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Article

Disentangling the effects of environmental conditions on wintering and breeding grounds on age-specific survival rates in a trans-Saharan migratory raptor

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Migratory species are subject to environmental variability occurring on breeding and wintering grounds. Estimating the relative contribution of environmental factors experienced sequentially during breeding and wintering, and their potential interaction, to the variation of survival is crucial to predict population viability of migratory species. Here we investigated this issue for the Montagu's harrier *Circus pygargus*, a trans-Saharan migrant. We analysed capture–recapture data from a 29-year long monitoring of wing-tagged offspring and adults at two study sites in France (Rocheftort-RO and Maine-et-Loire-ML). The study period covers a climatic shift occurring in the Sahel with increasing rainfall following a period of droughts (Sahel greening). We found that harriers' adult survival in RO (between 1988 and 2005) varied over time and was sensitive to the interaction between the amount of rainfall in the Sahel and the annual mean breeding success, two proxies of prey availability. The occurrence of adverse conditions on breeding and wintering grounds in the same year decreased survival from 0.70–0.77 to 0.48 ± 0.05 . Juvenile survival in RO was slightly more sensitive to conditions in Europe than in the Sahel. Unexpectedly, lower survival rates were found in years with higher mean breeding success, suggesting compensatory density feedbacks may operate. By contrast, adult survival in ML, monitored between 1999 and 2017, was higher compared to RO (0.76 ± 0.03 versus 0.66 ± 0.02), remained constant and unaffected by any proxy of prey availability. This difference seems consistent with the fact that harriers in ML experienced better and especially less variable environmental conditions during breeding and wintering seasons compared to RO. Overall, we showed that survival of a migratory bird is sensitive to the level of variability in environmental conditions and that adverse conditions on wintering grounds can amplify the negative effects of conditions during the previous breeding season on birds' survival.

Keywords: capture–recapture, *Circus pygargus*, long-distance migrant, Montagu's harrier, NDVI, raptor, Sahel rainfall



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Introduction

Migratory birds have to cope with two sequential – and geographically distinct – environments during their annual cycle. Environmental conditions encountered on breeding and wintering grounds can affect vital rates and entail potential cascading effects on population dynamics (Norris 2005, Ratikainen et al. 2008, Zwarts et al. 2009). It has often been assumed that the wintering period is the main limiting period for birds and particularly so for migrants (Lack 1954, 1968), although empirical tests remain rare to date.

Among the 495 bird species breeding in western Europe (Hagemeier and Blair 1997), about 25% cross the Sahara Desert to winter in the Sahel (Zwarts et al. 2009), and there is indeed accumulating evidence that population dynamics of migrating birds are affected by environmental conditions in the Sahel (review in Newton 2008, Zwarts et al. 2009). In this semi-arid region at the southern edge of the Sahara, the amount of rainfall during the rainy season (typically June–October, i.e. before the arrival of birds from Europe) is highly variable and drives to a large extent the variation in food resources available for birds (Zwarts et al. 2009, Schaub et al. 2011, Norman and Peach 2013, Ockendon et al. 2014). Rainfall is a major factor limiting vegetation growth and, in turn, the development of arthropod biomass, a key resource for many Palearctic migrants wintering there. Survival of migratory species has indeed been shown to positively correlate with rainfall (Kanyamibwa et al. 1990, Peach et al. 1991, Szep 1995, Boano et al. 2004, Cowley and Siriwardena 2005, Mihoub et al. 2010, Johnston et al. 2016). Other proxies have been used for measuring environmental conditions on their wintering grounds: annual survival has been shown to increase with vegetation greenness (normalized difference vegetation index – NDVI) in the white stork *Ciconia ciconia* (Schaub et al. 2005) or with the annual yield of cereals in the turtle dove *Streptotelia turtur* (Eraud et al. 2009). Understanding the environmental factors that affect population dynamics of migratory species is of paramount importance for conservation as a recent analysis has revealed that long-distance migratory birds of Europe are experiencing a more pronounced decline than non-migratory species (Sanderson et al. 2006, Both et al. 2010, Vickery et al. 2014).

To date however, most studies focused on a single phase of the annual cycle or, at the best, treated the sequential phases independently from each other (Kanyamibwa et al. 1990, Boano et al. 2004, Mihoub et al. 2010, Blackburn and Cresswell 2016a). Integrating all phases of the annual cycle, and potential effects associated with the sequential distribution of individuals across time and space, is likely to improve our understanding of population dynamics (Ratikainen et al. 2008, van de Pol et al. 2010). Studies trying to disentangle the relative contribution of breeding and wintering conditions on survival of migratory populations remain rare (Cowley and Siriwardena 2005, Schaub et al. 2005, Grande et al. 2009, Halupka et al. 2017) and, moreover, do not investigate the potential interaction between successive

seasons. Indeed, conditions in one area or season could affect the ability of individuals, not only to reproduce (i.e. carry-over or non-lethal effects, Norris 2005) but also to survive the next one (Webster and Marra 2005, Morrison et al. 2013). For instance, poor conditions experienced on the breeding grounds might render the individuals more sensitive to the conditions they will experience on their wintering grounds. On the opposite, good conditions in one area could aid individuals to buffer subsequent adverse conditions.

As an attempt to fill this gap, we investigated the relative contribution of food resource variation on breeding and wintering grounds, specifically testing for their potential interaction, on the survival of a trans-Saharan migratory bird of prey, the Montagu's harrier *Circus pygargus*. The Montagu's harrier is a long-distance migrant breeding across the open farming landscapes of the western Palearctic, from northern Morocco to western Russia and Kazakhstan. Harriers breeding in western Europe spend the wintering season (October–March) in the western Sahel (Limiñana et al. 2012, Trierweiler et al. 2013, 2014), where they prey mostly on grasshoppers (Trierweiler and Koks 2009, Trierweiler et al. 2014, Augiron et al. 2015, Schlaich et al. 2016). In France, harrier diet is mainly composed by common voles *Microtus arvalis* which densities strongly affect the number of breeding pairs, reproductive success and possibly survival (Millon and Bretagnolle 2008). Here we took advantage of two long-term capture–recapture datasets collected in two distinct breeding areas of western France, spanning 29 years, to investigate the response of harrier survival to environmental variation experienced during breeding and winter. Specifically, we estimated the relative contribution of environmental conditions experienced sequentially during the breeding and wintering periods on age- and sex-specific survival rates. During the study period occurred a regime shift characterised by an increase in rainfall during the rainy season (the so-called 'Sahel greening'; Dardel et al. 2014a). Therefore, we expected the strength of the relationship between wintering conditions and survival to be weaker as average environmental conditions improved and/or temporal variance decreased. Finally, we tested whether sequential environmental conditions interacted between each other to amplify, or alternatively buffer, the variation in survival. Specifically, we hypothesised that harsh environmental conditions successively experienced on breeding and wintering grounds might exacerbate reproduction costs and thus reduce adult survival.

Material and methods

Breeding areas and capture–recapture datasets

The study was carried out in two distinct areas of central western France. The marshes of Rochefort (hereafter RO, 45°57'N, 0°55'W) are an agricultural region of 190 km² covered by a mix of wet meadows and cereal crops (wheat and maize). This study area was monitored between 1988

and 2005 and hosted an average of 24 breeding pairs (range: 7–46). The second study area located in Maine-et-Loire (hereafter ML, 47°09'N, 0°14'W) covers 250 km² at the eastern margin of the large cereal plains of the Poitou-Charentes region. This area is covered by vineyards and woods on hill-tops whereas lower grounds are covered by annual crops, mostly wheat. ML was monitored between 1999 and 2016 and hosted an average of 44 breeding pairs (range: 28–59; Supplementary material Appendix 1 Fig. A1). The two study sites are located about 140 km apart from each other. The overall study period thus spans 29 years and the two areas share a common monitoring period of six years (1999–2005).

For each area, we built a capture–recapture dataset including birds marked as adults with a wing-tag attached to each patagium. We monitored a total of 180 individuals in RO (96 males, 84 females) and 429 in ML (256 males, 173 females). A third dataset was used for estimating juvenile (i.e. first-year) survival rates, gathering 456 birds wing-tagged as chicks in RO between 1988 and 1999 (i.e. 12 cohorts composed of 239 males and 217 females; sex identification based on dimorphism of iris colour and biometry; Leroux and Bretagnolle 1996). The period of resighting for juveniles extended until 2003. Twenty-eight individuals with undetermined sex were removed from the dataset. Birds marked as chicks that subsequently bred in RO were included in the adult dataset from their first breeding event onwards. Sites and capture methods remained similar throughout the study period. Birds were caught either at the nest during the chick-rearing period using a clap-net or with a lace on a pole located at the field margin. At the same time, and for each area, breeding data (localisation of breeding pairs, identification of wing-tagged individuals, clutch size, number of chicks fledged) were collected and nests were protected from harassing activities whenever required (Santangeli et al. 2015).

Proxies for food availability in summer and winter

Because direct estimates of food resources available to harriers were lacking on breeding and wintering grounds (except for RO, see below), we searched for relevant proxies of prey availability. In RO, Millon and Bretagnolle (2008) showed a strong log-linear positive relationship between mean vole density (estimated by live trapping) and annual mean breeding success (number of fledglings per pair). We therefore used the annual mean number of fledglings per pair for each area as a proxy for food availability during the breeding season and further checked consistency between models incorporating either breeding success or vole density in RO (on log scale).

We defined the wintering range of Montagu's harriers based on GPS-tracking data of 33 birds caught during breeding in west-European countries (France: five males/three females; Denmark: 3/3; Germany: 1/0, Holland: 14/4) between 2009 and 2015 (Schlaich et al. 2016). Each bird provided information regarding wintering locations for one to five years. The wintering area was derived from a total of 208 sites (two to 15 sites per bird), taking the centre of each site in which a bird

stayed for at least three days within a 15-km radius. For this, we calculated a 75% kernel of all wintering sites ($n=196$) using Kernel Density tool in ArcGIS ver. 10.3.1 and derived a map of the overall wintering range (ca 11°13'–18°11'N and 17°6'W–8°4'E; Supplementary material Appendix 1 Fig. A2).

We then produced three different proxies to estimate food availability on the wintering grounds. First, we used monthly rainfall anomalies occurring during the Sahel rainy season (June–October), assuming that a wetter rainy season typically induces higher vegetation growth which in turn results in higher abundance of herbivorous insects, such as grasshoppers (Cheke and Holt 1993, Todd et al. 2002). Rainfall anomalies were obtained at http://research.jisao.washington.edu/data_sets/sahel/ from 68 meteorological stations located throughout the western Sahel (10°–20°N, 20°W–10°E). Second, we used the normalized difference vegetation index (NDVI), a measure of vegetation greenness, averaged over the wintering range between September and March, assuming the greener the vegetation the more abundant phytophagous orthopterans. NDVI maps were downloaded from the Land Processes Distributed Active Archive Center (LP DAAC, <<https://lpdaac.usgs.gov>>) using two distinct datasets covering the entire study period: VIP15 (from 1980 to 2014) and MODIS13C1 (since 2014) and providing data every 16 d at a 5.6 km spatial resolution for the wintering period (September–March). Finally, we used a mechanistic approach based on the knowledge of harrier ecology during winter in the Sahel as an attempt to derive a more relevant index of environmental conditions in winter. The abundance of grasshoppers has been shown to positively correlate with NDVI (Augiron et al. 2015). Furthermore, the amount of time spent flying and hunting by GPS-tracked Montagu's harriers steeply increases in areas where NDVI values go below a threshold ranging between 0.19 and 0.25 (Schlaich et al. 2016). We considered that NDVI values below the median of this range (0.22) indicate low prey abundance and induced increased hunting effort. Considering this, we built an annual covariate, the aridity index, by summing $|\text{NDVI}-0.22|$ for all NDVI values falling below 0.22. This index integrates thus both the duration and intensity of harsh conditions on the wintering grounds (Supplementary material Appendix 1 Fig. A3). Finally, we checked for consistency between mean NDVI and aridity index for the wintering range derived from all birds versus from only the eight birds breeding in western France. Correlation coefficients between ranges were high for both covariates ($r=0.95$ and 0.99 , $p<0.001$, for NDVI and aridity index, respectively).

Statistical analysis

We adopted a Cormack–Jolly–Seber (CJS) formulation (Lebreton et al. 1992) as umbrella model for all datasets and to estimate apparent survival rate S and recapture probability p . We performed goodness-of-fit tests (GOF) to confirm the validation of CJS-related hypotheses with U-Care 2.3.2 (Choquet et al. 2009a). Details on GOF results, modelling

recapture and survival for these three datasets are presented in Supplementary material Appendix 1.

Capture–recapture models were fitted using E-Surge ver. 2.1.4 (Choquet et al. 2009b). We searched for the best model parameterisation according to a three-step process involving: 1) the simplification of p parameterisation keeping the survival one with the umbrella structure, 2) the search for the most adequate model structure for S regarding age and sex effects with the most parsimonious structure for recapture selected at step 1, and finally 3) the test for linear or logarithmic trends of the different environmental covariates related to breeding (average breeding success, vole density) and wintering conditions (western Sahel rainfall, NDVI and aridity index). Logarithmic trends would reveal an accelerated deterioration in survival below a given threshold (not used for aridity index). The difference in study period precluded a joint analysis of the two adult datasets. Environmental covariates were standardised such that their relative contribution can be evaluated by comparing their regression coefficients. All combinations of wintering and breeding proxies were tested in an additive way. In this last step, we tested for interactive effects between the best environmental covariates of each season in a ‘breeding-to-wintering’ sequence. Indeed, our monitoring based on resightings made in Europe did not allow us to test the ‘wintering-to-breeding’ sequence. For this purpose, environmental covariates were categorised as two-level factors (below/above average). We selected models based on the Akaike’s information criterion corrected for small sample size (AICc; Burnham and Anderson 2002). The statistical significance of covariates was evaluated using an analysis of deviance (ANODEV) according to the following formula (Skalski 1996, Grosbois et al. 2008):

$$F = \frac{\text{Dev}_{(i)} - \text{Dev}_{(\text{cov})}}{\text{Dev}_{(\text{cov})} - \text{Dev}_{(t)}} \times (k_i - k_{\text{cov}})$$

where k_i and k_{cov} are the number of estimable parameters of time-dependent model and the model with covariates respectively. $\text{Dev}_{(i)}$ refers to the deviance of a model assuming constant survival through time. We further evaluated the proportion of deviance explained by the covariates using:

$$\% \text{Dev} = \frac{\text{Dev}_{(i)} - \text{Dev}_{(\text{cov})}}{\text{Dev}_{(i)} - \text{Dev}_{(t)}}$$

Environmental covariates were standardised so as to evaluate the relative contribution of each covariate using the comparison of the absolute value of their respective slope (β).

Descriptive statistics are presented as mean \pm 1 SD (with coefficient of variation, hereafter CV) and effect size as mean \pm 1 SE, using R ver. 3.4.1 (R Core Team).

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.1gv4k74>> (Millon et al. 2019).

Results

Environmental variability on breeding and wintering grounds

On the breeding grounds, harriers in the two study areas experienced similar average breeding success, our proxy for summer food availability (Fig. 1a; RO: 1.65 ± 0.74 fledglings per pair, ML: 1.68 ± 0.39). However, RO experienced twice as high inter-annual variation of average breeding success compared to ML (RO: CV = 44.9%, ML: CV = 23.4%).

On the wintering grounds, harriers from RO encountered marginally harsher but especially more variable environmental conditions for the 1988–2005 period, compared

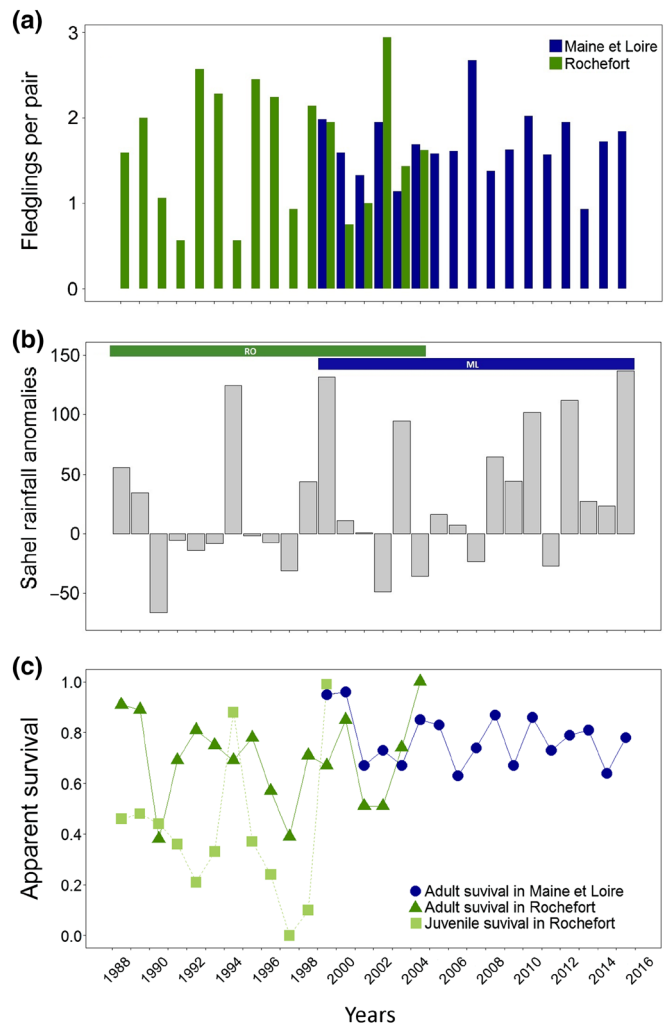


Figure 1. Time-series analyses of: (a) average annual breeding success (fledglings per pair) during the whole study period for Rochefort (green) and Maine et Loire (blue); (b) annual rainfall anomalies during the Sahel rainy season (June–October, in cm, with respect to the 1980–2009 mean) and (c) apparent adult (RO and ML) and juvenile (RO) survival rates of wing-tagged Montagu’s harriers. Estimates are taken from time-dependent models with no covariates (models a9, b6 and c14; Table 1).

Table 1. Results of model selection for age-specific survival of Montagu's harriers wing-tagged in Maine-et-Loire (ML, adult birds only, 1999–2016) and Rochefort (RO, adult birds, 1988–2005, juveniles with 12 cohorts, 1988–1999). Akaike's information criterion (AICc) and Δ AICc are provided (best model in bold) together with the number of parameters k . Apparent survival rates were modelled as constant (\cdot), age-dependent (a) or time-dependent (t). Time-dependent models were also fitted with several combinations and transformations of the following covariates: average annual breeding success (BS) as a measure of environmental conditions experienced in Europe, and the amount of rainfall received during the rainy season (rain), mean NDVI (NDVI) and aridity index (aridity) in the western Sahel. Interactions between seasonal covariates were tested after transforming them as two-level factors (e.g. f.BS \times f.rain, see Methods). Only a subset of key models is shown here, see Supplementary material Appendix 1 for a full list of models.

Model		AICc	Δ AICc	k
(a) Adult survival ML				
1	S (\cdot)	2040.34	0.00	7
3	S (aridity)	2042.62	2.28	9
4	S (log BS)	2043.96	3.62	9
5	S (rain)	2044.06	3.72	9
6	S (log rain)	2044.12	3.78	9
7	S (BS)	2044.19	3.85	9
8	S (BS+aridity)	2046.33	5.99	11
9	S (t)	2047.45	7.11	23
10	S (log BS+rain)	2047.70	7.35	11
11	S (log BS+log rain)	2047.74	7.39	11
12	S (BS+rain)	2047.92	7.58	11
13	S (BS+log rain)	2047.97	7.63	11
14	S (f.log BS \times f.aridity)	2048.11	7.77	13
(b) Adult survival RO				
1	S (f.BS\timesf.log rain)	843.90	0.00	5
2	S (BS+log rain)	845.76	1.86	4
3	S (BS+rain)	847.90	4.00	4
4	S (log rain)	848.79	4.89	3
6	S (t)	850.50	6.60	18
7	S (rain)	851.54	7.64	3
8	S (BS)	854.21	10.31	3
9	S (BS+aridity)	854.74	10.84	4
10	S (aridity)	855.23	11.33	3
11	S (log BS)	855.36	11.46	3
12	S (\cdot)	855.64	11.74	2
13	S (log NDVI)	857.06	13.16	3
14	S (NDVI)	857.24	13.34	3
(c) Juvenile survival RO				
1	S (BS+rain)	704.23	0.00	8
2	S (BS)	704.32	0.09	7
3	S (a (1, 2, 3))	704.65	0.42	6
4	S (BS+log rain)	704.73	0.50	8
5	S (log BS)	704.81	0.58	7
6	S (rain)	704.85	0.61	7
7	S (log rain)	705.79	1.55	7
8	S (BS+aridity)	706.37	2.13	8
9	S (aridity)	706.64	2.40	7
10	S (aridity)	706.68	2.44	7
11	S (log NDVI)	706.69	2.46	7
12	S (NDVI)	706.70	2.47	7
13	S (f.BS \times f.rain)	708.33	4.10	9
14	S (a (1).t+a (2, 3))	715.61	11.38	17

to those from ML between 1999 and 2016. Average rainfall during the rainy season indicated drier years during the earlier study period of RO compared to the later study period of ML, although this difference was not significant (RO: 16.4 ± 57.4 cm; ML: 37.4 ± 59.5 ; $\beta = -21.1 \pm 20$, $p = 0.30$; Fig. 1b). The coefficient of variation was however twice as large for RO compared to ML (351% vs 159%). The same pattern arose for mean NDVI (RO: 2.20 ± 0.18 , CV = 8.0%, ML: 2.31 ± 0.09 , CV = 3.7%; $\beta = -0.11 \pm 0.05$, $p = 0.03$) and the aridity index (RO: 3.47 ± 1.75 , CV = 50.5%, ML: 2.69 ± 0.49 , CV = 18.1%, $\beta = 0.78 \pm 0.44$, $p = 0.09$).

Environment-mediated variation in age-specific survival

Capture–recapture data for adults showed no deviation from CJS hypotheses in RO ($\chi^2_{70} = 56.9$, $p = 0.87$). However, trap-dependence in both males and females and transience in only females were detected in ML ($\chi^2_{116} = 143$, $p = 0.05$). Both sources of heterogeneity have been accounted for (Supplementary material Appendix 1). Adult survival in ML was constant over time and did not differ between males and non-transient females ($S_m = 0.76 \pm 0.03$, $S_{nt,f} = 0.76 \pm 0.02$; model a1, Table 1, Fig. 1c). We did not detect any significant effect of environmental covariates on both breeding and wintering grounds on adult survival. In contrast, adult survival in RO was lower than in ML, averaging 0.66 ± 0.02 (model b12, Table 1). As for ML, survival did not differ between males and females. However, we found a significant among-year variation in RO (Δ AICc = 5.1 compare models b6 and b12, Table 1, Fig. 1c). This temporal variation in adult survival was mainly driven by an interaction between environmental conditions experienced by harriers on breeding and wintering grounds (average annual breeding success and rainfall in the Sahel, respectively; model b1, Table 1). Adult survival dropped at 0.48 ± 0.05 in years combining low rainfall level in the Sahel and poor breeding success in Europe (Fig. 2). Five years showed this detrimental environmental sequence: 1990, 1991, 1997, 2001 and 2004 (Fig. 1c). In all other years, adult survival rates were closed to values observed in ML (0.70–0.77). This model, accounting for an interaction between average annual breeding success and rainfall in the Sahel, explained 46% of deviance in adult survival ($F_{3,13} = 11.13$, $p < 0.01$). We found no significant correlation between adult survival and NDVI or aridity index (model b14: $\beta = -0.08 \pm 0.12$ and model b10: $\beta = 0.20 \pm 0.13$, respectively). It is noteworthy that replacing mean annual breeding success by direct estimates of vole density produced similar results for RO (Δ AICc = 0.35; Supplementary material Appendix 1 Table A3). Despite this contrast between RO and ML, annual adult survival rates were relatively synchronous between areas during the six years in common (Fig. 1c).

Juvenile survival, estimated only in RO from a sample of harriers wing-tagged as chicks, was lower and more

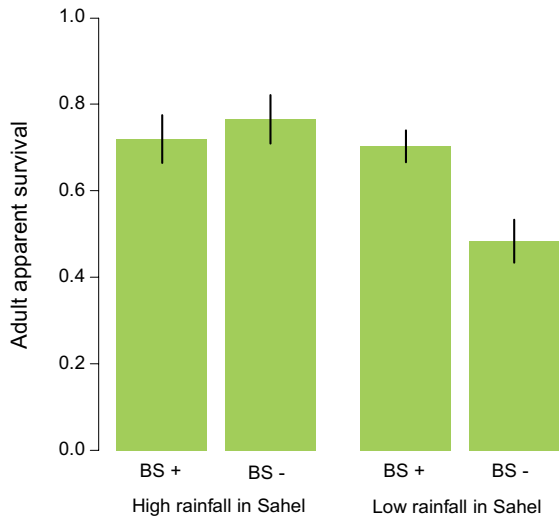


Figure 2. Variation in adult apparent survival of Montagu's harrier in Rochefort (1988–2005). Averaged estimates (± 1 SE) are taken from model b1 (Table 1) that includes an interaction between average annual breeding success (BS) as a proxy for environmental conditions in Europe and the amount of rainfall during the rainy season in the western Sahel (rainfall in Sahel) as a proxy of wintering conditions. Environmental covariates were categorised as two-level factors according to whether the annual value was above or below the average (BS+/BS-, high/low rainfall, see Methods).

variable than adult survival in the same area ($S_{a1} = 0.35 \pm 0.07$, $S_{a2+} = 0.62 \pm 0.05$, model c3, Table 1). As for adults, juvenile survival did not differ between males and females and its

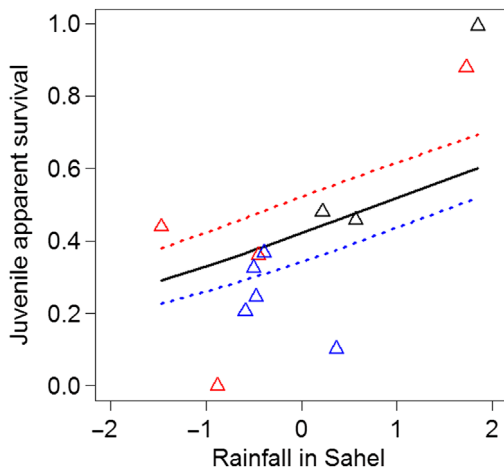


Figure 3. Relationship between apparent juvenile survival and the amount of rainfall during the rainy season in the western Sahel (standardised values) for 12 cohorts of Montagu's harriers tagged between 1988 and 1999 in Rochefort. Estimates were taken from models c1 (Table 1). This model also includes an additive effect of average annual breeding success. Black, red and blue lines indicate predicted values for the average, the first and third quartiles of average annual breeding success, respectively. Triangles present annual juvenile survival estimates from a time-dependent model without any covariate (same as in Fig. 1; model c14). Their colour refers to the categorisation described above.

temporal variation was driven by both breeding and wintering environmental conditions. Juvenile survival was positively correlated with rainfall in the Sahel (model c1, $\beta = 0.39 \pm 0.29$) but, in contrast to adults, was negatively correlated with mean annual breeding success (model c1, $\beta = -0.45 \pm 0.29$). Unexpectedly, chicks born in years with high mean breeding success (i.e. peak vole years) showed lower survival compared to chicks born in years with low mean breeding success. The best model, accounting for an additive effect of breeding success and Sahel rainfall during the rainy season, explained 38% of deviance ($F_{11}^2 = 6.03$, $p < 0.025$, model c1; Fig. 3). Average annual breeding success contributed more than rainfall to the variation in annual survival. Contrary to adults, we did not detect a significant interaction between covariates related to wintering and breeding environmental conditions (model 13, Table 1).

Discussion

Survival response to environmental variability

This long-term study allowed us to apprehend how changes in environmental variability affect survival of a long-distance migrant over the long-term. The two breeding areas in France were subject to different between-year variations in mean breeding success, putatively in link with the availability of harrier's main prey, the common vole (Millon and Bretagnolle 2008). If mean breeding success was similar between the two study areas, the coefficient of variation was twice as large in RO compared to ML. Over the course of the study period (1988–2016), the amount rainfall in the Sahel increased from the 2000s onwards, following three decades characterised by severe droughts at the end of the 20th century. This climatic shift, also called 'Sahel greening', has led to an enhanced primary production in the area (Olsson et al. 2005, Dardel et al. 2014b), although concurrent changes in land use and vegetation communities affect bird guilds differentially (Zwarts et al. 2015, 2018). Overall, environmental conditions during the whole annual cycle were thus more favourable (slightly higher average values for the wintering period), and especially less variable (reduced among-year variation in both breeding and wintering conditions) for harriers in ML (1999–2016) than for harriers in RO (1988–2005). Increased environmental variation is expected to reduce mean vital rates in most instances (Henden et al. 2008, van de Pol et al. 2010) and, in line with this, adult survival in ML was significantly higher than in RO (0.76 ± 0.03 vs 0.66 ± 0.02 , respectively). Furthermore, while we found significant effects of environmental proxies on adult survival in RO, survival in ML remained relatively constant over time. These results suggest the occurrence of a threshold in terms of environmental quality, below which adult survival becomes sensitive to the environment and starts to deteriorate.

Apparent survival, however, includes both true survival and permanent emigration outside the study area (Schaub and Royle 2014). Therefore, we cannot exclude that part of

the difference in adult survival rates between the two sites may arise from a higher dispersal propensity of birds breeding in RO, as a response to deteriorating breeding conditions (Millon and Bretagnolle 2008; see Supplementary material Appendix 1 Fig. A1 for time-series of breeding numbers). The positive effect of the recent increase in Sahel rainfall on bird survival is also apparent when comparing the results of studies conducted on different periods of time for the white stork (Kanyamibwa et al. 1990, Nevoux et al. 2008) and the sand martin *Riparia riparia* (Szep 1995, Cowley and Siriwardena 2005, Masoero et al. 2016).

Rainfall appeared as a better proxy than NDVI for environmental wintering conditions in the western Sahel. Mihoub et al. (2010) also found a positive effect of Sahel rainfall, but not of NDVI, on juvenile survival for the lesser kestrel *Falco naumanni*, a raptor with a similar wintering ecology. These results seem to be in line with other studies comparing the relative merit of NDVI and rainfall in the Sahel at a broad spatial scale (Ockendon et al. 2014). We expected that our aridity index, derived from NDVI but including a species-relevant threshold, would more closely reveal the quality of environmental conditions for harriers during the critical final stage of wintering. However, as for NDVI, we did not detect any significant correlation with harrier survival. Interestingly, NDVI does not strongly correlate with rainfall ($r = 0.49$), possibly due to different timing of rainfall in various regions and land-use types. Vegetation greenness alone does not directly explain food availability especially when considering that the recent re-greening of the Sahel includes non-native plants with little value for biodiversity (Herrmann et al. 2014). If NDVI has been previously associated with survival in some bird species, studies conducted on a finer scale using individual foraging data may shed some light on the contrasting results to date (Blackburn and Cresswell 2016b, Schlaich et al. 2016).

Both breeding and wintering environments contribute to age-specific variation in survival

Montagu's harriers spend about four months on their breeding grounds in Europe, migrate between Europe and Africa, crossing the Sahara Desert, for 1–2 months and winter in the Sahel region for the rest of the year (6–7 months; Augiron et al. 2015, Schlaich et al. 2016). Adult survival significantly varied among years in RO during the 1988–2005 period. Our results revealed the occurrence of an interactive effect of successive environmental conditions Montagu's harriers are coping with throughout their life cycle. Adult survival rates were above 0.70 providing birds experienced good conditions on either wintering or breeding grounds. However, in years with both low levels of rainfall in the Sahel and poor breeding success in France, adult survival rate dropped below 0.50. These two environmental proxies, likely to reveal the level of prey available for harriers during the two longest phases of the annual cycle (breeding and wintering season; Millon and Bretagnolle 2008,

Schlaich et al. 2016), explained almost half of the overall deviance in survival (46%).

Juvenile survival, estimated in RO only (12 cohorts from 1988 to 1999) was also sensitive to both rainfall in Sahel and annual breeding success in France, with a proportion of deviance explained however smaller than for adults (38%). In contrast with adult survival, we found no interactive effect and juvenile survival was found to be primarily sensitive to environmental conditions on the breeding grounds, with an additive effect of rainfall in the Sahel. Chicks were wing-tagged when ca 25 d old, i.e. about a week before fledging (note that some nests were fenced to protect them from harvesting activities, which also reduces predation risk before fledging). Juvenile survival thus included the critical phase of emancipation post-fledging where a peak of mortality typically occurs in many birds, with reduced flight ability putting young birds at risk of predation and starvation (Coles and Petty 1997, Cox et al. 2014). Unexpectedly, the effect of mean breeding success was negative, meaning that juveniles experienced lower survival when born in years with higher mean breeding success (i.e. higher vole density). As a consequence, juvenile and adult survival rates were not correlated (Fig. 1c). Three non-mutually hypotheses can account for this. First, density-dependent processes can increase mortality as population size increases, and young individuals are expected to suffer more than adults from increased competition. Both adults and juveniles feed mainly on voles and grasshoppers during the post-fledging period. The number of juvenile Montagu's harriers produced varies drastically among years in link with vole density (Millon and Bretagnolle 2008), and the variation can reach one order of magnitude (range in RO between 1987 and 2005: 4–112, mean: 44.6 ± 33.7). Following peak vole years, competition for food resources can then be high and result in elevated mortality for inexperienced juveniles during the critical phases of emancipation and migration. Second, it has been shown that juveniles fledging in years with high vole abundance were carotenoid-limited compared to juveniles born in poor vole years, the latter being fed with alternative prey, birds and insects mostly (Salamolard et al. 2000). This pigment is involved in the immune response and birds with higher levels may be fitter (Sternalski et al. 2010, 2012). Offspring fed with a lower proportion of voles may actually benefit from an improved immune condition helping them to survive the first winter, providing they overcome food limitation at birth. Third, in food-restricted years, breeding individuals are a non-random sample of the adult population, of high intrinsic quality, which are possibly able to compensate for food shortage and therefore produce offspring with higher survival probability. On the opposite, in poor vole years, most harriers are probably able to breed, including individuals of poor quality that may produce chicks with lower survival probability.

To date, few studies looked simultaneously at environmental conditions influencing migratory bird survival during wintering and breeding periods. In the Egyptian vulture *Neophron percnopterus*, Grande et al. (2009) found a positive

effect of environmental conditions on the breeding grounds on juvenile survival only, while environmental conditions on the wintering grounds affected survival in all age classes. Schaub et al. (2005) found that age-specific survival positively correlated with primary production measured by NDVI in the white stork, on a major stop-over for Polish and German populations in the eastern Sahel, whereas environmental conditions during breeding had no effect. In a French population of white storks, Nevoux et al. (2008) also found a greater impact on survival of Sahel rainfall than a climatic index on the breeding grounds (winter North Atlantic Oscillation). Interestingly in a shorter-lived species, the sand martin, annual survival rates (juveniles and adults combined) were negatively affected by rainfall on the breeding grounds, because wetter conditions reduce foraging, than by rainfall in the Sahel (positive effect with higher insect biomass in wetter years; Cowley and Siriwardena 2005).

We are not aware of any study looking at the possible interaction between environmental conditions experienced sequentially between breeding and wintering grounds on survival. Here we specifically tested for such an interaction, hypothesising that good conditions on the breeding grounds could allow birds to better cope with possibly adverse environmental conditions on the wintering grounds or that the succession of a low vole year in Europe and a low amount of rainfall in the Sahel would result in catastrophic mortality. We did find some evidence for such an interaction and more attention should be paid to the link between successive environments when investigating survival of migratory species. Note that the interaction of the alternative sequence (wintering–breeding) has been extensively studied regarding carry-over (i.e. non-lethal) effects on reproductive output (Norris 2005).

Based upon a sample of 69 individuals of three trans-Saharan migrating raptors tracked by satellite transmitters, Klaassen et al. (2014) were able to measure where and when mortality occurs during the whole annual cycle. For the Montagu's harrier, the two migration phases were associated with the highest daily mortality risk, especially during spring migration. When accounting for the duration of each phase however, mortality was roughly equally spread among the four phases of the harrier's annual cycle (breeding, autumn migration, wintering, spring migration). Mean annual mortality rates found in this study for the three species suggested, however, that the burden imposed by the transmitters may have increased mortality (0.59 for harriers tracked between 2005 and 2011 compared to our estimates of 0.76 ± 0.03 for ML). Our proxies for environmental conditions ignore the conditions during migration. In the light of this, the proportion of deviance explained by our breeding/wintering-related covariates (36–46%) were relatively high. Assessing the conditions during the time-restricted, but crucial, migration periods remains a challenge. Indeed, mortality during these periods seems to be associated to short-term, and spatially localised, weather conditions to which birds might be confronted to (Klaassen et al. 2014). Wind data, available

at global scale from the National Oceanic and Atmospheric Administration since May 2011 at a 0.5-degree resolution-scale, could be gathered in the future to test this hypothesis.

In conclusion, we found that adult and juvenile survival rates of Montagu's harriers were impacted by the conditions experienced on both breeding and wintering grounds, with evidence for an interaction between the two successive environments for adults. Increased variability in environmental conditions resulted, as expected, in lower survival rates. Studies looking at the relative contribution of breeding and wintering environments on vital rates, survival but also reproduction, are critically needed to understand the demography of long-distance migratory birds and improve their conservation. Future studies should particularly pay attention to provide results (standardised effect size) that would allow comparative work to be performed, such a synthesis being currently lacking.

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Supplementary material (available online as Appendix jav-02233 at <www.avianbiology.org/appendix/jav-02233>). Appendix 1.