. Indeed, brain mass residuals were negatively related to log-transformed migration distance ($F_{1,16}$=4.95, P=0.04, see figure 1a). Species habitat specialization index was negatively correlated to species thermal niche breadth ($F_{1,18}$=12.46, P=0.002, see figure 1b). Thus, habitat specialists are also thermal specialists because a high habitat specialization index refers to a narrow habitat niche. Log-transformed migration distance was significantly correlated to species adjustment capacities. Indeed, species wintering further away from their breeding grounds are less able to time their breeding cycle in relation with spring temperature ($F_{1,18}$=39.85, P<0.001, see figure 3b). The mean annual brood number was not significantly related to species PAC ($F_{1,18}$=0.95, P=0.34). Species niche habitat and thermal niche breadth measures were related to the PAC as species with wider thermal ranges and low habitat specialization indices were better able to cope with climatic variability (TSI: $F_{1,18}$=18.14, P<0.001; SSI: $F_{1,18}$=4.90, P=0.04 see figure 3a and 3d). Species with larger brain mass residuals were significantly more able to adjust their breeding phenology ($F_{1,16}$=5.14, P=0.04, see figure 3c) while there was no evidence that PAC was influenced by species diet ($F_{1,18}$=0.74, P=0.40). Because of the correlations between PAC predictors described here above (between both niche breadth measures and between log-transformed migration distance and brain mass residuals), only the best univariate PAC predictors were kept in a multiple GLS model, thus log-transformed migration distance and thermal niche width which effects on species PAC remained significant (see table 2). Hierarchical partitioning of the variance of species PAC confirmed the overlap between thermal niche width measures and between log-transformed migration distance and brain mass residuals (MigrDist: R^2=0.40, Z-score=4.83, P<0.001; TSI: R^2=0.13, Z-score=1.02, P=0.15; SSI: R^2=0.09, Z-score=0.35, P=0.36; BrainMass: R^2=0.06, Z-score=0.02, P=0.49).

Discussion

Climate variability is going to increase during the next century. Thus the frequency of extremely mild winters and hot springs will increase as well as the frequency of cold episodes (IPCC 2007). Thus the phenology of birds breeding environment should become increasingly variable and difficult to anticipate. All species should not be able to track these increasing fluctuations similarly. This study identifies migration distance as the main ecological correlate of species ability to time their breeding cycle in relation with temperature on their breeding grounds. All five species for which the PAC was positive are transsaharan migrants. Migratory species have long been considered as a group particularly vulnerable to climate change especially to resource mismatching (Sanderson et al. 2006; Jones and Cresswell 2010). Indeed, because the regional patterns of climate fluctuations are different (IPCC 2007), the rate of climate change on their wintering grounds can differ markedly from the one on their breeding grounds (Jones and Cresswell 2010). Yet migration phenology sets constraints on the breeding phenology in such species. In the Pied Flycatcher (Ficedula hypoleuca), laying date has advanced over the past two decades but the selection differential towards earlier laying, and the absence of any temporal trend in migratory return dates suggest that migration phenology impairs adequate breeding responses to the local increase in temperatures (Both and Visser 2001). At least two different mechanisms can help understanding such phenological inflexibility in long distance migrants. First, a number of studies show that migration timing is controlled endogenously by daily and circannual rhythms (Berthold 1984; Gwinner 1996) and relate to environmental information that is not related to climate change such as photoperiod (Both 2010). Such determinism is more pronounced in species wintering close to the equator because in these areas, environmental constancy does not provide valuable timing cues to the birds (Gwinner 1996). The wintering areas of the six transsaharan migrant species included in this study, namely the Reed Warbler, the Common Withethroat, the Garden Warbler, the Willow Warbler, the Melodious Warbler and the Common Nightingale comprise equatorial regions although the birds breeding in France might rather spend winter nearer to the tropics. Thus, these species could time their migratory return based on such non informative cues and their laying date could thus not relate to the climate on their breeding grounds. The second mechanism which could impair long distance migrant species to adjust their breeding times to local climate also relates to meteorological constraints during their journey back to their breeding grounds. In order to achieve such long return journeys, long-distance migrants rely on different stopover sites where they refuel before heading towards their breeding grounds (Saino et al. 2007). Climatic conditions might show substantial inter annual variations on these sites, thus altering the quality and quantity of resource which can delay the departure of the birds. Moreover, degraded meteorological “en route” can also force birds to stop (Tottrup et al. 2008). All climatic conditions the birds experience during their journey do not obviously relate to the climate conditions on their breeding grounds and could thus act as severe constraints on phenological adjustment of the breeding time to climate fluctuations (Marra et al. 2005; Both 2010). Although large-scale climatic coupling might to some extent exist between Africa and Europe as it has been suggested in one study (Post and Forchhammer 2002) and investigated in another one (Saino and Ambrosini 2008), such phenomena should only provide migrants with very rough information. But in a context of rapid and uneven climate change, such information systems could become inefficient on a relatively short term and the climatic obstacles faced during migratory stopovers could also see their frequency increase.

Species with smaller brain mass residuals had reduced phenological adjustment capacities to climate on their breeding grounds. There is accumulating evidence that cognitive abilities are related to population trends in birds (Sol et al. 2007). In British birds, long term population growth rates were related to brain size and more specifically to telencephalon size (Shultz et al. 2005). Such structures may represent valuable surrogates for species abilities to respond behaviorally to large-scale environmental changes by means of behavioral flexibility facing novel resources or novel environments as suggested by the relation between relative brain size and invasion success in birds and mammals (Sol et al. 2005). Thus, in a changing environment or when facing harsh environmental conditions, species with higher cognitive abilities seem to suffer less. Yet the significant relation between brain mass residuals and log-transformed migration distances and the fact that we found no independent contribution of brain mass residuals to the PAC rather points out an underlying mechanism for the poor PAC of long-distance migrants. Indeed, previous work has shown that migrant species have smaller brain sizes than resident species (Sol et al. 2010). Contrary to resident species which have evolved costly cognitive strategies to cope locally with seasonality and climate fluctuations, migrants face these issues by leaving inhospitable grounds which probably involved the development of different costly physiological abilities. Indeed, whereas migratory species do not face adverse winter conditions on their wintering grounds, this is the case for resident species which often have to change resources. Such cognitive abilities could then be useful when timing the breeding phenology in relation with local climate (Sol et al. 2010). Different evolutionary pathways could have lead to such differences. One of these hypothesis involves trade-offs between cognitive functions and the migratory behavior for which specific physiological abilities are required (Sol et al.

2010). The cost of developing these physiological capacities could now outweigh the benefits they provide to migratory species in the context of a rapidly changing and increasingly unpredictable environment. The high degree of phylogenetical inertia of the migratory behavior could rapidly lead to important declines in long distance migrants because of a lack of response to the current directional selection, and could well account for part of their current observed declines (Sanderson et al. 2006; Moller et al. 2008).

The last important predictor of species PAC was their ecological niche breadth. Thus, species with wide thermal or habitat niches, in other words ecological generalist, were more able to track climate fluctuations in their breeding phenology than ecological specialists. The pattern of ecological generalists better able to cope with ongoing global changes has been ascertained by a number of studies concerning plants (Fischer and Stocklin 1997), fish (Munday 2004), insects (Kotze and O'Hara 2003; Goulson et al. 2005), birds (Julliard et al. 2004) and mammals (Fisher et al. 2003). It is also known that habitat, as well as thermal generalists suffer smaller population declines than both habitat and thermal generalists (Jiguet et al. 2007; Jiguet et al. 2009). Species with wide thermal ranges are also able to face extreme climatic events such as heat waves (Jiguet et al. 2006). Ecological specialization is thought to have evolved in stable and highly predictable environments (Futuyma and Moreno 1988; Kassen 2002) as there are true advantages for this ecological strategy in such environments (Egan and Funk 2006). Indeed, ecological generalism involves the development of complex information gathering systems which costs can outweigh the benefits in environments where resources abundance and distribution are predictable (Dall and Cuthill 1997; Tosh and Ruxton 2008). Moreover, living on a variety of resources requires the development of physiological abilities such as digestive flexibility (Futuyma and Philippi 1987). Thus the general pattern is that generalist species will be favored during substantial changes in the environment or in highly heterogeneous environments where specialist species are expected to decline. Our results show that different forms of flexibilities are to some extent correlated. This suggests the existence of an “ecological flexibility syndrome”, where on average habitat generalists are thermal generalists and phenological generalists (Clavel et al. in press). This hypothesis tends is reinforced by the significant correlation found between habitat and thermal niche breadth and by the hierarchical partitioning of variance analysis which does not disentangle the both effect on species PAC. Moreover, habitat generalists, thermal generalists and phenological generalists currently seem to experience smaller declines on the long term (Julliard et al. 2004; Jiguet et al. 2009). Given the predictions under which such generalists should perform better in changing environments (Futuyma and Moreno 1988), their current fate brings evidence about how intensively global changes impact ecosystems. Moreover, because the gradual changes in phenology (Moller et al. 2008) as well as the PAC (Moussus et al. in prep) have both been related to species large scale population growth rates, these results provide evidence for one of the numerous putative mechanisms by which functional biotic homogenization is currently contributing to alter plant and animal communities (Devictor et al. 2007; Clavel et al. in press).

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Tables

Table 1. Phenological Adjustment Capacities (PAC) and the different explanatory variables used in this study for 20 common passerine species. SSI : Species habitat Specialization Index, TSI : Thermal Specialization Index, MigrDist : log mean migration distance, Brood : average annual number of broods and Diet.

Species	PAC (SE)	BrainMass	SSI	TSI	MigrDist	Brood	Diet
Acrocephalus Scirpaceus	1.26 (1.83)	-0.097	2.19	11.02	3.65	1.2	Insectivorous
Aegithalos caudatus	-6.6 (1.80)	-0.010	0.62	13.06	-0.89	1	Insectivorous
Certhia brachydactyla	-2.58 (2.20)	NA	0.62	11.36	0.05	2	Insectivorous
Cyanistes caeruleus	-2.34 (1.95)	0.098	0.35	13.44	1.24	1.2	Omnivorous
Erithacus rubecula	-1.3 (1.15)	0.010	0.48	14.34	2.03	2	Insectivorous
Fringilla coelebs	-1.58 (2.69)	-0.003	0.27	14.82	1.39	1	Omnivorous
Hippolais polyglotta	1.37 (1.47)	NA	0.72	11.66	3.70	1	Insectivorous
Luscinia megarhynchos	1.15 (0.80)	0.008	0.47	10.72	3.58	2	Insectivorous
Parus major	-2.68 (1.05)	0.196	0.29	14.99	1.29	1.5	Omnivorous
Parus montanus	-1.99 (3.07)	0.247	1.39	11.88	-1.00	1	Omnivorous
Parus palustris	-0.76 (2.25)	0.031	0.99	11.52	0.33	1	Omnivorous
Phylloscopus collybita	-2.06 (1.45)	-0.127	0.46	13.22	3.07	2	Insectivorous
Phylloscopus trochilus	0.87 (1.07)	-0.228	1.12	12.27	3.68	1	Insectivorous
Prunella modularis	-2.42 (1.58)	0.0004	0.50	13.00	1.90	2	Insectivorous
Sylvia atricapilla	-1.36 (1.20)	-0.023	0.32	13.82	2.99	1	Omnivorous
Sylvia borin	0.25 (1.37)	-0.054	0.69	13.74	3.72	1	Omnivorous
Sylvia communis	-0.49 (1.34)	-0.046	0.65	12.73	3.60	1	Omnivorous
Troglodytes troglodytes	-5.24 (1.71)	-0.017	0.37	14.93	1.11	2	Insectivorous
Turdus merula	-1.13 (2.13)	-0.061	0.23	14.46	1.88	2.5	Omnivorous
Turdus philomelos	-2.83 (2.94)	0.075	0.40	13.35	2.70	2.5	Omnivorous

Table 2. Effects of different explanatory variables on species Phenological Adjustment Capacity (PAC) to spring temperature. The relationships between PAC and the different variables were investigated using Generalized Least Squares (GLS) models. The effects of the variables significantly related to PAC were then tested adjusted to each other.

Explanatory Variable		**F**	**df**	**P**	**slope (SE)**
SSI		4.90	1.18	0.04	2.36 (1.06)
TSI		18.14	1,18	0.0005	-0.80 (0.19)
TSI	**adjusted**	8.82	1.17	0.009	-0.49 (0.16)
Brood		0.95	1,18	0.34	-1.13 (1.16)
MigrDist		39.85	1,18	<0.0001	1.29 (0.20)
MigrDist	**adjusted**	30.18	1,17	<0.0001	1.04 (0.19)
Diet		0.74	1,18	0.40	
BrainMass		5.14	1,16	0.04	-10.43 (4.60)

Figure legends

Figure 1. Significant relationships between the potential predictors of species phenological adjustment capaticity (PAC) for 20 common passerine species. (a) Relation between log-transformed migration distance and brain mass residuals and (b) between Thermal (TSI) and habitat (SSI) niche breadths. Regression lines from the GLS models are shown.

Figure 2. Relationships between the phenological responses of the breeding time to average temperatures (January-May) for 20 common passerine species and (a) the thermal range (TSI), (b) the log mean migration distance (MigrDist), (c) the brain mass residuals (BrainMass) and (d) the habitat specialization index (SSI). The regression line is shown as the four relationships are statistically significant.

Figures

Figure 1.

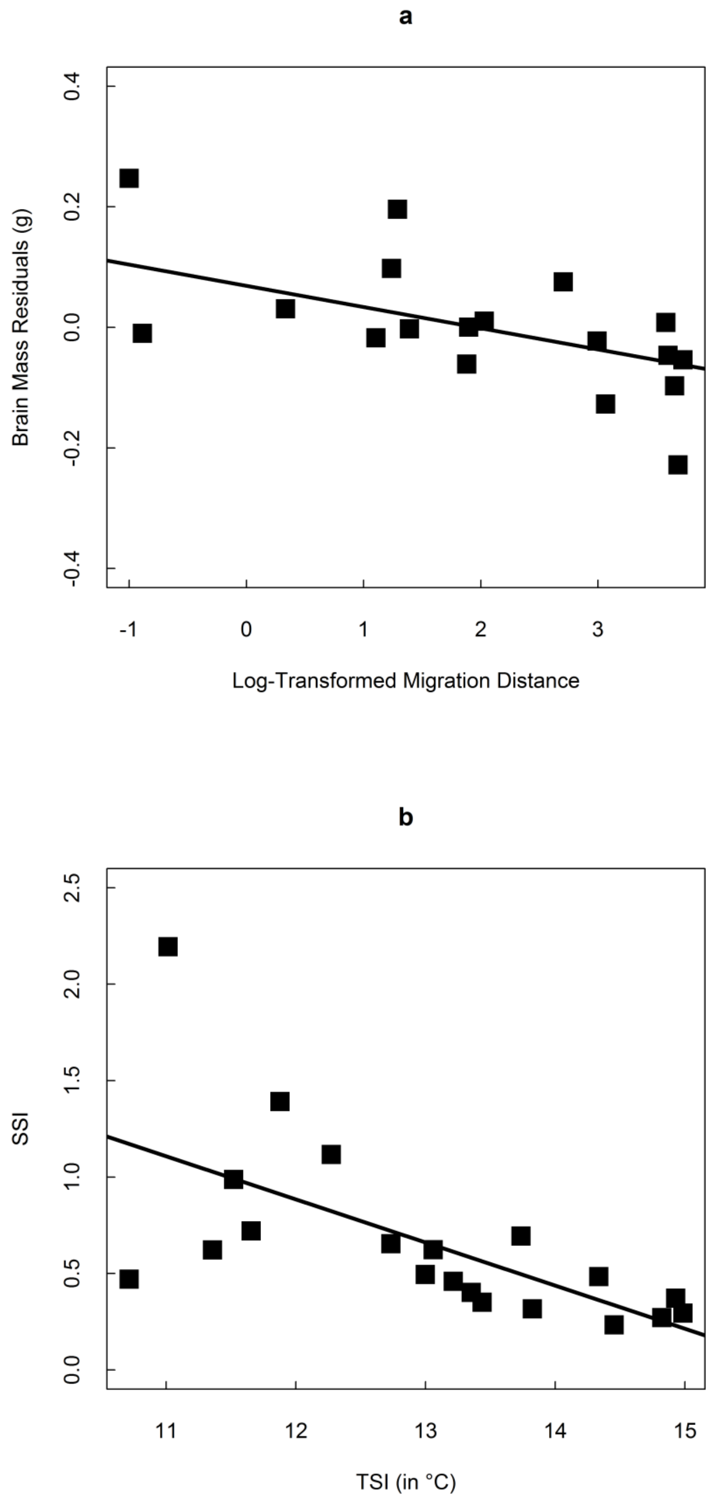
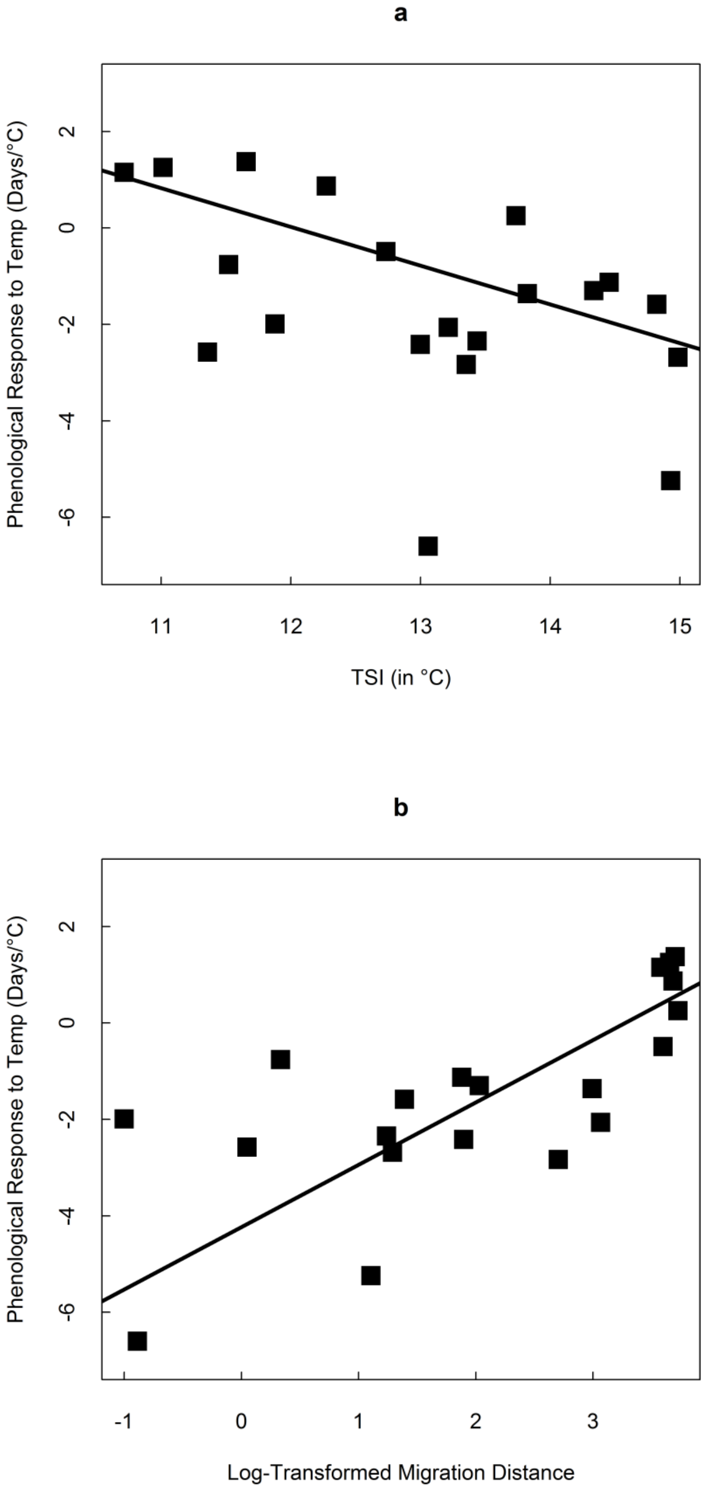
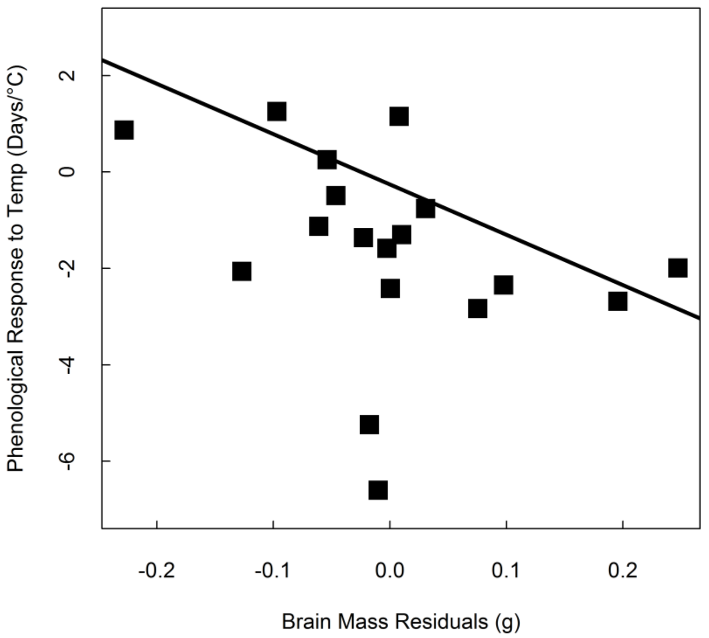


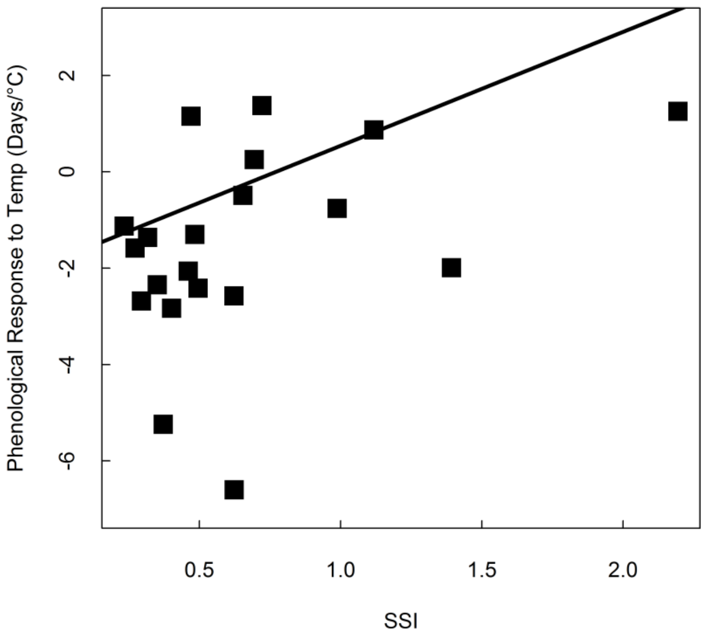
Figure 2.


a
Phenological Response to Temp (Days/°C)
2
0
-2
-4
-6
11
12
13
14
15
TSI (in °C)
b
Phenological Response to Temp (Days/°C)
2
0
-2
-4
-6
-1
0
1
2
3
Log-Transformed Migration Distance

c


Phenological Response to Temp (Days/°C)
2
0
-2
-4
-6
-0.2
-0.1
0.0
0.1
0.2
Brain Mass Residuals (g)

d


Phenological Response to Temp (Days/°C)
2
0
-2
-4
-6
0.5
1.0
1.5
2.0
SSI

Manuscrit 8

Differential sensitivity of population dynamics to climate across the distribution, a case study with the Cetti's Warbler.

Soumis à *Global Change Biology*

Differential sensitivity of population dynamics to climate across the realized climatic niche, a case study with the Cetti's Warbler.

Running title: Climatic forcing along a species distribution

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Key-words: survival, climate change, constant effort site, productivity, range shift, biogeography

Abstract

Biogeography raises increasing interest as species ranges have begun to shift and are expected to shift even more as a consequence of ongoing climatic changes. Simultaneously, the monitoring of bird demography thanks to Breeding Bird Surveys (BBS) and Constant Effort Site (CES) schemes has enabled to understand how climate drives species demographic rates at national or continental scale. Yet measuring precisely how demography varies across species climatic niche has not yet been investigated although this question is of fundamental importance to understand the mechanisms underlying species range expansions or contractions. In this study, we show how combining data from BBS, CES and species distribution models outputs provides interesting insights into the relationships between climate, position within the climatic niche and demography and apply the analysis to a sedentary warbler reaching the boundary of its current range in France (Cetti's Warbler, *Cettia cetti*). CES data from 31 sites covering the 2000-2009 period enable the estimation of annual survival rates and productivity while BBS data across the period 2001-2009 were used to produce annual abundance estimates. Species distribution models were used to estimate a Site Climatic Suitability (SCS) for the CES sites. We show that spring abundance is strongly related to annual survival rates which are themselves driven by fall and winter temperatures. The sensitivity of survival rates to temperature tended to increase along a gradient of SCS suggesting differences in the demographic regimes along the species climatic niche. These results improve our understanding of the current northward range shifts observed for many species and propose an insightful framework to combine species demography and biogeography modelling efforts which could help improving species future distributions predictions facing the ongoing climatic changes.

Introduction

The influence of climate on bird populations has raised major scientific interest over the past decade (Parmesan 2006; Visser 2008). A wide range of ecological responses to climate have been found or are predicted to occur particularly concerning phenology (Crick & Sparks 1999; Sparks *et al.* 2005; Moller *et al.* 2008; Both *et al.* 2009; Visser *et al.* 2009), geographical distribution (Popy *et al.*; Marini *et al.* 2009; Zuckerberg *et al.* 2009) and population dynamics (Beale et al. 2006; Both et al. 2006). Because climate is currently changing rapidly (IPCC 2007), there is an urgent need to understand how bird populations react to different climatic parameters along their breeding cycle (Saether *et al.* 2003). Considerable effort has been made during the past two or three decades to monitor bird populations and produce valuable abundance indicators which are used by policy makers to address the issue of a declining biodiversity (Walpole *et al.* 2010). Indeed Breeding Bird Surveys (BBS) are now running in many European countries (EBCC 2008) and allow bird population abundance to be followed at large spatial scales (Gregory et al. 2007; Jiguet et al. 2009) and abundance data have been recently used to develop a climate change impact indicator on European bird populations (Gregory et al. 2009). Nevertheless if abundance indicators represent a summarized measure of broad-scale population health, they do not provide information about the ecological and demographic processes underlying abundance variations (Grosbois et al. 2008). Constant Effort Site programs (CES) are designed to enable the computation of population demographic rates on the long term and at regional or national geographical scales, by building capture-mark-recapture databases from ringed birds to further estimate demographic parameters. Thus average survival and productivity of common passerine species can be studied (Peach *et al.* 1996; Julliard *et al.* 2004b; Grosbois *et al.* 2006). The recent development of multi population dynamics models associated with an increase in computation power has provided insightful tools to analyze ringing data originating from numerous sites as it is the case for CES datasets (Grosbois et al. 2009). Moreover, Bayesian hierarchical modeling has been applied to abundance and capture-mark-recapture datasets allowing an integrated population modeling (Besbeas et al. 2002; Freeman et al. 2007a). Such modeling approaches have enabled researchers to quantify the relative contributions of productivity and survival to species abundance (Freeman et al. 2007b; Gauthier et al. 2007). Once the most influential demographic processes on species abundance are known, it is possible to look for climate influences on these processes (Grosbois et al. 2008). Examples of studies addressing these questions show that the importance of breeding success and survival are variable from one species to another (Siriwardena et al. 2000) and that climate influences on these demographic rates also highly depend on the species considered (Peach et al. 1999; Robinson et al. 2007a). The sensitivity of species demographic rates to climate variables can vary across their distribution ranges. Indeed populations established at the edge of a species' geographical range, can have different population dynamics from those populations located in the core range of the distribution (Mehlman 1997; Angert 2006, 2009).

In this study we address the issue of the demographic mechanisms by which climatic variables shape the abundance of a sedentary passerine bird. The Cetti's Warbler (*Cettia cetti*) is an insectivorous passerine widespread along the Mediterranean coast and across the Iberian peninsula (Hagemeijer WJM 1997). Its breeding distribution extends northwards along the Atlantic coastline and the Channel to the Netherlands and southern England. The French part of the distribution lies close to the edge of the species northwards and continental extension. Unlike its European Warbler relatives, the Cetti's Warbler is mainly sedentary, though it is currently extending its distribution northwards (Balmer 2005; Robinson et al. 2007b). Thus, one aim of this study is to provide demographic mechanisms potentially driving distribution changes at the range boundary. The other purpose of this work is to examine the influence of climate on Cetti's Warbler survival and breeding success and to examine whether the sensitivity of the most influential demographic rates changes across the French range. To our knowledge the relation between demography and its climatic drivers and the position of the species within its climatic niche remain to be addressed. It is known that Cetti's Warbler populations suffer important losses during extremely cold winters (Robinson et al. 2007b). However, the mechanisms underlying this trend have never been investigated, and a linear effect of winter climate on demographic rates has yet to be evidenced. Using the French Constant Effort Site ringing scheme, we estimate Cetti's Warbler productivity and annual survival between 2001 and 2009. Cetti's Warbler large scale's abundance indices are derived from the French Breeding Bird Survey scheme over the same time period. First, the relative contributions of survival and productivity to abundance variations are estimated. Given its diet and its wintering strategy we predict survival to be the most influent demographic driver of population abundance while productivity is predicted to play only a minor role. Second, the spatio-temporal pattern of survival rate sensitivity to climate is investigated at the northern boundary of Cetti's warbler's distribution range.

Materials and Methods

Ringing data

Data originate from the French Constant Effort Site Program (CES) (Julliard et al. 2004b). CES are standardized bird ringing schemes using mist-netting during the breeding period. Standardization on CES relies on a fixed position and number of nets used per site (between 10 and 50), and on a fixed number and similar dates of capture sessions per site between years (usually between three and five, depending on the site, with dates ranging from the beginning of May to the end of July, and covering at least two months for a given site). The scheme started in 1989. The data used in this study cover the period 2000-2009. In the field, each bird captured is individually ringed to avoid double counting, and the species and age (breeding adults or young of the year) are determined unambiguously from plumage by experienced volunteer bird ringers. This represented 31 sites and a total of 1127 individually ringed birds and 167 recaptures. The sites were distributed across the entire French part of the Cetti’s Warbler’s range (See Figure 1).

Abundance data

The French BBS program is based on volunteer ornithologists counting birds in spring on permanent plots. Surveyed sites are 2 × 2 km squares randomly selected within a 10-km radius around a locality specified by the volunteer. Random selection (one of *c.* 80 possible squares) ensures that surveyed habitats closely match their actual availability (Jiguet et al. 2007). In each square, observers carry out 10 point counts (separated by at least 300 m) of 5 min duration each. Counts are done twice in spring (from 1st April to 8th May, then from 9th May to end of June) in order to detect both early and late breeders, with 4-6 weeks between both counts. For a given site, counts are repeated yearly by the same observer at the same points, on approximately the same date (± 7 days within April to mid-June), and at the same time in the day (± 15 min). Here, maximum counts (between both sessions) for the 10 points within each square were summed before analysis. Cetti's Warblers were contacted at least once on 258 sites (See figure 1).

Climatic data

Mean daily minimal temperatures were used as climatic covariates to investigate the annual variations of the most important demographic rate accouting for Cetti's Warblers spring abundance variations. Data were downloaded from the website of the European Climate Assessment & Dataset (ECA&D) (http://eca.knmi.nl). For each temperature index, climate data from 8 meteorological stations were averaged (Dunkerque, Abbeville, Cap de la Hève, Nantes, Poitiers, La Rochelle, Nîmes and Bastia see figure 1 for the locations). These meteorological stations are located across the entire French range of the species. In order to limit the number of tests and therefore the number of spurious correlations with climatic variables, a single broad climatic predictor was chosen, the average daily temperature from October to May.

Estimating Site Climatic Suitability

The current climate suitability index of the species across its distribution was obtained through climate suitability modeling techniques. Such techniques require presence - absence data and climatic variables across the species distribution. The presence - absence data was obtained by geo-referencing and digitizing maps from the handbooks of the birds of the Western Palearctic (BWPi 2006). As for the climatic variables needed for the niche modeling, we used the following eight variables: (1) annual mean temperature, (2) mean temperature of the warmest month, (3) mean temperature of the coldest month, (4) temperature seasonality, (5) annual precipitation, (6) precipitation of the wettest month, (7) precipitation of the driest month and (8) precipitation seasonality. The seasonality is the coefficient of variation of the monthly means. These variables were derived from the monthly mean temperatures and precipitations over the intervals 1961-1990 (http://worldclim.org) and interpolated (bilinear interpolation) to a 0.5°×0.5° latitude×longitude grid over the Western Palearctic. Temperature and precipitation are expected to impose direct or indirect constraints on bird distributions (Root 1988 (Araujo et al. 2009). We realized the projections for seven different niche-based modeling techniques, performed with the BIOMOD computational framework (Thuiller et al. 2009): (1) generalized linear model (GLM), a regression method with polynomial terms for which a stepwise procedure is used to select the most significant variables, (2) generalized additive model (GAM), another regression method with four degrees of freedom and a stepwise procedure to select the most parsimonious model, (3) classification tree analysis (CTA), a classification method running a 50-fold cross-validation to select the best trade-off between the number of leaves of the tree and the explained deviance, (4) artificial neural networks (ANN), a machine learning method, with the mean of three runs used to provide predictions and projections, as each simulation gives slightly different results, (5) multivariate adaptive regression splines (MARS), a regression method, (6) generalized boosting model (GBM), a machine learning method which combines a boosting algorithm and a regression tree algorithm to construct an 'ensemble' of trees, and (7) Random Forest (RF), a machine learning method which is a combination of tree predictors such that each tree depends on the values of a random vector sampled independently and with the same distribution for all trees in the forest. In order to evaluate the predictive performance of a species distribution model, for each species, we used a random subset of 70% of the data to calibrate the model, then used the remaining 30% for evaluation, using a threshold independent method, the area under the relative operating characteristic curve (AUC)(Fielding & Bell 1997). The data splitting approach was then replicated five times from which we calculated the mean AUC of the cross-validation. The final calibration of every model for making predictions used 100% of available data. We then used an ensemble forecast technique which aims at taking into account the variability among species distribution models and climate models, in order to get the central tendency (Araujo & New 2007; Thuiller 2007). The current consensus distribution of the Cetti's Warbler was obtained by calculating the weighted mean distribution: the models were ranked according to their predictive performance, and a decay of 1.6 gave the relative importance of the weight (Coetzee et al. 2009; Marmion et al. 2009). From the current modeled distributions, the climatic suitability index for each CES site was extracted and hereafter named Site Climatic Suitability (SCS).

Modeling annual survival

Annual capture histories of each of the 1127 birds were built, then summarized into site specific so-called M-arrays (Williams et al. 2002). For each site the M-array is a (n-1) x n matrix where n is the number of years the site was monitored. The first column of the M-array is the number of individuals released each year, and subsequent columns are based on terms we denoted $a_{i,j}$ i.e. the number of birds that were released at year i and first recaptured at year j. The likelihood of the M-array can be expressed as a product of multinomial distributions:

$$\prod_{i=1}^{n-1} \mathrm{M_i}(\mathrm{q_1}, \dots, \mathrm{q_{n-1}}, q_0, N_i)$$

where M_i is the multinomial distribution modeling the fate of individuals released at year *i*, N_i is the number of released individuals at year *i*, q_j the probability of individuals released at year *i* to be first recaptured at year *j* and q_0 the probability of individuals released at year *i* to never be recaptured. The *q* probabilities are complex non-linear functions of survival and detection probabilities (e.g. (Gimenez et al. 2009)).

Survival probabilities were modeled using the following random effect model:

$$\mathrm{logit}\,(\phi_{ik}) = \log\left(\frac{\phi_{ik}}{1-\phi_{ik}}\right) = \mu_i + \alpha_k + \varepsilon_{i,k}$$

where ϕ_{ik} is the probability that an individual from site *k* survives from year *i* to year *i+1*, μ_i is a fixed effect of year *i* on survival rate ϕ_{ik} and, α_k a random effect of site *k* on survival rate ϕ_{ik} and $\varepsilon_{i,k}$ is a residual error term $\varepsilon_{i,k}$~N(0, σ^2_{error}). The α_k's and $\varepsilon_{i,k}$'s were assumed to be normally distributed α_k~N(0, σ^2_{site}) and $\varepsilon_{i,k}$~N(0, σ^2_{error}) with σ^2_{site} and σ^2_{error} a standard deviation parameters to be estimated. The potential impact of climate covariates on survival probabilities was investigated using:

$$\mathrm{logit}\,(\phi_{ik}) = \beta_0 + \beta_1 \times \mathrm{climate}_i + \alpha_k + \varepsilon_{i,k}$$

where the β's are regression parameters to be estimated. To investigate spatial patterns in the response of populations to climate, survival probabilities were modeled using:

$$\mathrm{logit}\,(\phi_{ik}) = \beta_0 + \beta_1 \times \mathrm{climate}_i + \beta_2 \times \mathrm{climate}_i \times \mathrm{SCS}_k + \alpha_k + \varepsilon_{i,k}$$

where SCS_k is the site climatic suitability of site *k*.

Detection probabilities were considered as site-specific only:

$$logit\,(p_{i,k}) = \pi_k$$

where $p_{i,k}$ is the detection probability of a given individual at year i at site k and π_k the mean detection probability at site k. We assumed that detection probabilities did not vary from one year to the other because CES protocol uses the same number of nets, the same number and the same timing of the sessions from one year to another.

Goodness of fit

Fitting models to capture-recapture data requires certain assumptions (Cormack & Jupp 1991; Lebreton *et al.* 1992). Standard goodness-of-fit testing procedures for capture-recapture data measure to what extent a model with time-dependence on both survival and detection probabilities fit the data (see (Pradel et al. 2005) for a review). Overall goodness-of-fit tests for the data of each site were performed using program U-CARE (Choquet et al. 2009). P-values associated with those tests did not show any violation of the usual assumptions, at least for those sites where enough data were available.

Setting model priors

Because site effects were treated as random effects, it was more convenient to fit capture-recapture models in a Bayesian framework (e.g. Gimenez et al. 2009). Estimation of annual survival and slopes of climate and site effects were performed using Markov Chain Monte Carlo methods (MCMC). Bayesian inference requires prior distributions for model parameters to be provided. β_0, β_1 and β_2 were given vague normal priors N(0, 1000) , π_k were given vague Uniform prior distributions U(0,1) while σ_{site} and σ_{error} , were given vague uniform priors U(0,5). Models were run with two chains for 100 000 iterations (discarding the first 50 000 as burnin). We assessed convergence by calculating the ratio of between-chain variance and within-chain variance known as R-hat (convergence was reached for R-hat < 1.1). Bayesian analyses using MCMC simulations were performed using program JAGS (available for download at http://www-fis.iarc.fr/~martyn/software/jags/ that was called from R (Team 2008).

Modeling annual productivity

Annual productivity indices for the Cetti's Warbler were estimated using a logistic regression in which the number of juveniles captured during year *i* at site *k* was assumed to follow a binomial distribution $Juv_{i,k} \sim B(Prod_{i,k}, Total\ Captures_{i,k})$ where $Total\ Captures_{i,k}$ represents the total number of Cetti's warblers captured during year *i* at site *k* and $Prod_{i,k}$ the probability of capturing a Juvenile during year *i* at site *k*. $Prod_{i,k}$ was then modeled as:

$$\text{logit}\left(Prod_{i,k}\right) = \pi_i + \rho_k + \varepsilon_{i,k}$$

where π_i is a yearly fixed effect and ρ_k is a site random effect and $\varepsilon_{i,k}$ a residual term.

Modeling annual abundance

Annual abundance indices for the Cetti's Warbler were estimated by fitting log-linear Poisson regressions to the count data. The counts at year *i* and site *k* were assumed to follow a Poisson distribution $P(\eta_{i,k})$ with

$$\log(\eta_{i,k}) = \kappa_i + \nu_k + \varepsilon_{i,k}$$

where κ_i is a yearly fixed effect, ν_k is a site random effect and $\varepsilon_{i,k}$ a residual term.

Relationships between demographic rates

Relationships between abundance and demographic rates (annual productivity and survival) were investigated using Generalized Linear Models. Because the dependent variable (abundance) was itself an estimate, linear regressions were weighted by the inverse of the squared standard deviation of abundance estimates. Linear temporal trends in demographic rates were investigated using GLMs weighted by the inverse squared standard deviation of demographic rates estimates. The significance of effects of climate, site covariates and their interactions on survival was assessed using the 95% confidence intervals estimated from the MCMC simulations.

Results

We did not observe any significant linear temporal trend in the abundance of Cetti's Warblers across the period ($F_{1,7}$=1.81, P=0.22, see Figure 2). Survival rates did not show any temporal trend through the study period ($F_{1,7}$<0.01, P=0.98, see Figure 2a) while productivity declined significantly between 2001 and 2009 ($F_{1,7}$=8.54, P=0.02, see Figure 2b). There was a very strong positive relationship between Cetti's Warbler's annual abundance and its annual survival rate ($F_{1,7}$=19.92, P=0.003, see Figure 2a). On the other hand we found no relation between annual abundance and productivity during the year preceding the counts ($F_{1,7}$=0.67, P=0.44, see Figure 2b). The main demographic mechanism influencing abundance being survival, we investigated the effect of climate on this demographic rate. Mean daily temperatures from October through May were significantly related to annual survival (slope=0.67, 95% credible interval (CI) limits [0.29; 0.96]; see figure 3). Site Climatic Suitability estimates for the 31 CES sites ranged between 0.65 and 0.95 (within the [0;1] interval). The weighted average of SCS was worth 0.79, see table 1. Investigating the variations of survival rates along the SCS gradient revealed no relationship between these rates and SCS (slope=1.17 ,95% CI [-3.35; 5.34]; see figure 4). There was a tendency for the sensitivity of survival rates to fall and winter climate to increase with Site Climatic Suitability (slope=0.18, 95% CI [-0.24; 0.63]; see figure 5). Thus climate explained survival rate variations better on high climatic quality sites.

Discussion

Demographic contributions of survival and productivity to population size

Cetti's warbler population sizes appear to be driven almost exclusively by fall and winter survival. As expected given the wintering strategy of this warbler species, productivity played only a minor role in shaping local abundance. Similar results were found for the Spotted Flycatcher (*Muscicapa striata*) for which productivity only played a minor part in the decline across Britain while survival rates - especially first-year survival - seemed much more involved (Freeman & Crick 2003). This pattern seems quite variable since other studies outline the importance of breeding success in shaping population abundances especially those suffering from the degradation of their habitat (Siriwardena et al. 2000).

Influence of climate variables on Cetti's Warbler demographic rates

Cetti's Warblers are known to suffer important losses during very cold winters (Robinson et al. 2007b). Unlike most European Warbler, it winters on its breeding grounds. Its insectivorous diet is the most important reason why low winter temperatures affect population sizes. Nevertheless, our results show that Cetti's Warbler's survival rates are linearly influenced by fall and winter temperatures. The fact that temperatures from October to May were significantly correlated to annual survival rates, suggests that population limiting by survival occurs already during fall when temperatures start to decrease. Because we did not differentiate first winter survival from adult survival it is also possible that this sensitivity be due to un-experienced first-year birds, although this is not supported by a preliminary analysis showing that the age effect on survival rates is mainly additive (data not shown). Moreover, spring temperatures also account for annual survival and breeding numbers (as counted with BBS protocols). This suggests that the temporal window immediately preceding the breeding period is of crucial importance in determining population size, probably because birds spend an important amount of energy to prepare the breeding season. Our data show no relations between annual productivity indices and climate variables. This is surprising since numerous studies have shown important breeding success variations in relation with winter or spring temperatures and rainfall (Morrison & Bolger 2002; Pearce-Higgins *et al.* 2009). A moderate decline of the species productivity was observed throughout the study period for which we did not identify any climatic driver.

Spatio-temporal variation in survival rate sensitivity to climate

Cetti's Warbler survival rates did not show clear spatial patterns. Results showed no significant alteration of survival rates towards the edge of the species climatic niche. This absence of a clear pattern has already been found previously for abundance. Indeed, no geographical covariate significantly explained abundance patterns along the British range of 22 woodland passerines (Blackburn et al. 1999) while similar results were found for the European robin (*Erithacus rubecula*) at its southern range boundary (Perez-Tris et al. 2000). However, these studies focused on geographical covariates such as easting or northing and not on a measure of the position of the site within species climatic niche. Although some degree of correlation is expected between both sets of variables, this shortcoming might have impaired the detection of geographical covariate effects on species abundance. Conversely Song thrushes (*Turdus philomelos*) and Blackbirds (*Turdus merula*) showed lower breeding success at higher latitudes (Paradis et al. 2000). The present study was carried out on a restricted portion of Cetti's Warbler breeding range. Although Cetti's Warblers are present in stable populations in the southern part of France, the species distribution includes the entire Mediterranean basin. Thus, it is possible that part of the climatic niche gradient lacks in this analysis which could have also impaired the clear detection of the climatic suitability effect on survival rates.

Survival rates tended to differ in their sensitivity to climate variables across the species French part of the breeding range. Populations living on the edge of the distribution (low SCS) tended to have less sensitive survival rates than populations located nearer to the core of the range (high SCS). Important variations of climate influence on survival rates were also detected in the Blue Tit in its Mediterranean range. In this species winter climate was not the only driver of annual survival rates (Grosbois et al. 2006). Summer climate also explained part of annual survival variations. However, a likely interpretation of our result is that the interaction coefficient between SCS and climate represents an apparent sensitivity to climate in populations located in low climatic quality sites. Indeed, this pattern would be expected if part of the species distribution, in other words its realized ecological niche, is located outside the species fundamental ecological niche (Pulliam 1988, 2000). Indeed, populations located beyond the fundamental niche could be mostly driven by Source-Sink population dynamics and experience frequent local extinctions as a result of particularly unfavorable climatic events (Dias 1996). Between the time when a species becomes locally extinct and the time when individuals originating from nearby source populations recolonize less favorable sites, survival rates are not sensitive to climate. Thus, according to this hypothesis, survival rates are predicted to be less sensitive in less suitable sites (low SCS).

Northward expansion of Cetti's Warblers

The frequency of extreme climatic events such as heat waves or cold spells is predicted to increase in the future as a result of the recent and rapid climate change. Mean temperatures - especially mean minimum temperatures - are also predicted to increase in this context. During past decades, Cetti's Warbler has markedly extended its distribution range northwards (Balmer 2005; Robinson et al. 2007b). This northward expansion is in accordance with our results showing that Cetti's Warbler abundance is mainly driven by winter climatic conditions via survival. Indeed, minimal temperatures have already started to increase in France and more generally in Western Europe (Spagnoli *et al.* 2002; IPCC 2007). Our results suggest that the ongoing climatic changes will favor the northwards expansion of Cetti's Warblers and bring evidence for the demographical mechanisms which should mainly be involved in this predicted expansion (Huntley et al. 2007). The rate at which this northward extension will occur should not only depend on climate but also on the interactions between Cetti's Warblers and other passerine species sharing similar ecological niches as well as dispersal abilities (Paradis et al. 1998).

Using Integrative population modeling to study population dynamics at broad spatial scales

Cetti's Warblers population dynamics appear to be mainly driven by annual survival and not by annual breeding success. Most studies addressing the question of the drivers of population dynamics are carried out on a single population. Therefore, generalizing results to other populations or to the species is not straightforward. In this study survival and productivity are estimated from 31 different populations scattered across the French part of the species distribution range. The development of integrated population modeling where data from completely independent sources can be combined at large spatial scales therefore offers very interesting opportunities to understand how population dynamics are driven within the global warming context (Besbeas et al. 2002; Grosbois et al. 2008; Grosbois et al. 2009). The strong relation between survival estimates and annual abundance indices calculated using a completely independent dataset shows that CES data can provide meaningful large scale survival estimates even if the monitored populations can differ markedly in their locations, and thus experience very different local environmental conditions. The importance of such data for the investigation of abundance and productivity variations had already been stated (Peach *et al.* 1996; Julliard *et al.* 2004a). It is also interesting to note that the Cetti's Warbler is far from being the most captured species in the French CES program. The small amount of ringed birds (1127 Cetti's Warblers ringed over ten years of survey and 31 sites) showed similar variations to the much larger amount of birds sampled with the BBS counts (258 sites, 2921 birds counted). Thus, our results suggest on the one hand that our sampled birds are representative of the behavior of the total northern population of Cetti's Warbler and on the other hand that such modeling approaches could be carried out on many other passerine species where much more data exists in order to identify clearer spatio-temporal patterns in demographic parameters. Such demographic gradients could then be integrated within niche modeling approaches (Araujo & Guisan 2006; Thuiller 2007) to refine the predictions of species range shifts under climatic scenarios.

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Figure legends

Figure 1. Locations of Breeding Bird Survey sites where at least one Cetti's Warbler was counted during 2001-2009 (grey circles), Constant Effort Sites where on average 5 different Cetti's Warblers were captured each year during 2000-2009 (black circles) and meteorological stations from which climate covariates were estimated (black stars).

Figure 2. Annual abundance indices of the Cetti's Warbler (*Cettia cetti*) estimated from the French Breeding Bird Survey data (dashed line) in relation with (a) annual survival rates (solid line) and (b) annual productivity (solid lines) estimated from the French Constant Effort Site Scheme. For clarity, error bars associated with abundance indices, survival rates and productivity indices are not displayed. The relationship between abundance and survival rates is statistically significant while the relation between abundance and productivity is not.

Figure 3. Relationships between annual survival rates (2001 through 2009) and mean temperature (October through May) for the Cetti's Warbler (*Cettia cetti*). For clarity, error bars associated with abundance indices, survival rates and productivity indices are not displayed. The relationship is statistically significant.

Figure 4. Markov Chain Monte Carlo simulations output for the regression coefficient Site Climatic Suitability (SCS) as a covariate of Cetti's Warbler annual Survival rates. . The estimated mean interaction coefficient is indicated by the solid line and the zero by the dashed line. The model was run for 100 000 simulations discarding the first 50 000 as burnin. Zero is included within the 95 % credible interval.

Figure 5. Markov Chain Monte Carlo simulations output for the interaction between Site Climatic Suitability (SCS) and Temperature from October through May as a covariate of

Cetti’s Warbler annual Survival rates. The estimated mean interaction coefficient is indicated by the solid line and the zero by the dashed line. The model was run for 100 000 simulations discarding the first 50 000 as burnin. Zero is included within the 95 % credible interval.

Tables

Table 1. Values of Site Climatic Suitabilities (SCS) for the CES sites considered in the study. SCS were estimated using species distribution models and an Ensemble Forecast procedure (BIOMOD) using presence/absence data from an independent dataset.

Site Climatic Suitability	Number of Sites
0.6451	5
0.6933	1
0.7472	1
0.7493	1
0.7520	3
0.7681	3
0.7813	1
0.7916	1
0.7955	2
0.8107	1
0.8143	1
0.8483	1
0.8485	1
0.8690	4
0.8721	1
0.9014	1
0.9429	1
0.9472	2
0.7919	**Weighted Average**

Figures

Figure 1.

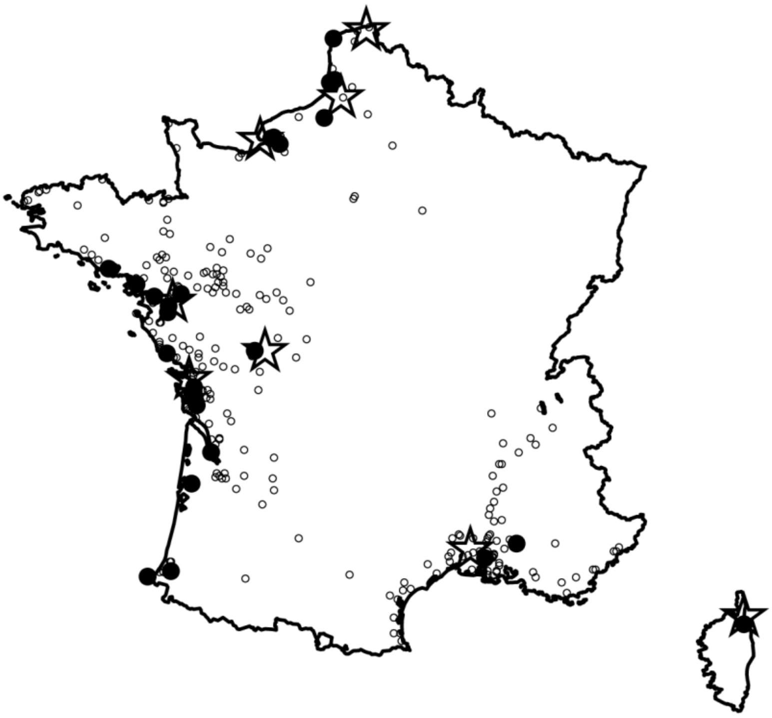


Figure 2.

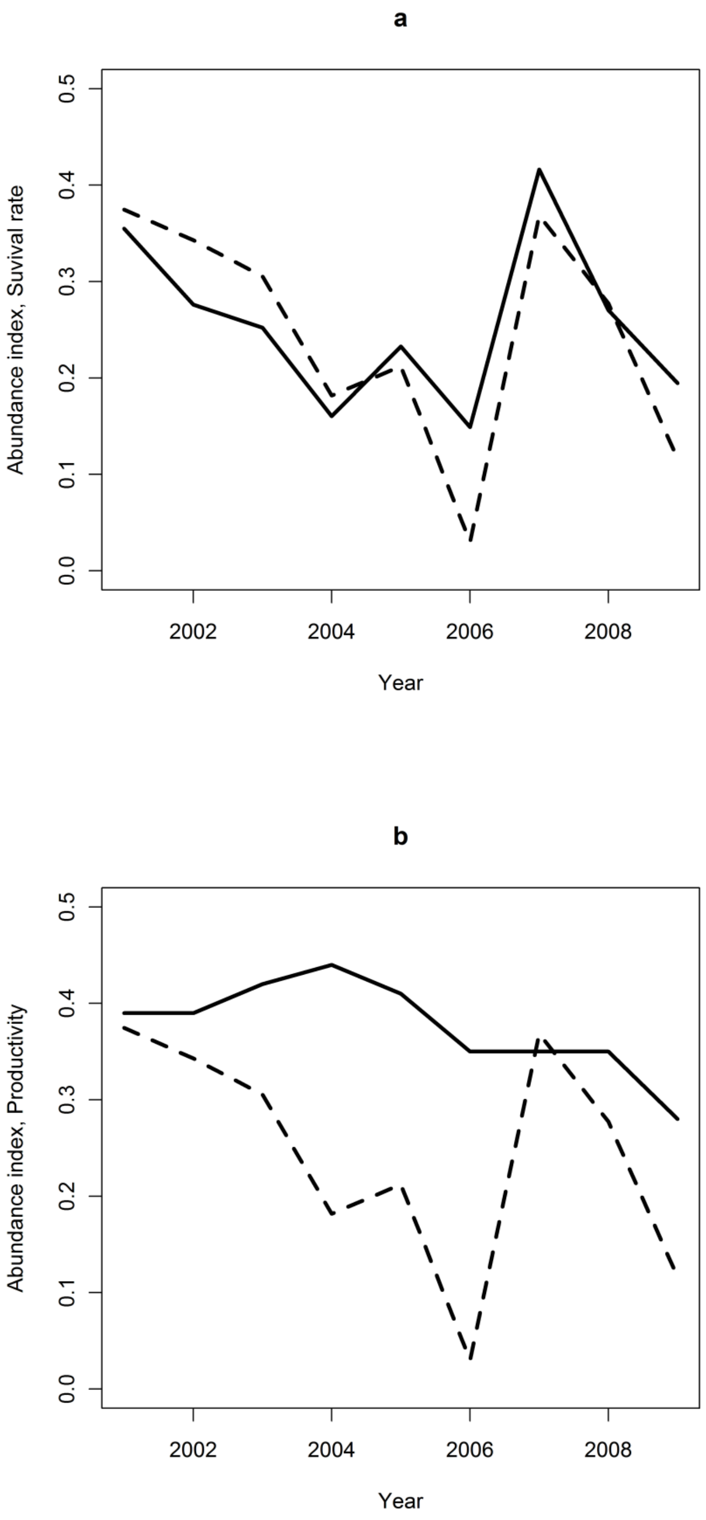

a
Abundance index, Suvival rate
0.0
0.1
0.2
0.3
0.4
0.5
2002
2004
2006
2008
Year
b
Abundance index, Productivity
0.0
0.1
0.2
0.3
0.4
0.5
2002
2004
2006
2008
Year

Figure 3.

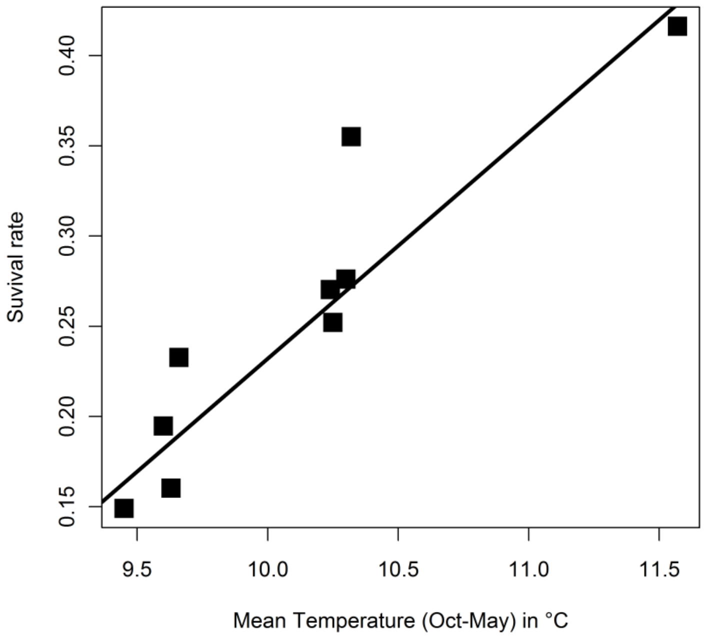

Suvival rate
0.15
0.20
0.25
0.30
0.35
0.40
9.5
10.0
10.5
11.0
11.5
Mean Temperature (Oct-May) in °C

Figure 4.

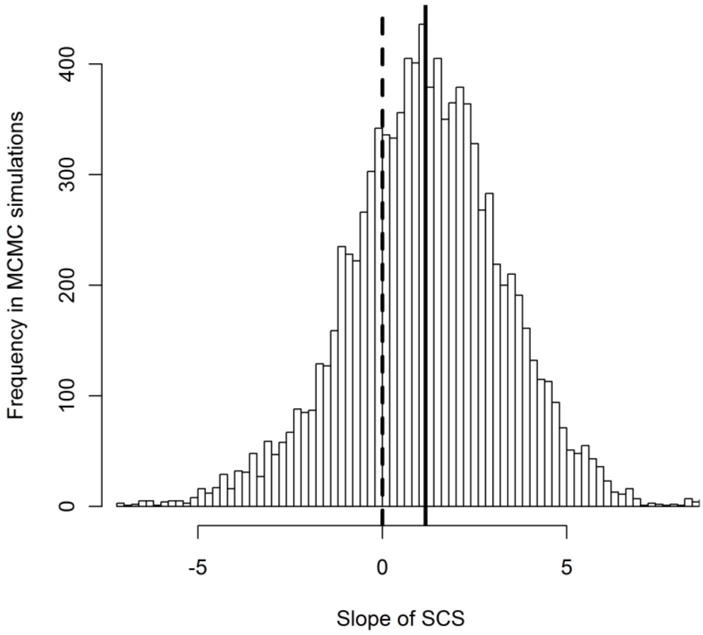
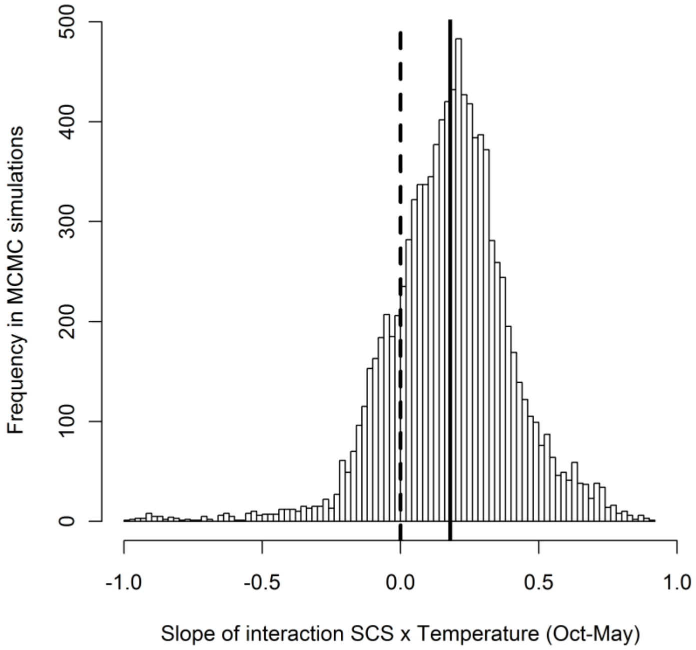

Frequency in MCMC simulations
0
100
200
300
400
-5
0
5
Slope of SCS

Figure 5.


Frequency in MCMC simulations
0
100
200
300
400
500
-1.0
-0.5
0.0
0.5
1.0
Slope of interaction SCS x Temperature (Oct-May)

Manuscrit 9

Measuring the sensitivity of abundance to climate towards the range limits, a way of distinguishing between fundamental and realized climatic niches?

En preparation

Climate dependent dynamics at the range margin, a way of distinguishing between fundamental and realized climatic niches?

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Abstract

Climate is a broad scale driver of species geographical distribution. Yet the precise relations between species climatic niche and species distribution still remain to be further investigated, especially species distributions are currently shifting and are predicted to shift even more as a result of ongoing climatic changes. Although there is evidence for some species that the realized climatic niche is congruent to the fundamental climatic niche, evidence for species occurring outside their fundamental climatic niche has not yet been found. Here we test the existence of such populations for three highly climate dependent passerine species at the margin of their distribution using the sensitivity of populations to climate fluctuations along their climatic niche. We show that population size in sites with poor climatic suitability appears less sensitive to winter climate as in sites with higher climatic suitability. This suggests that the actual sensitivity of population size to climate in poorly suitable sites is masked by colonization and extinction. We also identify a climatic suitability threshold above which populations are highly sensitive to climate fluctuations and under which this sensitivity is much lower. This threshold could reflect the boundary between species fundamental and realized climatic niches. Eventually we compare the future predicted distributions of the three species under climatic scenarios while accounting or not for such differences in population dynamics.

Introduction

Understanding species geographical distributions has always been one of the major challenges of ecological research (Darwin 1859; Brown *et al.* 1995; Brown *et al.* 1996; Sexton *et al.* 2009). The factors which determine the limits of species ranges can be very different (Angert 2006). Indeed, for some species, obstacles such as mountain chains, plains or oceans set obvious constraints on their distribution, while in many other species, the limit of the distribution seems to relate to environmental variables varying continuously across wide areas such as temperature, humidity, or other abiotic parameters (Case *et al.* 2005; Angert 2009; Sexton *et al.* 2009). Climate plays an important part in limiting species distributions (Root 1988; Araujo *et al.* 2009). This consensual observation suggests that the latitudinal and altitudinal boundaries of species observed distributions reflect the limits of its realized climatic niche. If range limits are driven by climatic patterns, population dynamics are expected to be more dependent on climatic fluctuations towards these range boundaries. However, this assumption is only valid if a species distribution is at equilibrium with the current climate which defines it climatic niche (or potential range). Previous work has shown that this was often not the case (Araujo & Pearson 2005). Thus, tree distributions in Europe are on average far smaller than the predicted potential range (Svenning & Skov 2004), while this is also the case for reptiles and amphibians (Araujo & Pearson 2005). Birds seem on average to occupy geographical areas closer to their predicted range equilibrium (Araujo & Pearson 2005). From these examples, it could be assumed that species always occur within their climatic niche. Yet the concept of a climatic niche can be regarded as an extrapolation of the ecological niche concept. Indeed, the ecological niche was defined at much lower scales. A species fundamental ecological niche includes all environmental conditions that allow a species to persist on the long term at a given site has thus been defined as its fundamental or grinnellian ecological niche (Colwell & Fuentes 1975; Devictor *et al.* 2010). The area where a species is actually present in the field defines its realized ecological niche. Further developments of this concept have led to the consideration of inter specific relations which can either narrow, in case of competition (Case & Gilpin 1974), or broaden, in case of facilitation (Bruno *et al.* 2003), the original N dimensional space defined by Hutchinson (1957) on the basis of abiotic parameters only (Hutchinson 1957). However, the relations between species fundamental and realized ecological niches remain unclear (Davis *et al.* 1998). Indeed, until recently, a species realized niche was thought to be always congruent to its fundamental ecological niche (James *et al.* 1984) notably because of dispersal limitations within the fundamental niche (Lawton & Woodroffe 1991; Beisner *et al.* 2006). Yet, developments of the niche concept suggest that a species might actually be found outside its fundamental niche (Pulliam 1988; Holt & Keitt 2000; Pulliam 2000). Indeed, individuals originating from sites in the fundamental niche, where births exceed deaths might disperse and establish in sites which could normally not allow the persistence of the species on the long term (Dias 1996). In such places, named population sinks, population dynamics are mainly driven by the flow of individuals coming from stable populations located within the species fundamental ecological niche, named population sources. Thus, in population sinks, population dynamics lead to colonization and extinctions due to unfavorable environmental conditions. By definition, source-sink dynamics occur at local scales because they rely on individual’s dispersal (Howe *et al.* 1991; Thomas & Kunin 1999). The purpose of this study is to test whether the assumption that species can occur outside their ecological niches is also applicable to their climatic niches which drive their distribution at much broader scales. Indeed accurately featuring a species climatic niche has recently become a major challenge in the context of climate change. Indeed, as a result of global climate warming, species fundamental climatic niches are shifting geographically (Parmesan *et al.* 1999; Warren *et al.* 2001). This causes species distributions to shift more or less accordingly (Pease *et al.* 1989; Davis & Shaw 2001; Devictor *et al.* 2008; Svenning *et al.* 2008). Predicting species future distribution has focused tremendous modeling effort during the past decade and has led to the development of species distributions models (Thuiller *et al.* 2005; Araujo & New 2007; Thuiller *et al.* 2009). These models currently assume that the fundamental climatic niche of species is accurately measured as a function of environmental variables. Species abundance variations can relate to temporal environmental fluctuations such as temperature (Jiguet *et al.* 2006). If a species realized climatic niche is included in the species fundamental climatic niche, the sensitivity of population dynamics to such environmental fluctuations can be predicted to increase towards the edge of the realized niche (Mehlman 1997). Indeed, in such cases, environmental conditions allow species to persist on the long term across its entire distribution but populations located in the least favorable conditions would be more sensitive to environmental fluctuations. On the contrary, if part of the realized climatic niche (measured by the species geographical distribution) lies outside the species fundamental climatic niche, because these particular populations will tend to behave as population sinks, the apparent sensitivity to environmental fluctuations will be masked by colonization and extinction processes. Indeed, during periods when species disappears from unfavorable areas following particularly adverse climatic episodes, the sensitivity of its abundance to environmental fluctuations is worth zero. In such cases the apparent sensitivity of population dynamics to environmental variations should decrease along a gradient of environmental suitability for the species. Moreover, if part of the realized climatic niche is not included in the fundamental climatic niche, the sensitivity of population dynamics to climate should show non linear patterns along a species realized climatic niche. Thus, when crossing the boundary between species realized and fundamental niches, the sensitivity of abundance temporal variations to climatic fluctuations should also change markedly. The climatic suitability threshold defined by such a change in population dynamics apparent sensitivity to climate could thus be interpreted as the limit between species fundamental and realized climatic niche. Thus, the apparent sensitivity of population dynamics to a given environmental variable along a spatial suitability gradient should provide information about the relations between a species realized and fundamental climatic niches. We apply this approach to three common passerine species, the Cetti’s Warbler (*Cettia cetti*), the Dartford Warbler (*Sylvia undata*) and the Fan-tailed Warbler (*Cisticola juncidis*). These three species are strict insectivorous sedentary warblers widespread across the Mediterranean region but sharing different habitat types. In France where the study is conducted, they all reach the boundary of their current distribution range. We first show in a preliminary analysis that their population dynamics is mostly driven by winter climate, particularly winter temperatures using abundance data from the French Breeding Bird Survey. We then investigate how the sensitivity of population dynamics to winter climate varies across the French part of their distribution range and along a gradient of climatic suitability estimated from species distribution models. Lastly, we compare the outputs of species distribution models accounting or not for such differences in population dynamics.

Methods

Abundance data

The French BBS program is based on volunteer ornithologists counting birds in spring on permanent plots. Surveyed sites are 2 × 2 km squares randomly selected within a 10-km radius around a locality specified by the volunteer. Random selection (one of *c.* 80 possible squares) ensures that surveyed habitats closely match their actual availability (Jiguet *et al.* 2007). In each square, observers carry out 10 point counts (separated by at least 300 m) of 5 min duration each. Counts are done twice in spring (from 1st April to 8th May, then from 9th May to end of June) in order to detect both early and late breeders, with 4-6 weeks between both counts. For a given site, counts are repeated yearly by the same observer at the same points, on approximately the same date (± 7 days within April to mid-June), and at the same time in the day (± 15 min). Here, maximum counts (between both sessions) for the 10 points within each square were summed before analysis. The monitoring sites were distributed across the entire French part of the 3 warbler species' range.

Climatic data

Monthly mean daily temperatures were used as climatic covariates to population abundance. Data were downloaded from the website of the European Climate Assessment & Dataset (ECA&D) (http://eca.knmi.nl). For each temperature index, climate data from 8 meteorological stations were averaged (Abbeville, Bastia, Cap de la Heve, Dunkerque, La Rochelle, Nantes, Nîmes and Poitiers). These meteorological stations are located across the entire French range of the species including Corsica. Temperature averages for December, January and February were considered. Because the three species could have different climatic sensitivities, a preliminary analysis was run to identify the most influential climatic temporal window. Thus for each species, abundance was modelled using a linear mixed effects model between log transformed count data and all 6 possible climatic temporal windows involving monthly temperatures from December to February. The climatic window which maximized the z-score for each species was kept in further analyses.

Modeling annual abundance

In order to test the sensitivity of species abundance to temperature, the following model was fitted to the log-transformed count data:

$$Log\left(\alpha_{i,j}+1\right)=\beta_0+\beta_1\times Temperature_i+\gamma_j+\varepsilon_{i,j}$$

Where $\alpha_{i,j}$ represents the number of birds contacted at year *i* on site *j*, $Temperature_i$ the average temperature at year *i*, γ_j the random effect of site *j* on abundance $\alpha_{i,j}$, β_0 and β_1 the regression parameters to be estimated and $\varepsilon_{i,j}$ the residual error term.

Modeling species current and future distributions and estimating Site climatic suitability

The current and future climate suitability index of the species across its distribution was obtained through climate suitability modeling techniques. Such a technique requires presence - absence data and climatic variables across the species distribution. The presence - absence data was obtained by geo-referencing and digitizing maps from the handbooks of the birds of the Western Palearctic (BWPi 2006). As for the climatic variables needed for the niche modeling, we used the following eight variables: (1) annual mean temperature, (2) mean temperature of the warmest month, (3) mean temperature of the coldest month, (4) temperature seasonality, (5) annual precipitation, (6) precipitation of the wettest month, (7) precipitation of the driest month and (8) precipitation seasonality. The seasonality is the coefficient of variation of the monthly means. These variables were derived from the monthly mean temperatures and precipitations over the intervals 1961-1990 (http://worldclim.org) and interpolated (bilinear interpolation) to a 0.5°×0.5° latitude×longitude grid over the Western Palearctic. Future climate projections for 2050 were derived from five general circulation models (BCM2, ECHAM5, HADCM3, MIROHI and MK3) under two or three special reports on emission scenarios (A1, A2 and B1 for HADCM3 and ECHAM5, and A1 and B1 for BCM2, MIROHI and MK3), available from the IPCC fourth assessment. Because the future predictions were only available at a rough scale, they were downscaled to the 0.5° resolution, according to the method described in http://www.worldclim.org/downscaling. Temperature and precipitation are expected to impose direct or indirect constraints on bird distributions (Root 1988; Araujo *et al.* 2009). We realized the projections for seven different niche-based modeling techniques, performed with the BIOMOD computational framework (Thuiller *et al.* 2009): (1) generalized linear model (GLM), a regression method with polynomial terms for which a stepwise procedure is used to select the most significant variables, (2) generalized additive model (GAM), another regression method with four degrees of freedom and a stepwise procedure to select the most parsimonious model, (3) classification tree analysis (CTA), a classification method running a 50-fold cross-validation to select the best trade-off between the number of leaves of the tree and the explained deviance, (4) artificial neural networks (ANN), a machine learning method, with the mean of three runs used to provide predictions and projections, as each simulation gives slightly different results, (5) multivariate adaptive regression splines (MARS), a regression method, (6) generalized boosting model (GBM), a machine learning method which combines a boosting algorithm and a regression tree algorithm to construct an 'ensemble' of trees, and (7) Random Forest (RF), a machine learning method which is a combination of tree predictors such that each tree depends on the values of a random vector sampled independently and with the same distribution for all trees in the forest. In order to evaluate the predictive performance of a species distribution model, for each species, we used a random subset of 70% of the data to calibrate the model, then used the remaining 30% for evaluation, using a threshold independent method, the area under the relative operating characteristic curve (AUC)(Fielding & Bell 1997). The data splitting approach was then replicated five times from which we calculated the mean AUC of the cross-validation. The final calibration of every model for making predictions uses 100% of available data. We then used an ensemble forecast technique which aims to take into account the variability among species distribution models, climate models and climate scenarios, in order to get the central tendency (Araujo & New 2007; Thuiller 2007). For each species, we obtained 40 (8 models × 5 GCM) modeled current distributions and 96 (8 models × 12 (GCM×SRES)) modeled future distributions. The current and future consensus distributions were obtained by calculating the weighted mean distributions: the models were ranked according to their predictive performance, and a decay of 1.6 gave the relative importance of the weight (Coetzee *et al.* 2009; Marmion *et al.* 2009). In order to transform the results of species distribution modeling from climatic suitability to presence/absence distribution, we used the “sensitivity-specificity equality approach” threshold (Liu *et al.* 2005). From the current modeled distributions, the presence probability at each BBS site was extracted and hereafter named Site Climatic Suitability (SCS).

Estimating climate sensitivity thresholds along a climate suitability gradient

In order to investigate potential climate sensitivity thresholds for species abundance along a gradient of SCS, the following algorithm was applied to the log transformed abundance data of each species:

(a) A given SCS threshold t was selected iteratively within the different values of SCS corresponding to the different sites in the species abundance data.

(b) To the count data, the following model was fitted

$$Log\left(\alpha_{i,j}+1\right)=\beta_0+\beta_1\times Temperature_i+\gamma_j+\varepsilon_{i,j}$$

Where the different symbols refer to those used previously, except that $Temperature_{\text{i}}$ was set at 0 for those sites with a climatic suitability below t. Thus, for those sites, climate influence on annual abundance was omitted.

(c) The AIC (Akaike 1981) of each model (corresponding to each t) was recorded. Because all fitted models had the same number of parameters, minimizing AIC is equivalent to maximizing likelihood. The climate sensitivity threshold along the gradient of SCS was defined at the climate suitability which yielded the best fit for the model described above.

Comparing species current and future distribution models

When the outputs of species distributions models are used to produce maps of the predicted current and future distributions, a suitability threshold based on a “sensitivity-specificity equality approach” is applied. Thus, sites which SCS is estimated beneath this threshold are not considered in the modeled distribution. The overall rationale of this statistical threshold is to maximize the probability of predicting the presence of a species where it is known to occur (from the presence /absence data used to run the species distribution model) while minimizing the probability of predicting the presence of the species where it is not known to occur (also from the presence / absence data). This approach does account for any differences in population dynamics across the species range. On the other hand, the climate sensitivity threshold estimated using the algorithm described above could represent the limit between the fundamental niche and the realized niche if the latter is larger than the former. We compared the current and future distributions produced by applying both thresholds to the current and future predicted distributions.

Results

Spring counts of all three warbler species was significantly positively influenced by winter temperatures yet the best fitting climatic temporal window was slightly different between species (Cetti's Warbler: Temperature average from December to February $F_{1,992}$=16.09, P<0.001; Fan-tailed Warbler : January average temperature $F_{1,889}$=23.56, P<0.0001 and Dartford Warbler: December average temperature $F_{1,309}$=4.86, P=0.03, see Figure 1). Because the Site Climatic Suitability index (SCS) was calculated using presence absence data from an independent dataset, we tested the relation between Breeding Bird Survey data and SCS. There was a highly significant correlation between all three species abundance and SCS (Cetti's Warbler: $F_{1,992}$=23.54, P<0.0001; Fan-tailed Warbler $F_{1,889}$=27.82, P<0.0001 and Dartford Warbler: $F_{1,309}$=19.14, P<0.0001, see Figure 2). The sensitivity of abundance to winter climate varied significantly across the distribution for all three species (Cetti's Warbler: $F_{1,991}$=12.86, P<0.001; Fan-tailed Warbler $F_{1,888}$=20.54, P<0.0001 and Dartford Warbler: $F_{1,308}$=22.69, P<0.0001), for all species, this linear interaction between winter climate and site climatic suitability was positive. Thus the apparent sensitivity of the species abundance to annual fluctuations of winter climate was lower in sites with poorer species climatic suitability. Looking for thresholds in the climatic sensitivity of the warbler populations revealed an optimum for the fit of a model relating abundance to winter climate when sites with climatic suitability beneath a given threshold were not considered. These thresholds were very similar for the Cetti' Warbler and the Dartford Warbler (0.85 and 0.83 respectively) and much lower for the Fan-tailed Warbler (0.58), see figure 3 for the global AIC minimum.

When the outputs of species distributions models are used to produce maps of the predicted current and future distributions, a suitability threshold based on a "sensitivity-specificity equality approach" is applied. Thus, sites which suitability is estimated beneath this threshold are not considered in the modeled distribution. The overall rationale of this threshold is to maximize the probability of predicting the presence of a species where it is known to occur (from the presence /absence data used to run the species distribution model) while minimizing the probability of predicting the presence of the species where it is not known to occur also from the presence / absence data). Comparing the current and future distributions produced with the two different probability thresholds revealed marked differences for the Cetti's and Dartford Warblers for which the climatic suitability thresholds were high. For both species the current distribution was much smaller than the distribution predicted using the classical statistical presence probability threshold. For the Fan-tailed Warbler, both current distributions were not very different. Accordingly, the future predicted distributions for the Cetti's and Dartford Warblers were very different according to the considered presence probability threshold while the difference was again much smaller for the Fan-tailed Warbler (See figure 4).

Discussion

Species geographical ranges are often considered as the spatial projection of their fundamental ecological niche (Brown *et al.* 1996; Angert 2006, 2009; Sexton *et al.* 2009). In this view, range limits are associated with environmental conditions at the boundary of species ecological tolerances (Merriam 1894; Case *et al.* 2005; Sexton *et al.* 2009). Thus, a geographical distribution could represent the species fitness gradient from a core towards an edge especially regarding climatic conditions which vary on a large scale (Purves 2009). Nevertheless, dispersal can substantially alter this pattern in two ways. First, for species with poor dispersal abilities, the distribution range might not fill all the suitable areas predicted by the species fundamental niche just because individuals do not easily reach these suitable places (Lennon *et al.* 1997; Beisner *et al.* 2006; Svenning *et al.* 2008). On the other hand, species which show large dispersal ability can temporarily establish outside a species fundamental niche in so called sink populations (Pulliam 1988; Holt & Keitt 2000; Pulliam 2000). The long term persistence of sinks depends on the balance between births and deaths in such populations and on the rate of immigration from sources (Howe *et al.* 1991; Dias 1996; Thomas & Kunin 1999). There is evidence suggesting that sinks should occur more frequently at the margin of species geographic distribution (Wilson *et al.* 2002; Nielsen *et al.* 2008; Gaston 2009) but the identification of such populations at large spatial scales remains a challenge (Gaston 2009).

In this study, clear spatiotemporal patterns of climate sensitivity of abundance are identified for three passerine species along a site suitability gradient. These significant interactions between the climatic suitability of the Breeding Bird Survey sites and the sensitivity of the population abundance at these sites to climate could be interpreted as a result of differential population dynamics across the distribution. Indeed, the observed decrease in abundance sensitivity to winter climate when site suitability decreases could reflect local extinction and colonization processes. In case of unstable populations relying on immigration from population sources, extinctions lead to periods where the species is absent (Dias 1996) and therefore not detected during BBS counts sessions. The regression coefficient between abundance and climate during these periods is obviously zero. Thus, when considered on longer time scales, the sensitivity of abundance to climate appears to be lower in such poor suitability sites than in sites where the species is always present and where the effect of climate fluctuations is measured each year. It is therefore only the apparent sensitivity to climate that is lower in sinks and not the actual sensitivity because local extinctions are a result of environmental fluctuations (Dias 1996; Gaston 2009). The results presented here show that one can estimate a threshold of apparent climate sensitivity of abundance for all three species. The actual value of this threshold is perhaps not the most important fact to consider. Rather, the meaning of this threshold deserves more attention. The iterative algorithm designed to investigate the existence of such climate sensitivity thresholds assumes that species abundance of an increasing part of the sites where birds are detected is not sensitive to climate fluctuations. The best fit of the model is reached when sites where null apparent climate sensitivity and non null apparent climate sensitivity are best told apart. If the sensitivity of abundance to winter climate was not spatially distributed, the threshold would be equal to zero. Therefore, the most likely interpretation of this climate sensitivity threshold is that it represents the boundary between areas mostly occupied by long-term viable populations, mainly sources, and areas where the proportion of population sinks are more numerous (Wilson *et al.* 2002). This interpretation of the results leads to the conclusion that for those three warblers, the realized niche measured by the BBS counts is not congruent to the fundamental niche. Thus, populations do exist outside the fundamental niche. There is evidence for such meta population functioning on more local scales (Järvinen & Väisänen 1984; Wilson *et al.* 2002; Nielsen *et al.* 2008), yet addressing the spatial gradient of population dynamics through the distribution range has hardly been addressed.

Our results suggest that the extent to which the realized niche spreads outside the fundamental niche depends on the species. For the Cetti's and the Dartford Warblers, the climate sensitivity thresholds are relatively high within the [0,1] interval for climatic suitability (respectively 0.85 and 0.83). Thus, for both species the core range representing their fundamental niche is small compared to the range margin. Alternatively, the relatively low climate sensitivity threshold of the Fan-tailed Warbler seems to indicate a rather small difference between fundamental and realized climatic niches for this species.

For numerous species, the climatic conditions defining their fundamental niche are currently shifting as a result of global warming. The accurate estimation of how species are able to track spatial shifts of their climatic niche in such a context remains unclear. Species distribution models can produce valuable future distributions models under climatic scenarios (Pearson & Dawson 2003; Araujo & New 2007) but they do not yet account for heterogeneity in population dynamics and species interactions (Davis *et al.* 1998; Guisan & Thuiller 2005; Thuiller *et al.* 2008). As a result, the predicted future distributions often show large areas where the climatic suitability is far lower than the source-sinks dynamics thresholds estimated from the approach developed in this study and could result in flawed inferences (Davis *et al.* 1998). This is because, classical suitability thresholds are not estimated on the basis of population functioning but rather to maximize the match between the predictions of the current distributions and the current presence/absence data used to run the species distribution models (Liu *et al.* 2005). The presence/absence data are a rough image of a species distribution which does not account for differences between the dynamics of populations located within the range core and at the margin (Davis *et al.* 1998). Our findings raise the question of the meaning of large areas of moderate climatic suitability in the future distributions. If the apparent climate sensitivity thresholds identified here actually relate to source-sinks population dynamics, it is unlikely that such large areas as those predicted to possibly host a species will effectively do so, given the dispersal abilities from source populations (Lawton & Woodroffe 1991; Lennon *et al.* 1997; Svenning & Skov 2004; Beisner *et al.* 2006). Moreover, either considering range shifts and range size changes of all populations or only of the populations located within a species fundamental niche is not equivalent depending on the apparent climate sensitivity threshold. Indeed, for the Cetti's Warbler and the Dartford Warbler for which the thresholds were high, the core of the distribution is predicted to shrink dramatically within the next 50 years whereas, based on the classical thresholds, the entire potential distribution is predicted to increase through the same period. For the Fan-tailed Warbler, the differences are much smaller because the climate sensitivity threshold is not very different from the climate suitability index under which no more birds are present. Although applying these climate sensitivity thresholds to the species predicted distributions allows interesting insights, this approach also suffers from some shortcomings. Indeed, the sensitivity of population size to winter climate was only assessed on a small part of the species total geographic range. It is thus possible that some populations located outside the studies area respond differently to climatic fluctuations. Moreover, the climate dependency was estimated between 2001 and 2009 which might have not captured all possible climatic fluctuations. Lastly, drawing inferences on the geographic distribution of a species fundamental niche using this approach assumes no intrinsic changes of this niche due to evolutionary processes although the ecological niche boundaries are known to be labile (Roughgar.J 1972; Futuyma & Moreno 1988; Sexton *et al.* 2009). In that sense, the predicted distribution probably represents the most pessimistic view of a species future distribution.

To conclude, this study identifies highly significant variations of the apparent sensitivity of population size to temporal climatic fluctuations in three warbler species. Such spatiotemporal patterns, opposed to the common sense that populations should be more dependent on climate at the edge of their distribution, are likely to be driven by differences between sources and sinks population dynamics across species distribution. The existence of a site climatic suitability threshold for climate sensitivity allowed us to provide an estimate for the position of the boundary between each species fundamental and realized ecological niches. Besides bringing evidence for large-scale source sinks dynamics at the climatic edge of three species, this study raises important questions concerning the prediction of climate change consequences on species distributions.

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Figure legends

Figure 1. Relationships between winter temperature and population abundance for three Warbler species (a) the Cetti's Warbler, (b) the Fan-tailed Warbler and (c) the Dartford Warbler. The figures were produced using Generalized additive models (GAM) assuming a Poisson Error. All the relations are statistically significant. 95 % confidence intervals are represented in dotted lines.

Figure 2. Relationships between Site Climatic Suitability (SCS) and population abundance for three Warbler species (a) the Cetti's Warbler, (b) the Fan-tailed Warbler and (c) the Dartford Warbler. The figures were produced using Generalized additive models (GAM) assuming a Poisson Error. All the relations are statistically significant. 95 % confidence intervals are represented in dotted lines. SCS was estimated using an independent presence/absence dataset.

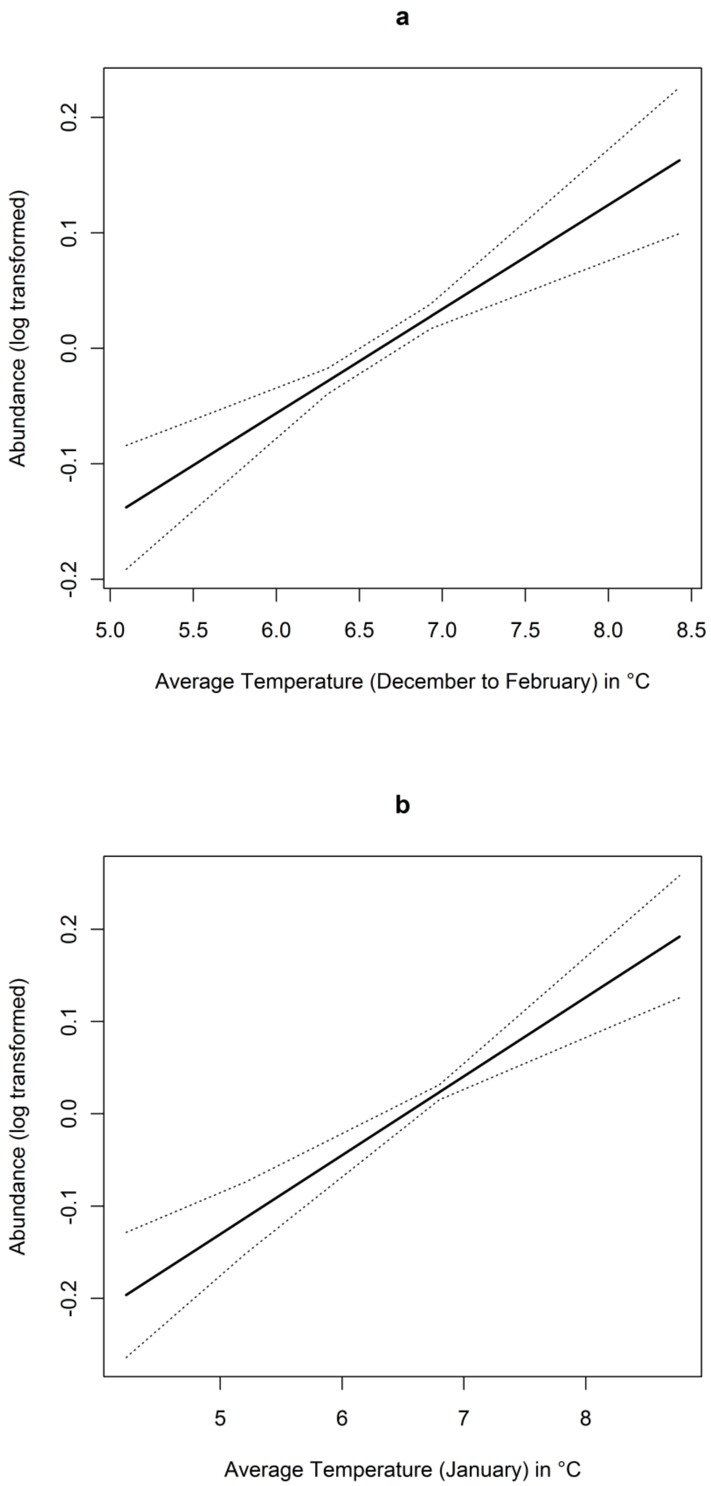
Figure 3. Detection of thresholds of the sensitivity of population abundance to climate along a gradient of Site Climatic suitability (SCS) for three warbler species (a) the Cetti's Warbler, (b) the Fan-tailed Warbler and (c) the Dartford Warbler. Each point on the figures represents the AIC of a model relating abundance to winter temperature where temperature is set at 0 for those sites with a Climatic suitability under a given threshold. This procedure was applied iteratively to all climatic suitability values. The global minimum of this AIC versus SCS function represents the SCS threshold under which the apparent sensitivity of abundance to climate decreases.

Figure 4. Predicted current and future distributions for three Warbler species. The figures show the current and future (2050) distributions produced by species distribution models

(described in the methods section). Figures on the left (total) show distributions for which the climatic suitability threshold applied is based on classical assumptions concerning the prediction accuracy of the current distributions. Figures on the right (core) represent the current and future distributions of the climatic suitability for sites belonging to the fundamental niche (Site climatic suitability above the threshold estimated in this study). (a) Cetti's Warbler, (b) Fan-tailed Warbler and (c) Dartford Warbler.

Figures

Figure 1.



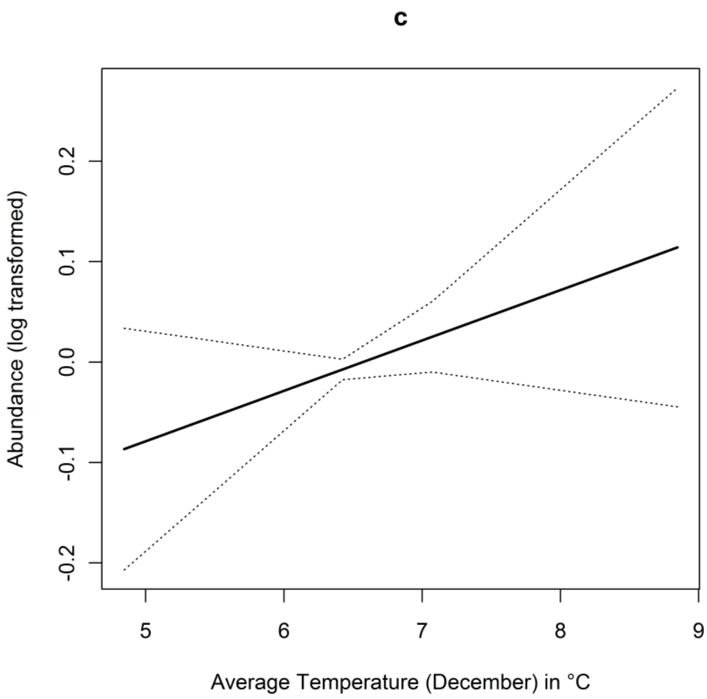
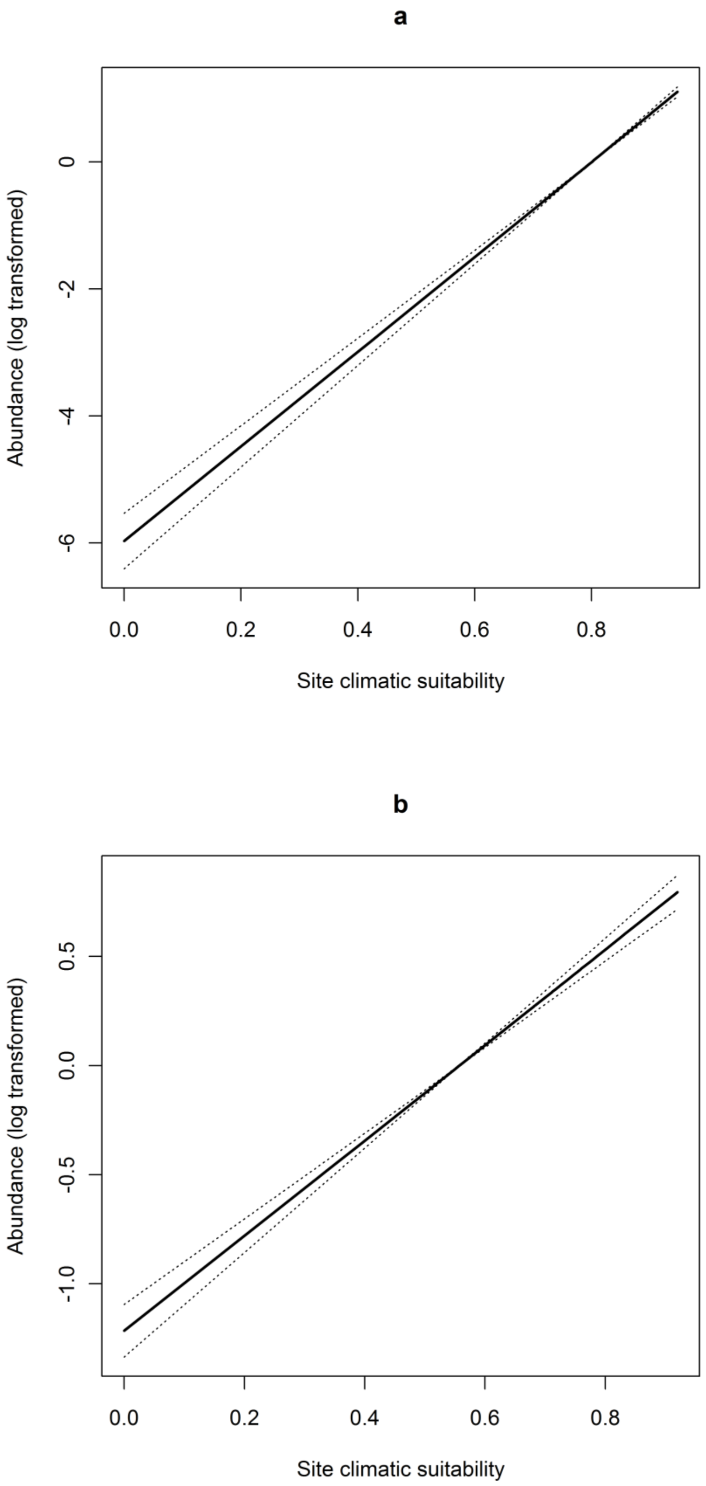

c
Abundance (log transformed)
0.2
0.1
0.0
-0.1
-0.2
5
6
7
8
9
Average Temperature (December) in °C

Figure 2.


a
Abundance (log transformed)
0
-2
-4
-6
0.0
0.2
0.4
0.6
0.8
Site climatic suitability
b
Abundance (log transformed)
0.5
0.0
-0.5
-1.0
0.0
0.2
0.4
0.6
0.8
Site climatic suitability

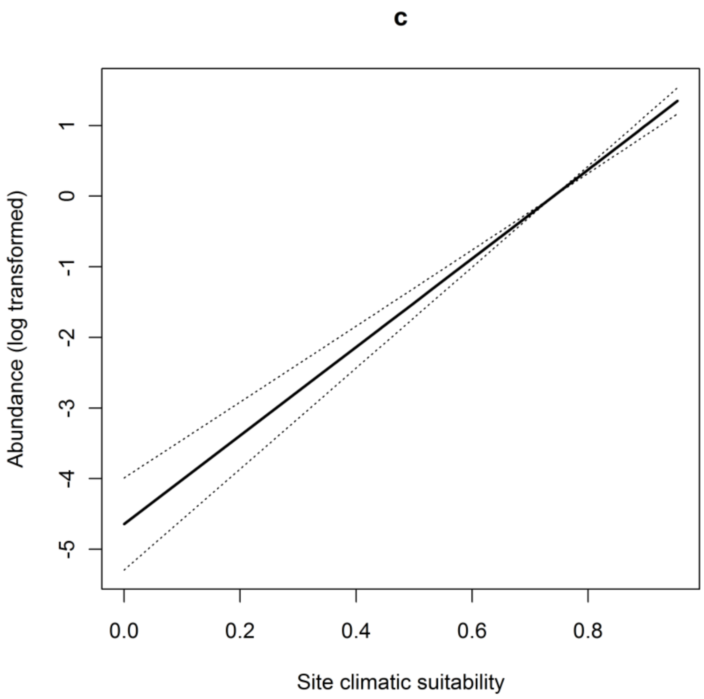
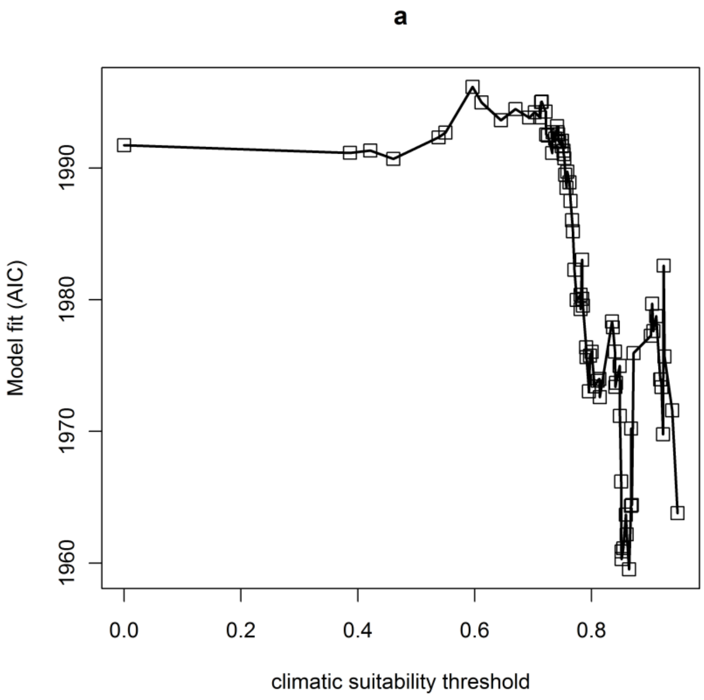
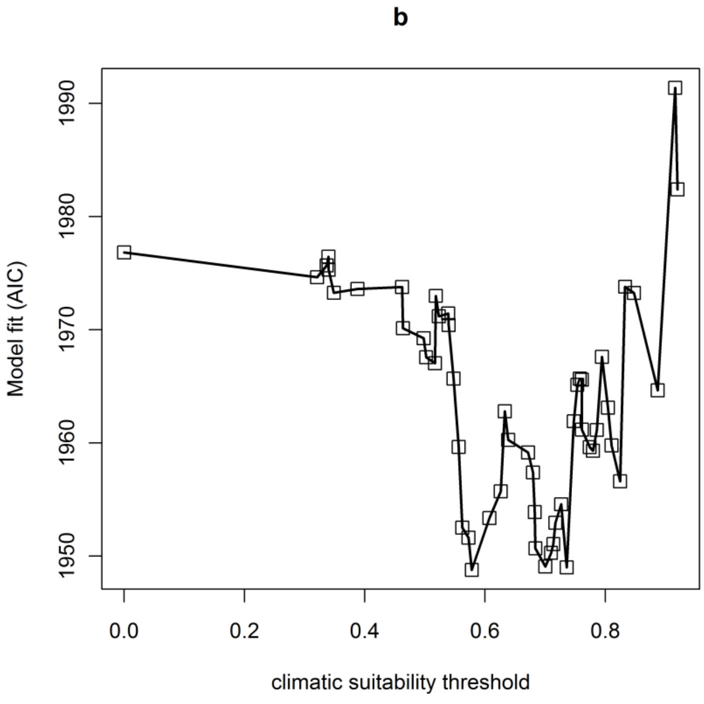

c
Abundance (log transformed)
1
0
-1
-2
-3
-4
-5
0.0
0.2
0.4
0.6
0.8
Site climatic suitability

Figure 3.


a
Model fit (AIC)
1960
1970
1980
1990
0.0
0.2
0.4
0.6
0.8
climatic suitability threshold


b
Model fit (AIC)
1950
1960
1970
1980
1990
0.0
0.2
0.4
0.6
0.8
climatic suitability threshold

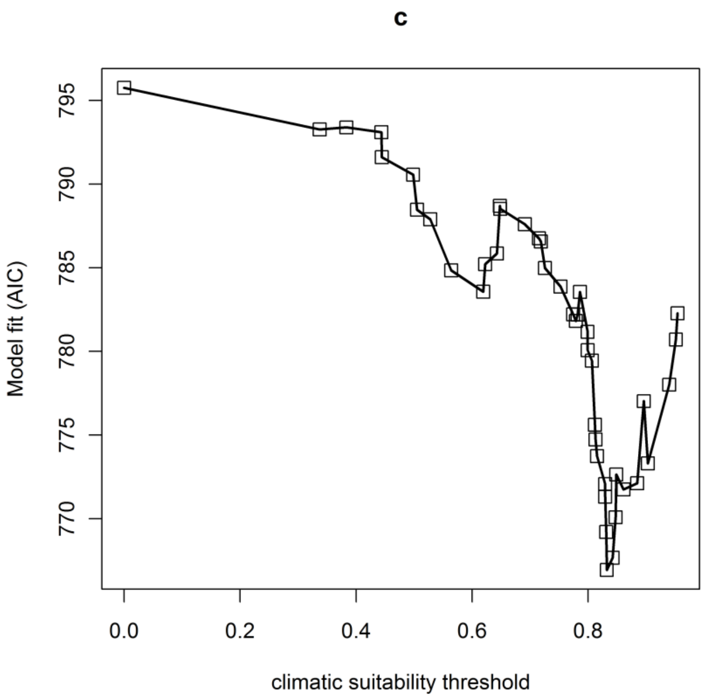
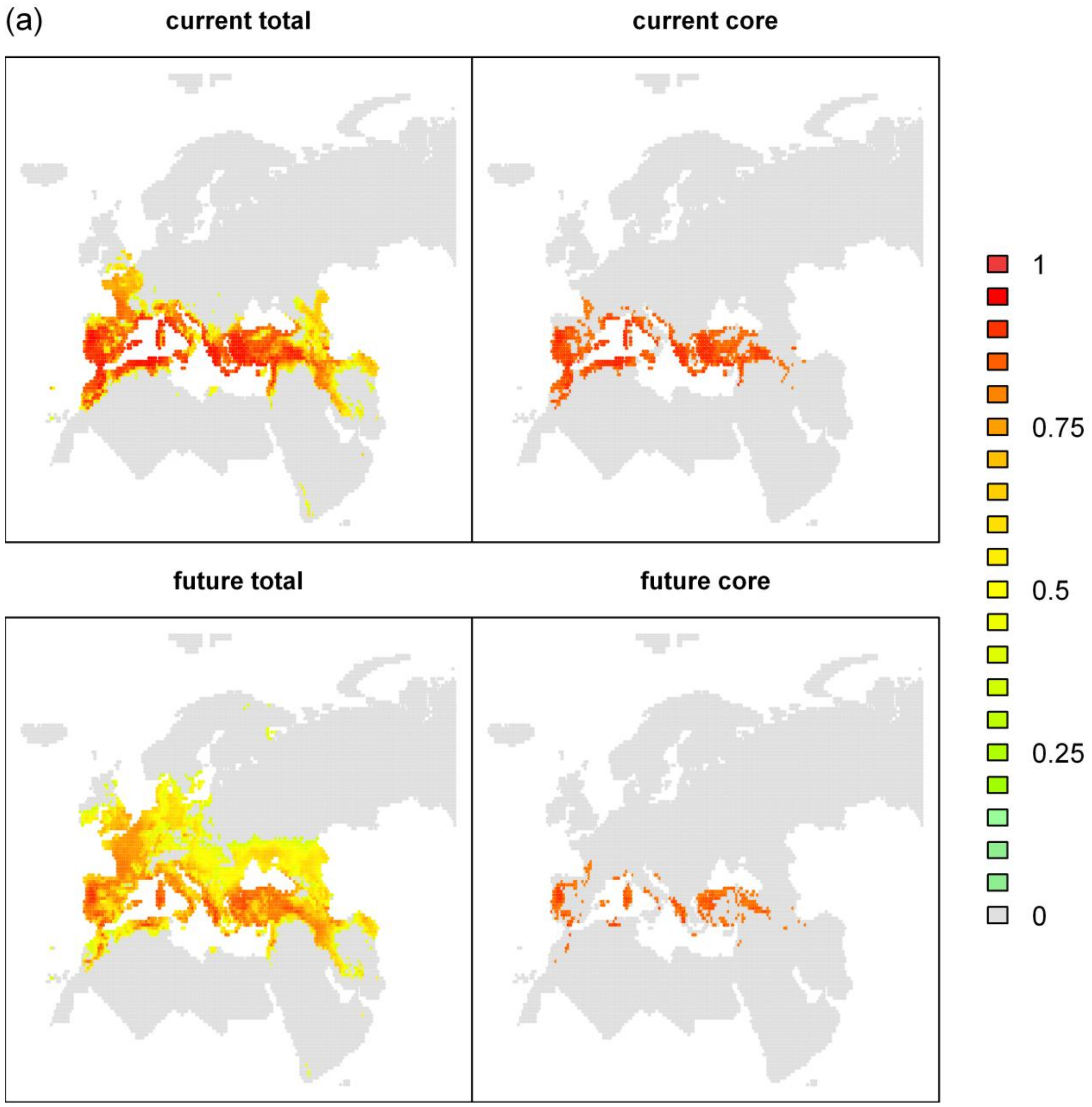
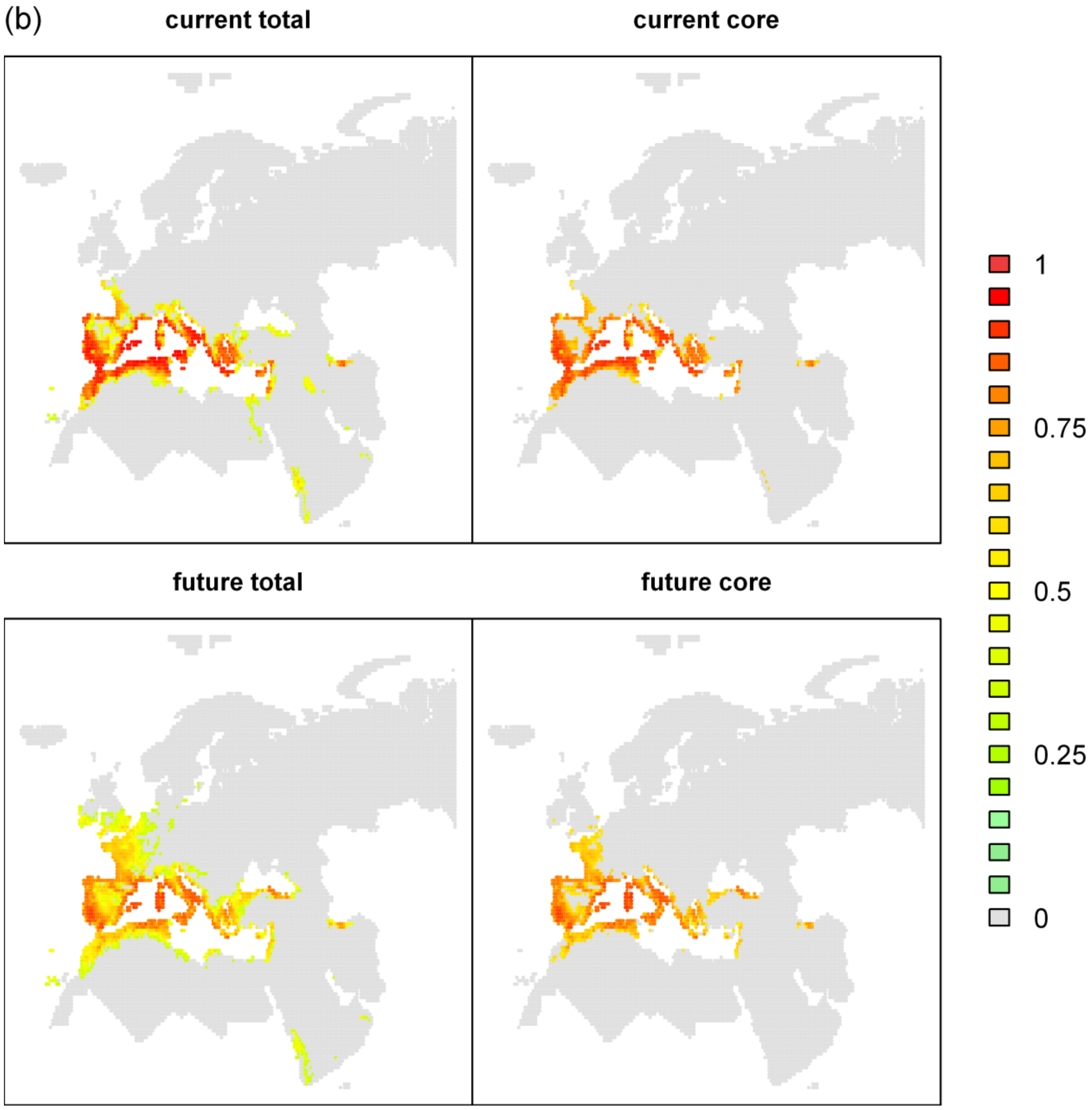
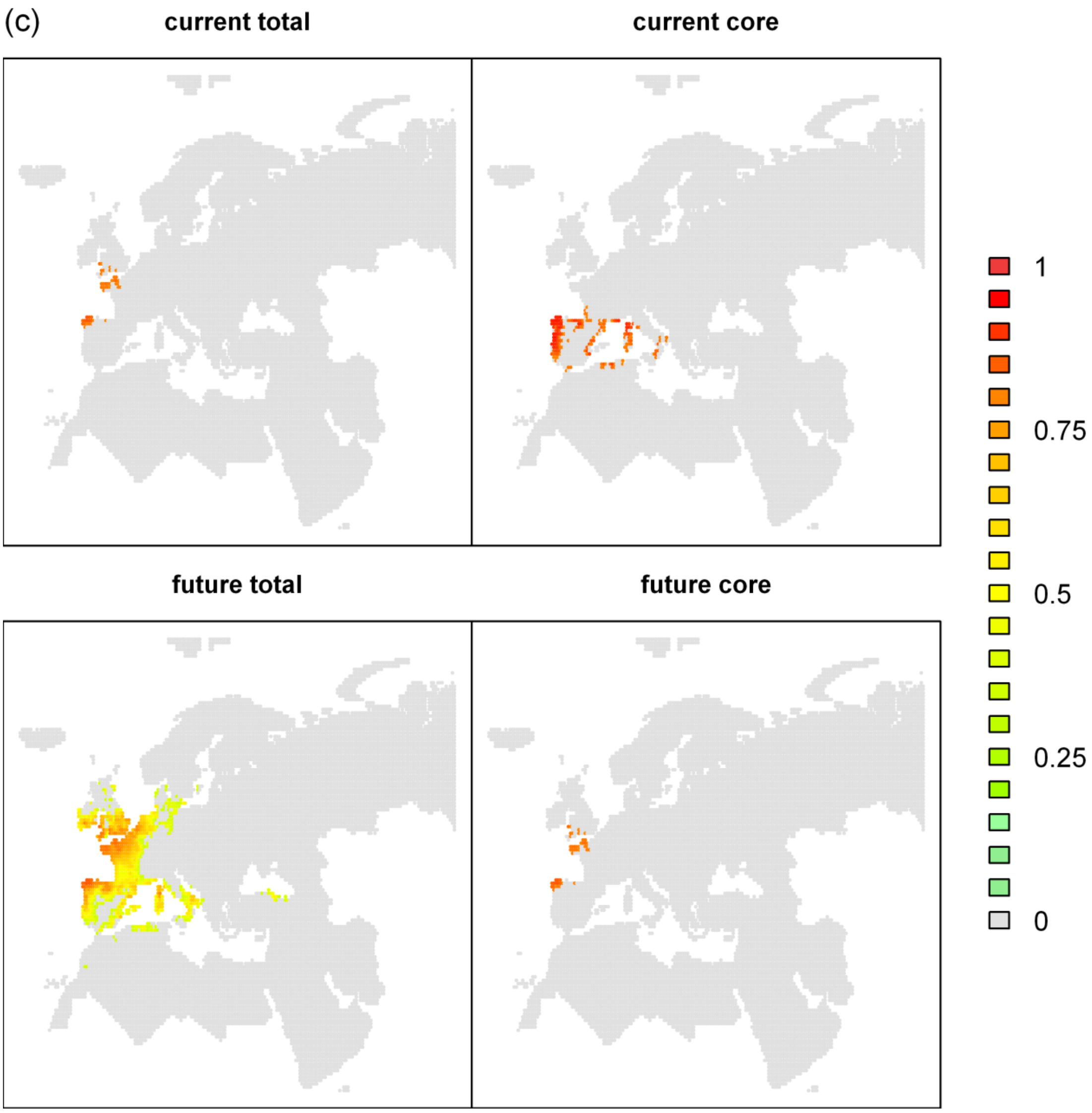

c
Model fit (AIC)
770
775
780
785
790
795
0.0
0.2
0.4
0.6
0.8
climatic suitability threshold

Figure 4.


(a)
current total
current core
future total
future core
1
0.75
0.5
0.25
0


(b)
current total
current core
future total
future core
1
0.75
0.5
0.25
0


(c)
current total
current core
future total
future core
1
0.75
0.5
0.25
0