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Short communication

# Survival of Turtle Doves *Streptopelia turtur* in relation to western Africa environmental conditions

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For several trans-Saharan migrant species, it is well established that the environmental conditions experienced on their wintering grounds may significantly affect their annual survival rates (Møller 1989, Kanyamibwa *et al.* 1990, Peach *et al.* 1990, Szép 1995, Barbraud *et al.* 1999, Schaub *et al.* 2005). Relatedly, it is hypothesized that food access and quality might be among the major proximate environmental factors shaping the survival of birds on their African wintering grounds (Newton 2004). However, as direct estimates of food availability are unavailable, covariates are generally used as surrogates for food availability (Wilson & Cresswell 2006). For instance, temporal variation in survival rates has been shown to be positively correlated with environmental covariates such as rainfall (Møller 1989, Kanyamibwa *et al.* 1990, Peach *et al.* 1990, Szép 1995, Schaub *et al.* 2005) and primary production indices (Schaub *et al.* 2005). As a consequence, firm support for the link between survival and food resources is lacking for species investigated to date.

The aim of this study was to investigate the link between overwinter survival and food conditions on wintering grounds. The Turtle Dove is a long-distance migrant that breeds in a large part of the western Palearctic and winters in sub-Saharan Africa (Jarry 1995). In its wintering quarters, it mainly relies for food on wild and cultivated seeds such as rice *Oriza* spp., millet *Panicum laetum* and sorghum *Sorghum* spp. (Morel 1987, Jarry & Baillon 1991), for which yearly production statistics are available. Besides these aspects, the Turtle Dove is a challenging species from a conservation point of view as it has dramatically declined over the whole of western Europe from the mid-1970s onwards (Baillie *et al.* 2001). Several factors are suspected to be responsible for this observed decline, including the degradation of both breeding and wintering habitats (Browne & Aebischer 2004, Browne *et al.* 2005). However, whether changes in breeding and wintering conditions may impact population dynamic parameters, such as annual survival rates, is currently unknown.

We assessed annual variation in local survival rates of adult Turtle Doves breeding in western France and further examined whether survival was related to variation in environmental conditions experienced on their sub-Saharan wintering quarters. More specifically, we investigated the relationships between overwinter survival rates and (1) surrogates for food availability such as rainfall and primary production indices during the same winter, but also (2) a proximate estimation of food availability, namely yearly cereal production for sub-Saharan countries.

## METHODS

### Study area and field methods

The study was carried out on Oléron Island (175 km$^2$, 46°09′N, 0°58′W, Charente-Maritime, France) where the Turtle Dove is a common breeder. The island is a mix of arable land, marshes, small woods and villages. The study site was located near the Saint Pierre d'Oléron town in the northern part of the island. It consisted of several capture sites, arranged along a fixed circuit. Birds were caught with mist-nets or drop traps after being attracted by bait (cereal seeds). Capture sites and capture methods remained similar throughout the study period.

### Data collection

We used data collected between 1998 and 2004, a period when catching effort was held relatively constant (mean number of capture sessions per year ± se = 13.3 ± 2.4). During each session the traps were deployed from dawn to dusk. Each bird was ringed with a numbered aluminium ring. Bird age (adult or juvenile) was assessed by plumage examination (Cramp 1985). Each year, capture sessions started in early May and lasted until late August, thereby covering pre-breeding migration, breeding and post-breeding migration. To limit bias in survival estimates due to the capture of transient migrating birds, we truncated the dataset to exclude birds caught during pre- or post-breeding movements. Pre-breeding migration in France starts in

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early April and ends in mid-June (Jarry 1994). Most birds migrating over Oléron Island in spring breed in western and north-western Europe (Aebischer 2002). For these populations, pre-breeding migration ends in late May (Boutin 2001). Consequently, we were confident that the risk of catching pre-breeding migrating birds was negligible from mid-May (first catching date = 13 May). In France, post-breeding migration starts in late July (Boutin 2001). We thus excluded birds caught after 31 July. Overall, our dataset included 352 captures (annual mean ± se = 50.3 ± 1.5) and 45 recaptures (mean ± se = 7.3 ± 0.7).

## Data analysis

### *Definition of wintering area*

Sparse recovery data suggest that Turtle Doves breeding in western Europe winter in western Africa, south of the Sahara desert (Morel 1985, Aebischer 2002). Additionally, censuses of large roosts in western Africa have shown that many of them (77%) were located in an area lying 17°–0°W, 12°–17°N (Jarry 1994), i.e. Senegal, Gambia, south-west of Mali and Burkina Faso. Accordingly, this area was considered as the wintering area for Turtle Doves breeding on Oléron Island.

### *Environmental covariates on wintering grounds*

First we modelled overwinter survival as a function of rainfall indices from western Africa for August to October (the peak of wet season). The indices were obtained at http://www.jisao.washington.edu/data_sets/sahel/. Rainfall indices were used from this large area (10°–20°N, 15°W–10°E), which largely determines water levels in the Niger and Senegal rivers (Zwarts *et al.* 2005).

Secondly, we considered the normalized difference vegetation index (NDVI) on wintering grounds as a potential correlate of survival. The NDVI is a measurement of chlorophyll density obtained from satellites of the US National Oceanic and Atmosphere Administration (NOAA). High NDVI values correspond to high chlorophyll densities, and indicate dense vegetation and thus potentially high seed availability (Tucker *et al.* 1991). Initially, we aimed at using NDVI values obtained during the whole wintering period of Turtle Doves (i.e. from August to March). Unfortunately, NDVI values were not available from January to March 2004. We therefore used NDVI values from August to December. NDVI values were obtained at http://iridl.ldeo.columbia.edu/SOURCES/.UMD/.GLCF/.GIMMS/.NDVIg/.global/.ndvi/.

Thirdly, we used the sum of yearly production for rice, millet and sorghum as a covariate reflecting annual variation in food supply. When arriving on wintering grounds (August/September), the wet season prevails and birds first consume millet, sorghum and wild seeds until November. We therefore used production values in the same year that we estimated survival. Afterwards, as the dry season begins, they mainly feed on mature rice (Morel 1987). Because rice is harvested from November to January, the yearly production statistic in a given year ($t$) is available only during the following year ($t+1$). Values were obtained from the Food and Agriculture of the United Nations (FAO) at http://faostat.fao.org/app_support/. Data referred to total net yearly production (in $10^6$ tons), excluding processing losses, and were compiled at two different spatial scales. The first considered cereal production over the whole of western Africa, while the second was restricted to the production of Mali and Senegal, where most Turtle Dove roosts (66%) have been located (Jarry 1994).

## Survival analyses

We used the time-dependent Cormack–Jolly–Seber (CJS) model (Lebreton *et al.* 1992) as a convenient departure model for analyses. This model adequately fitted the data (goodness-of-fit test; $\chi^2_{14} = 4.89$, $P = 0.99$; Choquet *et al.* 2005) as we found evidence for neither trap dependence (Test2.CT: $\chi^2_4 = 0.56$, $P = 0.97$) nor transience (Test3.SR: $\chi^2_5 = 4.33$, $P = 0.50$) in our dataset. In a first step, we used the information-theoretic approach to build a reference model that provided adequate description of the pattern of temporal variation in survival ($\phi$) and recapture probabilities ($p$). A set of candidate models that expressed various parameterizations for $\phi$ and $p$ (i.e. time-specific, constant over time, catch effort-dependent) were then developed and we used the Akaike Information Criteria (AIC$_c$) to rank and select models (Burnham & Anderson 2002).

Results showed that the model addressing time-dependence on survival and constant recapture probability over the study period ($\phi_t$; $p_{(.)}$) received a similar support to a competing model assuming constant survival and time-dependent recapture probability ($\Delta$AIC$_c = 0.15$; see Table S1). However, with this later model, $p$ was poorly estimated, with very large bounds (Table S1). Additionally, we found no evidence that yearly variation in recapture probability was related to yearly variation in catch effort (Table S1). Accordingly, we retained the model ($\phi_t$; $p_{(.)}$) as the reference model to further investigate whether yearly variation in survival was related to yearly variation in environmental covariates (i.e. rainfall, NDVI, cereals production). In this second step, the significance of each covariate was assessed separately following a hypothesis-testing approach (Grosbois *et al.* 2008). More precisely, we first assessed the fit of the covariate model (cov) relative to that of the time-dependent model ($t$) using deviance statistics (Dev) and the following likelihood ratio test: $\text{LRT}_{\text{cov}/t} = \text{Dev}(\text{model}\phi_{\text{cov}}) - \text{Dev}(\text{model}\phi_t)$. When $\text{LRT}_{\text{cov}/t}$ failed to detect variation in annual survival unexplained by the covariate (i.e. $P > 0.05$), we evaluated the statistical significance of the covariate by comparing the fit of the covariate model relative to that of the constant model, as follows: $\text{LRT}_{(.)/\text{cov}} = \text{Dev}(\text{model}\phi_{(.)}) - \text{Dev}(\text{model}\phi_{\text{cov}})$. Conversely, when $\text{LRT}_{\text{cov}/t}$ detected variation in annual survival rate that was unexplained by the covariate (i.e. $P < 0.05$), we evaluated the statistical significance of the covariate by using an analysis of deviance (ANODEV) and *F*-test statistics (Skalski *et al.* 1993, White & Burnham 1999). Here, the fraction of temporal variation in survival accounted for by the effects of covariates was assessed using the following formula:

$$R^2_{\mathrm{Dev}} = \frac{\mathrm{Dev}(\mathrm{model}\phi_{(.)}) - \mathrm{Dev}(\mathrm{model}\phi_{\mathrm{cov}})}{\mathrm{Dev}(\mathrm{model}\phi_{(.)}) - \mathrm{Dev}(\mathrm{model}\phi_{t})}$$

Environmental covariates were all standardized [(values – mean)/sd] to allow a direct comparison of their relative importance. All survival analyses were performed using the program MARK (White & Burnham 1999).

## RESULTS AND DISCUSSION

### Estimation of survival and recapture probabilities

Under the best fitting model ($\phi_t$; $p_{(.)}$), the recapture probability (± se) reached 0.20 ± 0.04. Survival estimates showed important year-to-year variations over the study period. On average, survival probability was 0.51 ± 0.15 with values ranging from 0.29 ± 0.18 to 0.99 ± 0.002. Overall, these were close to those estimated by Murton (1968) on the basis of ring recoveries from British Turtle Doves ringed until 1960 (i.e. adult annual survival of approximately 50%), as well as those gauged by Siriwardena *et al.* (2000) over the 1962–95 period. However, in this latter study, the authors distinguished survival rates between periods of stable (1962–78) and declining population trends (1979–95), respectively estimated at 0.623 and 0.525. Our estimates correspond to a period during which the abundance of the French breeding population over the last 15 years had ceased to decline and was slightly increasing (Juillard & Jiguet 2005). Several hypotheses might explain this paradox. In our study, survival rates were estimated using a capture–recapture scheme that did not allow us to separate mortality from permanent emigration. Contrary to Siriwardena *et al.* (2000) who used ring recovery data, we may have underestimated survival rates. This paradox might also suggest that important demographic traits other than survival drive population trajectories. Indeed, previous studies (Browne & Aebischer 2004, Browne *et al.* 2005) suggested that the reduction in the number of breeding attempts, and hence the number of young produced per pair, could have contributed significantly to the population decline of British Turtle Doves between 1941 and 2000.

### Environmental factors influencing survival

Among the four environmental covariates investigated, only NDVI and cereal production in Mali and Senegal were positively correlated (Pearson correlation; $r_4 = 0.83$, $P = 0.041$). The hypothesis-testing approach revealed that variation in the amount of cereal seeds produced annually in the Mali-Senegal area was a significant predictor of survival rates over the 1998–2004 period ($\mathrm{LRT}_{\mathrm{cov}/(.)}$: $\chi^2_1 = 7.80$, $P = 0.005$; Table 1). Examination of survival estimates with regard to cereal production showed that high annual survival probabilities matched years with high cereal production (Fig. 1), clearly indicating a positive relationship between these two variables (Table 1). Interestingly, this relationship remained significant when considering the amount of cereals harvested over western Africa (Table 1), suggesting either that birds breeding in Oléron Island overwintered in the Mali-Senegal area or alternatively that throughout the whole winter these birds could also rely on food supply located over a much larger area than these two countries. In support of this latter hypothesis, Morel (1986) reported that Turtle Doves may leave some wintering areas in Senegal in October and November to come back in December. Additionally, movements have been recorded during the wintering period, particularly towards Guinea (Morel 1987).

**Table 1.** Results of the hypothesis testing approach investigating whether yearly variation in survival over the 1998–2004 period was related to yearly variation in environmental covariates. Models are ranked according to deviance statistic and $\Delta\mathrm{AIC}_c$. $w_i$ refers to $\mathrm{AIC}_c$ weight and $n_p$ to the number of parameters in models. The fit of the covariate model (cov) relative to that of the time-dependent (*t*) and constant (.) survival models is assessed using likelihood-ratio tests ($\mathrm{LRT}_{\mathrm{cov}/t}$ and $\mathrm{LRT}_{\mathrm{cov}/(.)}$, respectively). *F*-statistics and *P* values are results from an analysis of deviance (ANODEV). The fraction of temporal variation in survival accounted for by covariates is shown ($R^2$), along with the slope of the parameter (Slope).

| | | | | $\mathrm{LRT}_{\mathrm{cov/t}}$ | | | $\mathrm{LRT}_{\mathrm{cov/(.)}}$ | | | ANODEV | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Models | Deviance | $\Delta\mathrm{AIC}_c$ | $w_i$ | $\chi^2$ | df | $P$ | $\chi^2$ | df | $P$ | $F$ | $P$ | $R^2$ (%) | Slope | $n_p$ |
| $\phi$ (Cereals production in W. Africa) $p_{(.)}$ | 38.40 | – | 0.50 | 5.69 | 4 | 0.22 | 7.95 | 1 | 0.005 | – | – | 58.3 | 0.64 | 3 |
| $\phi$ (Cereals production in Mali & Senegal) $p_{(.)}$ | 38.55 | 0.15 | 0.47 | 5.84 | 4 | 0.21 | 7.8 | 1 | 0.005 | – | – | 57.2 | 0.89 | 3 |
| $\phi$ (August–October rain index) $p_{(.)}$ | 45.10 | 6.70 | 0.02 | 12.38 | 4 | 0.015 | – | – | – | 0.41 | 0.6 | 9.2 | 0.31 | 3 |
| $\phi$ (August–December NDVI) $p_{(.)}$ | 46.08 | 7.68 | 0.01 | 13.37 | 4 | 0.001 | – | – | – | 0.08 | 0.8 | 2 | 0.15 | 3 |

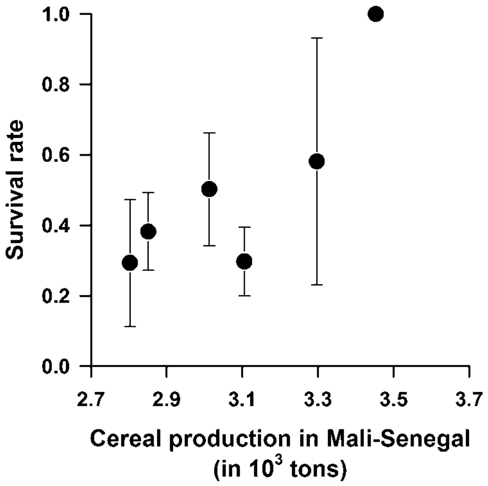

**Figure 1.** Relationship between annual production in cereals (rice, millet and sorghum) in Mali and Senegal and mean annual survival rates of adult Turtle Doves estimated from model $\phi_t$; $p_{(.)}$. Error bars represent ± se.

None of the remaining environmental covariates explained a significant amount of the temporal variation in survival (rainfall index ANODEV: $F_{1,3} = 0.41$, $P = 0.60$; NDVI ANODEV: $F_{1,3} = 0.08$, $P = 0.80$; Table 1). Interestingly, these findings contrast with previous studies showing a positive relationship between survival and rainfall (Møller 1989, Kanyamibwa *et al.* 1990, Peach *et al.* 1990, Szép 1995; Schaub *et al.* 2005) or between survival and NDVI index (Schaub *et al.* 2005). This suggests that, whilst these indirect estimates of food resources may be useful for a number of species, particularly insectivorous ones, variables more closely related to food availability such as cereal production may be more pertinent in the case of granivorous species such as the Turtle Dove. NDVI may be a poor proxy for food availability for doves as it corresponds to chlorophyll density assessed over a large variety of habitats, some of which may be unsuitable.

To conclude, the present study affords new insights into the population dynamics of Turtle Doves, particularly in response to environmental conditions experienced on their wintering grounds. Our results highlight the sensitivity of this species to agricultural changes over its wintering quarters. Although we speculate that our results could hold for other populations in western Europe (United Kingdom, Netherlands, Belgium and Luxembourg), we also recognize that more work is needed before drawing firm conclusions. In particular, the initiation of additional capture–recapture studies should be encouraged on other populations such as eastern ones. Indeed, these populations are suspected to winter in different parts of the sub-Saharan region (Jarry 1994) and accordingly, they might potentially experience different environmental constraints.

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## SUPPORTING INFORMATION

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

**Table S1.** Ranking of models for the analysis of Turtle Dove survival over the 1998–2004 period. ϕ refers to survival, *p* to recapture probability, (*t*) to time dependence, (effort) to trapping effort and (.) to constant. The best fitting model is shown in bold.