Population dynamics of two endangered bird species, *Upupa epops* and *Jynx torquilla*, in Valais (Switzerland)

Inauguraldissertation
der Philosophisch-naturwissenschaftlichen Fakultät
der Universität Bern

vorgelegt von

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von Schwyz

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Contents

1 General introduction 1

2 Analysis of European ring recoveries 15

3 Stable isotopes reveal wintering grounds in Hoopoes 37

4 Stable isotopes and migratory connectivity in Wrynecks 65

1

General Introduction

1.1 Population dynamics and conservation

The dynamics and sizes of populations are governed by temporal variation of demographic rates, as those fluctuate due to stochastic, density independent effects (e.g. environmental variation), or due to deterministic, density dependent effects (Leirs et al. 1997; Sæther & Engen 2002; Sibly et al. 2002). Declines of various animal populations gave raise to the declining population paradigm (Caughley 1994) and have alerted conservationists and population dynamicists: they have thus started working together in an attempt to understand the underlying demographic mechanisms of population changes (declines) and to propose targeted corrective measures. The key unifying variable linking various facets of population ecology is the local population growth rate (Sibly et al. 2002), which is a function of the demographic rates (survival, reproduction, immigration, emigration; Williams et al. 2002). If the local population growth rate experiences a change over time, at least one of the four demographic rates must have changed. A complete understanding of population dynamics requires therefore the study of the variation of demographic rates over time and how much a change of a particular demographic parameter impacts the population growth rate. By including all available knowledge on the ecology and the dynamics of a species (i.e. including vital rates and very importantly the factors limiting/influencing these rates), tailored conservation measures can be drawn to effectively restore endangered populations.

In recent years, many European bird populations have undergone dramatic declines (Berthold 1993; Tucker & Heath 1994). Among other reasons, habitat degradation or loss, as well as climate change with its consequences have been made responsible for negative growth rates in bird populations (Norris et al. 2004b; Lemoine et al. 2007a; Lemoine et al. 2007b; Robinson et al. 2007; Whittingham et al. 2007). In migratory birds, unlike in sedentary ones, the population dynamics can be influenced by conditions (environment and density) in more than one part of the world, namely by conditions in the breeding and wintering areas, as well as during migration or by all of the above (Newton 2004). Local food availability mediated through environment or competition seems to exert a big influence on demographic parameters affecting one or several demographic rates, either in immediate or in delayed ways. Examples of immediate effects on vital rates due to low food availability (resulting from e.g. adverse weather conditions or farming intensification) include reduced reproductive output and survival during breeding (McDonald et al. 2004; Cowley & Siriwardena 2005; Britschgi et al. 2006; Geiser et al. 2008), or increased mortality during non-breeding (Schaub et al. 2005). Delayed effects, which for example can result from unfavourable conditions during one stage affecting a subsequent or later stages of the annual cycle have been termed carry-over effects (Marra et al. 1998; Norris et al. 2004a; Saino et al. 2004; Newton 2004), and can have important consequences on the population dynamics (Norris 2005). In order to study the population dynamics of migratory birds and link stochastic and deterministic effects with varying population sizes, it is essential to take the different life cycle stages (and the conditions during those) into account. This requires, first of all, good demographic data, and, second, that the locations of the different stages of these species are known during their annual cycle.

1.2 The Hoopoe and Wryneck as model species

In Switzerland, populations of the long-distant migratory species *Upupa epops* (Linnaeus 1758) of the Upupidae family and *Jynx torquilla* (Linnaeus 1758) of the Picidae family have declined during the second half of the 20th century. These species are on the national Red List (Keller et al. 2001) and belong to the 50 priority species (Swiss Ornithological Institute) for which action plans are under development. Once widely distributed in the whole of Switzerland, the core breeding population of Hoopoes is restricted nowadays to the Canton of Valais (Arlettaz & Fournier 1998), whereas the Wryneck is mainly breeding in the Cantons Valais, Grisons and Ticino (Schaub & Lüthy 1998). Both species are secondary cavity breeders (they rely on existing cavities as they are unable to excavate nesting holes by themselves), inhabiting semi-open to open landscapes in arable land, and are specialized foragers feeding on ground-dwelling arthropods (Glutz von Blotzheim & Bauer 1966). Wintering areas of these two species are assumed to be south of the Sahara Desert in the Sahel, with some populations remaining in southern parts of Europe in the Mediterranean area. However, wintering grounds of particular breeding populations are generally not identified. Besides the known variability of reproductive output in both species, most probably resulting from variable climatic conditions (Geiser et al. 2008; Schaad 2002), other demographic parameters (i.e. survival, immigration) for the Swiss and generally also for other populations remain completely unknown. Consequently, the demographic reasons for the population changes are unidentified.

The University of Bern and the Swiss Ornithological Institute Sempach have launched in collaboration a project to restore the local Hoopoe population and to study the population dynamics of the two species on the plain of the Rhone river Valley in the lower part of the Canton Valais. The plain is dominated by intensive agriculture, including orchards, vineyards and vegetable plantations. Between Sierre and Martigny (approximately 46° 14’ N, 7° 22’ E) over 700 nestboxes were installed in small agricultural sheds in orchards on the plain between 1998 and 2002; the study site extends over an area of approximately 62 km^2. The nestboxes should have the effect that Hoopoes have shorter travelling distances between breeding sites and foraging areas, since the main prey of Hoopoes (molecrickets) is very abundant on the plain but natural cavities for breeding occurred almost exclusively on the slopes. Reducing this extra energy expenditures induced by commuting costs during foraging should increase the birds breeding performance. Shortly after the implementation of these conservation measures, Hoopoes started to breed successfully in the provided nestboxes (Arlettaz et al. in prep.) and monitoring of the nestbox population began. In 2002, after noticing that the endangered Wrynecks also occupy the nestboxes, breeding Wrynecks were also monitored. Various demographic data (capture-mark-recapture, breeding phenology and success) were continuously collected during the breeding seasons (April – July) throughout summer 2008.

The objective of the study at hand was to investigate how the two local populations (nestbox populations) in Valais were regulated. A better understanding of the population changes can, in a further step, lead to formulating conservation measures to protect and preserve these locally endangered species. As elaborated earlier, the dynamics of migrants can be influenced by conditions during different life cycle stages, hence the locations and stochastic effects during these different stages need to be taken into account in population dynamical modelling. Thus, in order to conduct a comprehensive study on the population dynamics of Hoopoes and Wrynecks, we first needed to assess where these two species winter. Secondly, important features of the known habitat (breeding ground) must be investigated. Then, demographic data (population counts, capture-mark-recapture data, and data on fecundity) needed to be collected, which was prerequisite to population dynamical studies. As a final step of this demographic analysis, we studied the temporal variation of demographic parameters, and investigated how much each demographic rate contributed to the population growth rate change. Furthermore, we tried to link stochastic effects occurring during the different life cycle stages with the observed population changes.

1.3 Wintering locations

The knowledge of migratory connectivity, i.e. about particular areas where breeding populations winters or stop-over during migration, plays an important role in population dynamics and conservation of migratory birds (Webster et al. 2002; Norris 2004). In order to establish these spatio-temporal links, animals need to be tracked for collating information about their whereabouts. There exists a wide array of tracking techniques comprising several extrinsic and intrinsic markers, such as phenotypic variation, radio- or satellite transmitters, genetics, to mention just a few (summarized in Hobson & Norris 2008). A traditional and very wide-spread approach of tracking migratory birds involves applying individually recognisable ring-bands (extrinsic marker) of which the recoveries produce spatially very accurate information on the birds' movements (Norris et al. 2006). A drawback of this technique is the necessity of recapture (recovery) of the ringed individual. An intrinsic approach, which does not suffer from such a drawback is the analysis of stable isotopes in bird feathers. Here, each initial capture simultaneously is a "recapture", since feathers store the spatially distinct isotopic value of the place of feather growth indefinitely after their formation ('you are (isotopically) what you eat', DeNiro & Epstein 1981). With the help of known isoscapes (spatially explicit isotopic landscapes; e.g. Bowen et al. 2005) and known isotopic discrimination factors which account for the isotopic fractionation along the food chain (DeNiro & Epstein 1981; Hobson & Clark 1992), previous locations of birds (i.e. where feathers have been grown) may be identified.

We applied both techniques, the analysis of ring recoveries (Chapter Two) and the analysis of stable isotopes in feathers (Chapter Three and Four), to delineate wintering areas of Hoopoes and Wrynecks. From ring recoveries, we expected a broad overview of wintering ranges of several Hoopoe and Wryneck breeding populations of Europe, whereas the stable isotope analysis should indicate wintering quarters of particular breeding populations.

1.3.1 Analysis of ring-recoveries

In **Chapter Two**, we studied where Hoopoes and Wrynecks winter by analyzing all available ring-recoveries (1905–2005) from birds ringed in Europe. The analysis clearly showed the intricacy of ringing data: recovery rates of small-sized birds are generally very low and thus the sample size is low. However, the available ring-recoveries showed distinct patterns of migration directions within Europe between the two species. For Hoopoes, there seems to be a migratory divide around 10-12°E, while for Wrynecks, we found a gradual shift of migration directions from west to east with increasing longitude of the ringing places. This resembles a common pattern among European migratory birds, with westerly breeders migrating more in south-western directions, whereas easterly breeding birds migrate more in south-eastern directions. Ring recoveries (including extrapolation of directions) generally seemed to support the literature about the wintering areas of the two species being partly located in southern Europe (southern Mediterranean areas) and trans-Saharan savannahs in the Sahel, but additionally also indicated the possibility of Hoopoes wintering more in eastern parts of the Sahel.

1.3.2 Migratory connectivity and stable isotopes

In **Chapter Three** and **Chapter Four**, we investigated migratory connectivity by means of stable isotope analysis (δD, $\delta^{15}N$, and $\delta^{13}C$) of wing feathers in two Hoopoe populations (Switzerland and Spain) and in two Wryneck populations (Switzerland and Germany). Collection year and age of the birds explained isotopic variance in winter-grown feathers in both species. A seasonally later winter moult on African wintering grounds could have led to differential isotopic values between second year (SY) and adult (AD) birds. In Hoopoes, stable isotopes further revealed that the Swiss breeding population likely winters in eastern Africa, while the breeding population of Spain consists of resident and migratory individuals.

East African isotopic values could be confirmed by analyses of δD in body feathers from museum Hoopoe specimens originally collected in these regions.

A comparison between the German and the Swiss Wryneck population suggested that Wrynecks follow a leap-frog migration: the more northerly German breeding population seems to exclusively winter in trans-Saharan Africa, while the more middle-European breeding population of Valais not only winters in the Sahel in trans-Saharan Africa, but also, partly, in southern Mediterranean areas.

1.4 Breeding habitat

Conservation of endangered species requires comprehensive knowledge of the habitat requirements, the assessment of territory quality, and the identification of population limiting factors; only then, effective conservation measures can be proposed and applied to restore and protect declining populations. We could study these habitat requirements on the breeding grounds of Swiss Hoopoe and Wryneck populations. Earlier studies on the micro-habitat use in the Canton of Valais have emphasized the importance of bare ground to these two species (Ioset 2007; Weisshaupt 2007). An optimal percentage of bare ground (at approximately 60%) is thought to facilitate access to the ground-dwelling arthropods on which Hoopoes and Wrynecks feed. However, not only micro-habitat use needs to be considered when trying to propose conservation measures, but also habitat configuration on a larger scale. Hence, the question about the key ecological features (Chapter Five) which most likely make these two populations thrive quite successfully in the intensively used agricultural land of lower Valais, still remained. Moreover, as the population of the Hoopoes dramatically increased since the installation of nestboxes (Arlettaz et al. in prep.), intra- and interspecific interactions (e.g. competition for nest sites) could occur, acting negatively on the populations (negative density dependence). Although we anecdotally report on such an interspecific interaction (Chapter Six), further studies will be needed to investigate the effect of interspecific nest site competition.

1.4.1 Key ecological features for Wrynecks

In **Chapter Five**, key ecological features on the macro-habitat scale were identified. Frequently occupied territories were occupied earlier in the season, which, according to the ideal despotic distribution leads to the assumption that these territories are of better quality than later occupied ones. Territory quality seemed to be positively correlated with the proportion of old pear orchards and the presence of conspecifics. Pear orchards were the favoured habitat type as they showed highest ant nest densities (ants and their broods are the main prey of Wrynecks) and higher proportions of bare ground, which facilitates accessibility to prey. Additionally, territories with a high proportion of cultivated areas (vegetable cultivations) seemed of inferior quality. For the persistence of a breeding population of Wrynecks in Valais, heterogeneously structured agricultural areas, preferentially with a high percentage of pear arboriculture, as well as artificial nesting sites should be promoted.

1.4.2 Hoopoes raising Wryneck brood

Hoopoes and Wrynecks are breeding in the same nestboxes in the study site in Valais (see above). Nestboxes are frequently installed in pairs, resulting in two close nestboxes in the same agricultural shed. On a few occasions so far, both nestboxes have been occupied simultaneously by Hoopoes and Wrynecks, which raises the question of interspecific competition for nestboxes. **Chapter Six** describes the rare, evolutionary maladaptive (!) phenomenon of adopting offspring foreign to one's species: a Hoopoe breeding pair raised a Wryneck brood after the failure of its own clutch. After the Wryneck nestling had hatched, first the Wryneck parents only, then Wrynecks along with both Hoopoe breeding birds of the neighbouring nestbox, and finally the Hoopoes only were feeding the Wryneck nestlings. Even though Hoopoes provided Wryneck nestlings with unsuitable prey (molecrickets are normally too large for the small Wrynecks chicks), three out of eight nestlings fledged.

1.5 Demography of Hoopoes and Wrynecks

Conservation demographic analyses of bird populations are usually done by ringing and recapturing ringed individuals of the focal population (Baillie 2001). Identifying changes in population parameters (e.g. brood numbers, breeding success) as well as in vital rates (i.e. survival, reproduction, immigration and emigration), and linking these changes to environmental or density dependent factors can lead to a better understanding of observed population fluctuations. A simple way of analyzing the demography of a species is to compare population parameters of spatially separated populations, for example to compare the clutch size of geographically distinct populations (Chapter Seven). On the other hand, quantifying stochastic events (e.g. weather conditions), as well as density dependence can help to identify how a demographic parameter (e.g. reproductive success) is affected by these stochastic/density-dependent events. However, this approach may only allude to the sensitivity of a demographic trait to certain events, such as climatic variability (e.g. Geiser et al. 2008). Trying to explain changes in population growth rates over time necessitates a modelling approach combining all the available demographic data. Integrated population modelling in combination with retrospective perturbation analysis (Horvitz et al. 1997; Caswell 2001; Besbeas et al. 2002) combines longitudinal demographic data with population counts and allows to estimate each of the vital rates, and the contribution of each rate to the observed population growth rate change.

1.5.1 Brood size variation between two Wryneck populations

The Wryneck population in Valais was slightly declining over the last 7 years (Chapter Nine), which reflects the declining population trend of the preceding decades. The study population in Germany (the same population as in Chapter Four), however, seemed quite stable over the last years. In both populations, the breeding density is quite high compared to other European breeding populations. **Chapter Seven** provides insights into the breeding parameters of these two geographically well separated populations. The clutch size of first broods was larger in the German than in the Swiss population, whilst clutch sizes of second broods different not between the two populations, but were generally lower than first broods. These results corroborate a described relationship between clutch size and latitude of breeding: the number of eggs increases towards northern latitudes compared to more southern locations, while additionally, the occurrence of second broods decreases probably due to shorter breeding seasons.

1.5.2 Weather dependent productivity in the Hoopoe

Investigations on the impact of weather variation and density-dependence on the reproductive output of Hoopoes in Valais (**Chapter Eight**) have revealed, that adverse weather conditions (rain) around the hatching date had a negative impact on the reproductive output, whereas higher temperatures enhanced the reproductive output. The effect of lower reproductive success could possibly be attributed to lower food provisioning rates (resulting also in less biomass supplied) of adults to nestlings during cool and rainy days. Additionally, higher breeding densities influenced reproductive output negatively. We thus concluded that population growth rate of the Hoopoes resulted from variation in reproductive output, which itself was determined by weather/climate variability.

1.5.3 Temporal variation of demographic parameters

In **Chapter Nine**, we analyzed the available data on capture-mark-recapture, fecundity and population counts (data collected over 7 years) with an integrated population model in the Bayesian framework to estimate the temporal variation of the different vital rates, and to assess how much each vital rate contributed to the population growth rate change. In both species, immigration seemed to be the driving force regulating the local population sizes. Population trajectories for the isolated Hoopoe population were positive (increase in population size after installation of nestboxes), whereas the Wryneck population in Valais slightly decreased. The differential dynamics of the two populations, which at first glance are quite similar regarding their ecology and life history, could be explained by differences in immigration. Furthermore, we tried to link the variation of correlates of food availability during winter and summer to the observed population changes. However, probably due to the short time series, we were not able to identify any clear effect of environmental covariates on vital rates (but see Chapter Eight).

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2

Migration patterns of Hoopoe *Upupa epops* and Wryneck *Jynx torquilla*: an analysis of European ring recoveries

Migration patterns of Hoopoe *Upupa epops* and Wryneck *Jynx torquilla*: an analysis of European ring recoveries

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2.1 Abstract

For many bird species, recovery of ringed individuals remains the best source of information about their migrations. In this study, we analyzed the recoveries of ringed European Hoopoe (*Upupa epops*) and the Eurasian Wryneck (*Jynx torquilla*) from 1914 to 2005 from all European ringing schemes. The aim was to define general migration directions and to make inferences about the winter quarters, knowing that hardly any recoveries are available from sub-Saharan Africa. For the autumn migration, there is evidence of a migratory divide for the Hoopoe in Central Europe, at approximately 10–12° E. Autumn migration directions of Wrynecks gradually change from SW to SE depending on the longitude (west to east) of the ringing place. In both species, only a few recoveries were available indicating spring migration directions, but they showed similar migration axes as for autumn migration, and hence no evidence for loop-migration. Due to a paucity of recoveries on the African continent, we can make only limited inferences about wintering grounds: extrapolating migration directions are only indicative of the longitude of the wintering area. The directions of autumn migration indicate a typical pattern observed in European long-distance migrants: west-European Hoopoes and Wrynecks are likely to winter in western Africa, while central- and east-European birds probably winter more in the east. Due to the migratory divide, for the Hoopoe, this phenomenon is more pronounced.

***Keywords*:** Connectivity • *Jynx torquilla* • Migration • Ring recoveries • *Upupa epops*

2.2 Introduction

Thanks to bird ringing over the past 100 years, we have gained a lot of insight into the biology of birds, especially for seasonal movement patterns (Bairlein 2001). Historically, the main interest of bird ringing was to describe migration routes and wintering ranges. Today, ringing data play a key role in many studies on ecology, behaviour, population dynamics and conservation of bird populations (Baillie 2001). The conservation of migratory bird species involves not only protecting crucial habitats in the breeding areas, but also on the wintering grounds (e.g. Pain et al. 2004; Holmes 2007; Walther et al. 2007). It is thus essential that we have as much information as possible on the spatio-temporal whereabouts of a species (Webster et al. 2002).

For many European migratory species, the breeding habitat and distribution ranges are well described and compiled in various handbooks (e.g. Cramp 1985; Glutz von Blotzheim and Bauer 1966; BirdLife International 2004). On the other hand, the non-breeding distribution is much harder to assess (Bibby 2003), as species might be very elusive, or simply because they are visiting regions where bird watchers and ornithologists are rare. Nevertheless, handbooks do contain broad descriptions of a species' wintering distribution, based mostly on observations. In most cases, we lack information about the connectivity between breeding grounds and wintering areas (Webster and Marra 2005), as well as which flyways different populations use when migrating southwards. Consequently, the wintering areas of many European long-distance migratory bird populations cannot be described as accurately as the breeding areas. In many cases, ringing has to date yielded insufficient information to determine the wintering grounds for many species and populations (Szép et al. 2006). Although they may be scarce and have many drawbacks (e.g. Pfister et al. 1992; Gauthier-Clerc and Le Maho 2001), ring-recovery data are still among the most spatially accurate sources of information on migratory movement (Norris et al. 2006) and connectivity (Webster et al. 2002).

Many species migrating to sub-Saharan Africa fly through the western (Iberia) and eastern (Middle East) land masses of the Mediterranean, rather than crossing the central Mediterranean Sea. This entails a gradual change of migration directions from SW orientation in western Europe to SE orientation in the east, or sometimes a clear-cut migratory divide (Schüz 1964). Especially in the latter situation, this clearly points to different winter quarters in sub-Saharan Africa.

In this study, we examined the migration directions of two non-passerine birds, the European Hoopoe (*Upupa epops*) and the Eurasian Wryneck (*Jynx torquilla*) from recoveries of ringed individuals. The Wryneck and the Hoopoe are currently on the IUCN Red List in category SPEC 3 (moderate recent decline; IUCN 2001). For both species, no European-wide ring-recovery analysis is available. Hoopoes and Wrynecks are assumed to winter mainly in the Sahel Belt in sub-Saharan Africa and occasionally in the Mediterranean. A migratory divide was previously postulated for Wrynecks, but not for Hoopoes (Glutz von Blotzheim and Bauer 1966; Cramp 1985). The latter seem to cross the Mediterranean Sea along its whole width (Glutz von Blotzheim and Bauer 1966). We focus in particular on the migration directions during autumn and spring migration across Europe and re-evaluate whether there is evidence of a migratory divide. Based on the mean migration directions within Europe, we hypothesize about the possible wintering areas of both species with the goal of learning more about the connectivity of the European breeding populations.

2.3 Material and Methods

From the EURING data base (European Union for Bird Ringing), we obtained recovery information on 117 Hoopoes and 331 Wrynecks spanning 92 years of ringing and recovery data (1914–2005). Because the EURING data base is incomplete, we added 16 Hoopoe and 12 Wryneck recoveries which are mentioned in the literature (Glutz von Blotzheim and Bauer 1966, and references therein) as well as three unpublished, recently reported Hoopoe and two Wryneck recoveries (Swiss Ornithological Institute, Sempach).

Birds were only included in the analysis if the recovery date was accurate to at least 2 weeks of either side of the recovery date mentioned in the raw data and if the accuracy of the ringing or recovery coordinates were within 50 km (Speek et al. 2006). We excluded all records with less than 100 km between the ringing and recovery sites in order to eliminate local, pre-migratory movements and returns to the natal area (e.g. birds roaming in the breeding area before leaving on their autumn migration). These selection criteria were more strict than in other publications and hence our recovery maps may exclude some recoveries published elsewhere (e.g. Saurola 1999).

Migration periods were defined according to Cramp (1985) and del Hoyo et al. (2001). Records were considered to reflect autumn migration movements if the birds were ringed between April and August and recovered between July and December (Hoopoe: n = 49; Wryneck: n = 121). Spring migration movements were defined by birds ringed in January to April, and recovered from March to July (Hoopoe: n = 30; Wryneck: n = 30). Records, which were not within these migration periods were excluded from further analyses. Additionally, we excluded records (Wryneck: n = 22), which were considered to be uninformative regarding general migration movements. These comprised records that were attributed to natal/breeding dispersal.

Records of birds that were ringed and recovered in the same year provided the best spatial information on migratory movements, still keeping in mind that the true flight path is likely not a straight line. Recoveries made in a later year can provide information on migration under the assumption that birds are philopatric to the breeding/hatching and/or wintering area. Recoveries from later years are grouped in two categories: (1) records falling within the defined migration periods, but the recovery was made in a later year; or (2) records falling within the above defined migration periods, yet the area the birds are presumably migrating to is the ringing site (e.g. ringed in breeding area, recovered during the following spring; hereafter "inverse season"). In order to get comparable bearings between same year/later year and inverse season recoveries, the migration directions were transformed by adding 180° to the calculated value.

Sex was not considered in the analysis, because in both species, sex is not easily assessed based on morphological characters. Migration patterns could potentially differ between age classes (e.g. Ketterson and Nolan 1983; Bairlein 2001); however, we did not include age in the analysis because we were primarily interested in general migration patterns and possible wintering quarters.

All analyses were performed with the statistical software package R (CRAN—The Comprehensive R Archive Network, Version R 2.6.1). Distance and direction were calculated using R codes obtained from http:// www.oikostat.ch (Korner-Nievergelt 2004, after Imboden and Imboden 1972). Recoveries were depicted on Mercator maps where loxodromic distances are straight lines (constant directions; Imboden and Imboden 1972).

Rayleigh tests were used to check for a significantly preferred migration direction (Batschelet 1981). To test whether birds from different locations show different migration directions, we fitted a regression model for a circular dependent (migration directions) and a linear independent variable (longitude of ringing place). A Welch two-sample t test was used to test for differences between the directions of birds ringed and recovered in the same year and birds ringed and recovered in later years. Statistics are presented as means ± 1 SD.

2.4 Results

2.4.1 Hoopoe

Mapping the autumn migration recoveries suggests a migratory divide running through Germany, Austria, Switzerland, and Italy (Fig. 1 a, b). Birds from these countries may, however, use either SE or SW directions. Only one individual was recovered in the described sub-Saharan wintering range (ringed on 19 April 1993 in Tuscany, Italy, reported dead on 1 November 1993 in Aderbissinat, Niger, distance 2,981 km). Table 1 shows the number of recoveries per ringing country grouped into geographic regions. The recoveries are from individuals ringed in western and central European countries, and are evenly distributed among these regions.

The mean direction for birds on autumn migration which were recovered in the same season was 193.7° (± 34.8°, *n* = 29; Fig. 1a). The directions showed a bimodal distribution with two peaks at approximately 165°and 225°. Directions were negatively related to the longitude of the ringing site (Fig. 2a). We achieved a good regression fit with the circular–linear regression model when both longitude and longitude squared were included in the model (longitude: estimate = 3.52, t = 2.60, p = 0.005; longitude^2: estimate = -0.35, t = 2.56, p = 0.005; Fig. 2a). Accordingly, a migratory divide can be set at 10–12°E. Birds ringed west of this divide differed significantly in direction (207.4 ± 31.6°, *n* = 15) from birds ringed east of the divide (178.7 ± 34.2°, *n* = 14; Welch two-sample t test with equal variances: t = -2.34, df = 26.4, p = 0.027).

Autumn recoveries from a later year confirmed the pattern shown by same year recoveries (mean direction of 187.6 ± 47.1°, *n* = 20; Fig. 1b). The directions were, however, not significantly impacted by the longitude of the ringing place (circular–linear regression with longitude: estimate = 0.90, t = 1.27, p = 0.102). There was no statistical evidence that the autumn migration directions differed between same and different year recoveries (Welch two-sample t test with equal variances: t = 0.49, df = 32.8, p = 0.625).

In general, Hoopoes showed similar routes in spring (Fig. 3) as in autumn. Only five recoveries could be attributed to spring migration during the same season (mean direction 47.5 ± 42.2°) whilst four individuals were recovered in later seasons (mean direction 93.2 ± 77.7°). However, because of the large scatter and small sample size, mean directions were not very informative. Birds ringed in the breeding area and recovered in a later spring (inverse season) were more numerous (*n* = 21). From these, we omitted recoveries <400 km from the ringing site in order to ensure the exclusion of any breeding and natal dispersal. We obtained a transformed mean direction of 356.8° (± 53.3°, *n* = 11). For all spring recoveries combined, mean direction is 24.6° [± 25.9°, *n* = 20: spring same year recoveries (5) + spring later year recoveries (4) + spring inverse season recoveries >400 km (11); Fig. 3]. There was no significant difference in mean migration axis between spring and autumn migration (all spring and autumn: Welch two-sample t test: t = 0.80, df = 24.3, p = 0.43; all spring and same year autumn: t = 0.65, df = 25.6, p = 0.52).

2.4.2 Wryneck

Mapping the autumn migration recoveries did not result in a clearly visible migratory divide (Fig. 4). Four birds were recovered on the African continent (longest distance of 3,720 km for a bird ringed on 13 May 1989 on Gotland, Sweden, recovered dead on 15 October 1989 in Ifrhassene, Morocco), but none in the sub-Saharan winter quarters. Table 1 shows the number of recoveries per ringing countries grouped into geographic regions. It appears that many recoveries are from individuals ringed in Scandinavia, thus our inference may be biased towards these regions.

The mean autumn migration direction of birds caught in the same season was 205.8° (± 21.0°, *n* = 83; Fig. 4a). Directions were significantly related to the longitude of the ringing site (circular–linear regression with longitude as variable: estimate = 0.71, t = 5.14, $p < 0.001$; Fig. 2a). There was no indication of a step in the regression line, but a slight gradual shift from SW in western Europe to S directions in eastern Europe (Fig. 2b). Autumn recoveries from later years again confirmed the pattern shown by same year recoveries (mean direction 209.8 ± 55.5°, *n* = 38; Fig. 4b). Direction was negatively related to the longitude of the ringing place (circular–linear regression with longitude: estimate = 0.01, t = 3.00, p = 0.001). We found no statistical evidence that the autumn migration directions differed between same and different year recoveries (Welch two-sample t test: t = -0.43, df = 41.9, p = 0.67).

The migration routes of Wrynecks in spring (Fig. 5) are similar to those in autumn. Only seven birds were recovered within the same year (mean direction 26.4 ± 150.5°) and just four individuals during spring migration of different years (mean direction 294.5 ± 139.3°). Nineteen birds were ringed in the breeding area and recovered in spring (inverse season). From these, we again omitted recoveries <400 km from the ringing site, due to the above-mentioned reasons. We obtained a transformed mean direction of 31.5 ± 24.3° *n* = 14). For all spring recoveries combined, mean direction is 27.0° [± 114.8°, *n* = 25 (spring same year recoveries + spring later year recoveries + spring inverse season recoveries >400 km); Fig. 5].

The mean migration axis between spring and autumn migration did not differ significantly (all spring and autumn: Welch two-sample t test: t = -0.003, df = 27.8, p = 0.98; all spring and same year autumn: t = 0.10, df = 25.9, p = 0.92).

2.5 Discussion

This study is one of the few European-wide analyses of ring recoveries, as asked for by several authors (e.g. Baillie 1995; Bairlein 2001). Information about migration patterns of the regionally threatened Wryneck and Hoopoe bear some conservation relevance. Although a substantial number of Hoopoes and Wrynecks have been ringed during the course of the last century (representative data for Germany and Switzerland: 8,643 Hoopoes, 19,665 Wrynecks), the number of recoveries remains scarce. This is due to the very low recovery rates (ca. 1.0% and 0.6% for Hoopoes and Wrynecks, respectively), with only one recovery (Hoopoe) available from the sub-Saharan wintering quarters. Hence, only indirect inferences about the location of wintering quarters of the different European breeding populations are possible.

2.5.1 Autumn migration

In contrast to previous suggestions (Glutz von Blotzheim and Bauer 1966), we found evidence of a migratory divide in Hoopoes (Fig. 1), with two distinct peaks in the distribution of migration directions (Fig. 1) as assessed by the circular–linear regression analysis (Fig. 2). We suggest that this divide lies between 10 and 12°E, as the migration directions of Hoopoes ringed west and east of these longitudes, respectively, differ significantly. Generally, western European populations migrate to the Iberian Peninsula with directions around 225° (SW), while eastern European populations migrate along the Balkan Peninsula [directions ca. 160° (SSE); del Hoyo et al. 2001]. In addition to these two flyways, it seems that an intermediate zone also exists, where Hoopoes migrate south over Italy, possibly crossing the Mediterranean Sea over Calabria and Sicily.

No clear migratory divide was evident in Wrynecks, but a gradual shift in migration directions was apparent depending on the longitude of the ringing site. Birds ringed in western Europe show more westerly migration directions compared to birds ringed in eastern Europe. This contradicts previous views summarized in Glutz von Blotzheim and Bauer (1966) but supports earlier statements by Rendahl (1963) about Scandinavian Wrynecks: individuals ringed in Sweden chose a more westerly route than individuals from Finland. However, a migratory divide further to the east may still exist for this species. Ringing and recovery data from eastern and south-eastern Europe is needed to clarify this hypothesis.

We found two outliers in migration directions in the Hoopoe data (see Fig. 1a: at approximately 60° and 290°): a bird ‘migrating’ to the east (nestling ringed in Switzerland, July 2005), and retrieved in Austria (August 2006), and a second bird ‘migrating’ to the north-west (ringed as after first-year bird in northern Italy, May 1994) and recovered at a distance of 180 km (northern Italy, September 1997). Possible explanations for this behaviour are: (1) the reverse migration hypothesis (e.g. Rabøl 1969; Thorup 2004), which states that, due to various reasons (Pfeifer et al. 2007), birds sometimes migrate 180° opposite to the expected direction; or (2) natal and breeding dispersal, which can be over extremely long distances in migratory birds (Paradis et al. 1998). We favour the latter explanation because these two birds were recovered in a later year. As personal observations show, Hoopoes exhibit high breeding site fidelity after natal dispersal. The same explanation can apply to one Wryneck outlier, which was ringed as a second-year bird in May 1998 in Sweden and recovered in August of the following year in Norway (direction 320°; Fig. 4b). On the other hand, a Wryneck captured and recaptured in northern Italy (May and October 1956, direction 100°; Fig. 4a) supports the hypothesis of a reverse migration.

2.5.2 Spring migration

Unfortunately, only very few same year recoveries were available. Thus, we combined all information on spring migration to describe migration directions. In both species, we found no indication that spring migration routes differed from autumn migration routes (Figs. 1, 3, 4 and 5, respectively), hence there is no indication for a loop-migration.

An outlier concerning migration directions in the Hoopoe data (ringed as nestling in Germany, June 1961, recovered on a freighter in the North Atlantic, April 1962) has already been mentioned in Seilkopf (1964), who suggested that this bird might have been diverted by the unusual atmospheric conditions and very strong winds. In the case of two Wrynecks which showed an intuitively wrong spring migration direction (approximately 110° in the Netherlands and 120° from Denmark to Sweden; see Fig. 5), we dismiss the reverse migration hypothesis. These two birds had been ringed in April and May, and recovered 1 and 14 days later, respectively. We suspect that these two birds were recovered rather early in their breeding area while they were still on the search for suitable breeding grounds.

2.5.3 Wintering sites

In the literature, wintering sites of Hoopoes and Wrynecks are described to be south of the Sahara Desert in the Sahel (Senegal to Ethiopia), with occasional overwintering in the Mediterranean area (Spain, Portugal and southern France), or northern Africa (Algeria, Morocco) (Glutz von Blotzheim and Bauer 1966; Cramp 1985; Fry et al. 1988; del Hoyo et al. 2001). Only one Hoopoe recovery was from within the described wintering areas (found in Niger). We therefore cannot delineate wintering grounds of these species based on the extant ring recoveries, and inferences on wintering areas are only possible by projecting (extrapolating) migration directions. As a result, only assumptions on the longitude of the wintering areas can be made, whereas inferences about latitude are impossible.

The directions from autumn migration indicate the usual pattern observed in other European long-distance migrants with comparable migration directions and documented wintering sites (Zink and Bairlein 1995). We suggest that west-European Hoopoes and Wrynecks are likely to winter in western Africa, while central- and east-European birds probably winter more in the east. This phenomenon would be more pronounced in the case of the Hoopoe, due to the migratory divide.

Despite using all available ring recoveries across Europe from almost one century, we were not able to make strong inferences about connectivity between breeding and wintering locations in Hoopoes and Wrynecks. Other methods, such as the use of stable isotopes in feathers (e.g. Hobson 1999; Procházka et al. 2008) or geo-data loggers (Phillips et al. 2007), appear to be promising approaches for inferring connectivity. We are currently applying these methods to populations in Switzerland and hope to be able to increase our knowledge about their wintering locations in the near future.

2.6 Zusammenfassung

Zugverhalten von Wiedehopf Upupa epops und Wendehals Jynx torquilla: Eine Analyse europäischer Ringfunde

Für viele Zugvogelarten sind Ringfunde die beste Quelle, um an Informationen über das Zugverhalten zu gelangen. In der vorliegenden Studie untersuchten wir Ringfunde von Wiedehopf und Wendehals zwischen 1914 und 2005, welche in der Europäischen Ringfundzentrale vorhanden sind. Das Ziel dieser Studie war die Beschreibung der Richtungen des Frühlings- und Herbstzuges, um Hinweise auf mögliche Überwinterungsorte zu bekommen. Beim Wiedehopf gibt es Anzeichen für eine Zugscheide in Zentraleuropa bei ungefähr 10–12° östlichen Längengrades: Vögel, die östlich dieser Zugscheide brüten ziehen in südöstlicher Richtung ab, Vögel die westlich davon brüten in südwestlicher Richtung. Die Herbstzugrichtungen beim Wendehals ändern sich allmählich von südwestlicher zu südöstlicher Richtung in Abhängigkeit des Längengrades des Beringungsortes (West nach Ost). Bei beiden Arten gab es nur wenige Ringfunde, welche die Richtungen des Frühlingszuges anzeigten. Jedoch ähnelten die Frühlingszugrichtungen jenen vom Herbstzug und somit bestehen keine Hinweise auf einen Schleifenzug. Die wenigen Ringfunde aus Afrika lassen nur sehr limitierte Aussagen über die Winterquartier zu: Extrapolation der Zugrichtungen können den Längengrad des Winterquartiers anzeigen. Die Herbstzugrichtungen widerspiegeln ein typisches Zugverhalten Europäischer Langstreckenzieher: Wiedehopfe und Wendehälse aus Westeuropa überwintern wahrscheinlich in Westafrika, während Vögel aus Zentral- und Osteuropa vermutlich mehr östlich überwintern. Dieses Phänomen ist beim Wiedehopf aufgrund der Zugscheide deutlicher ausgeprägt als beim Wendehals.

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Table 1 Number of recoveries of European Hoopoes (*Upupa epops*) (*n* = 49) and Eurasian Wrynecks (*Jynx torquilla*) (*n* = 121) on autumn migration grouped into geographic regions of ringing countries.

Ringing country	Hoopoe	Wryneck
Austria, Czech Republic, Hungary	8	7
Belgium, Luxembourg, Netherlands	2	3
Denmark, Finland, Norway, Sweden	1	82
France, Germany, Poland, Switzerland	33	12
Great Britain	0	4
Italy, Spain	2	5
Latvia, Lithuania, Russia	1	6
Romania, Serbia	2	1
Turkey	0	1

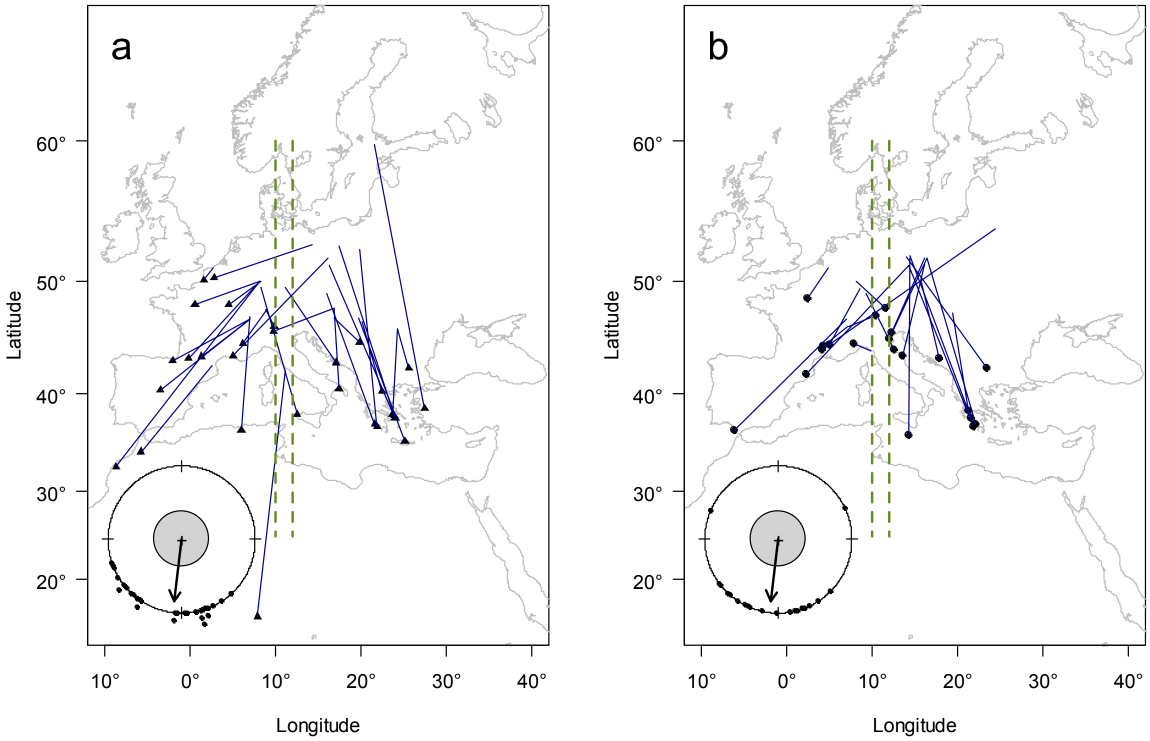

Figure 1 Recoveries of Hoopoes (*Upupa epops*) on autumn migration: a) ringed and recovered in the same season (*n* = 29); b) ringed and recovered in different seasons (*n* = 20). The *dashed lines* show a proposed migratory divide. *Symbols* indicate the recovery site. The *small circle* on the maps represents the result of the Rayleigh tests. The *arrow* indicates the mean migration direction of the recovered birds. The length of the arrow is a measure of the mean vector length (test statistics of Rayleigh test 0.83 and 0.74, respectively, p < 0.001); it is inversely related to the variance of the migration directions. The inner circle indicates the 1% significance level of the Rayleigh test.

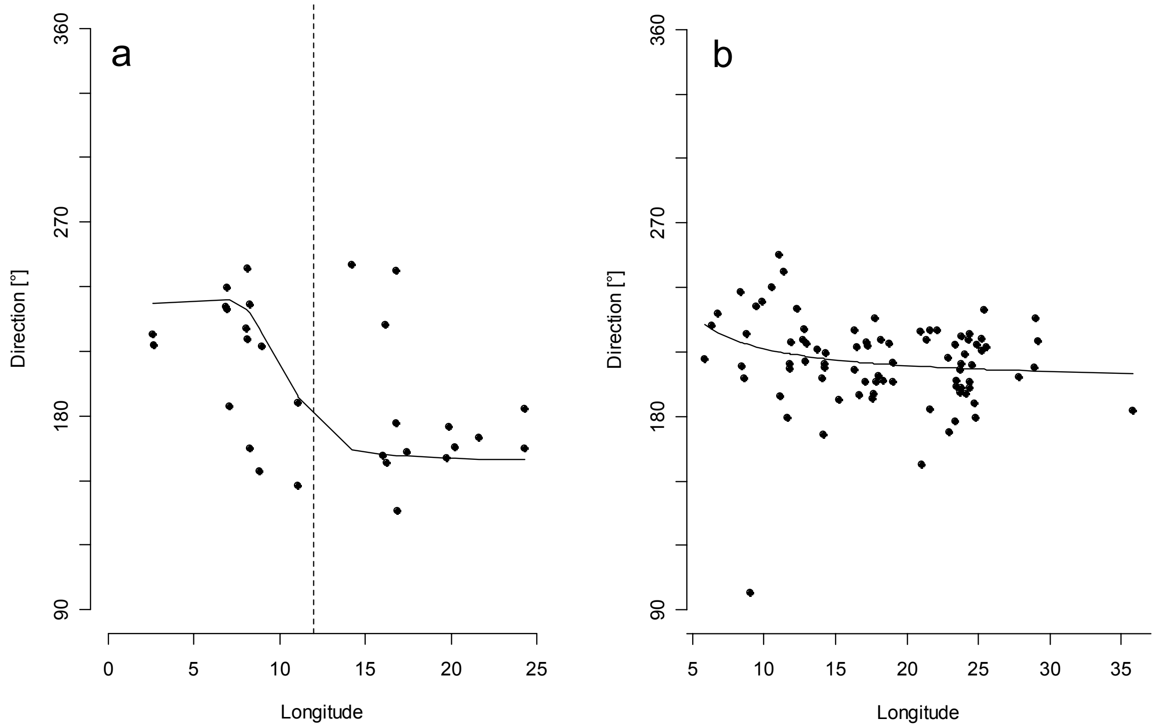

Figure 2 Autumn migration directions of birds ringed and recovered in the same season in relation to longitude of the ringing site: a) Hoopoe (*n* = 29): the step in the quadratic regression line indicates a possible migratory divide at ca 12° E (*dashed line*); b) Wryneck (*n* = 83): the line represents the circular-linear regression.

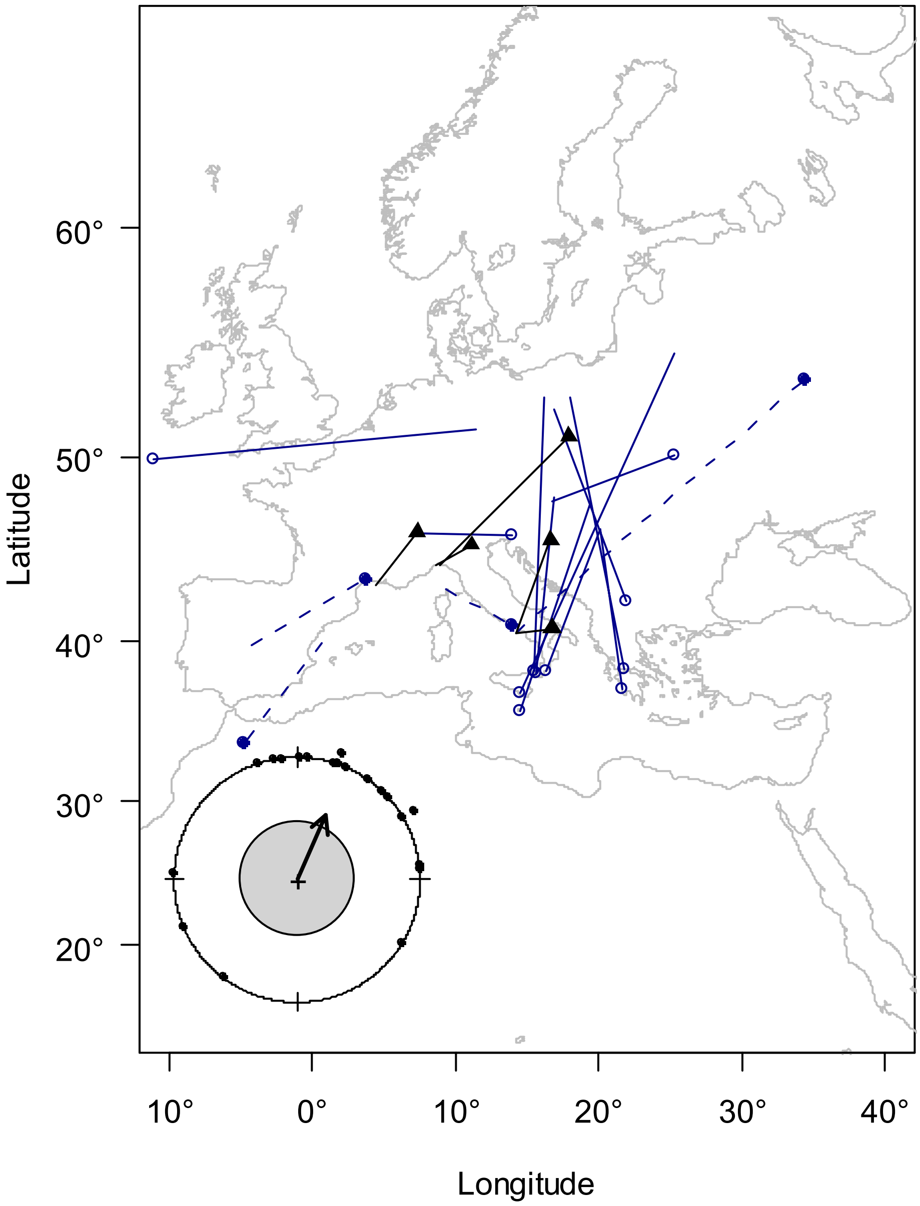

Figure 3 Recoveries of Hoopoes on spring migration. *Filled triangle* birds ringed and recovered in the same season (*n* = 5, *solid lines*); *filled circle* birds ringed and recovered in a later season (*n* = 4, *dashed lines*); *open circle* birds recovered in a later season, yet attributed to inverse spring migration (only recoveries with > 400 km between ringing and recovery site, *n* = 11, *solid lines*). *Symbols* indicate the recovery site. Test statistics of Rayleigh test 0.58, p < 0.001.

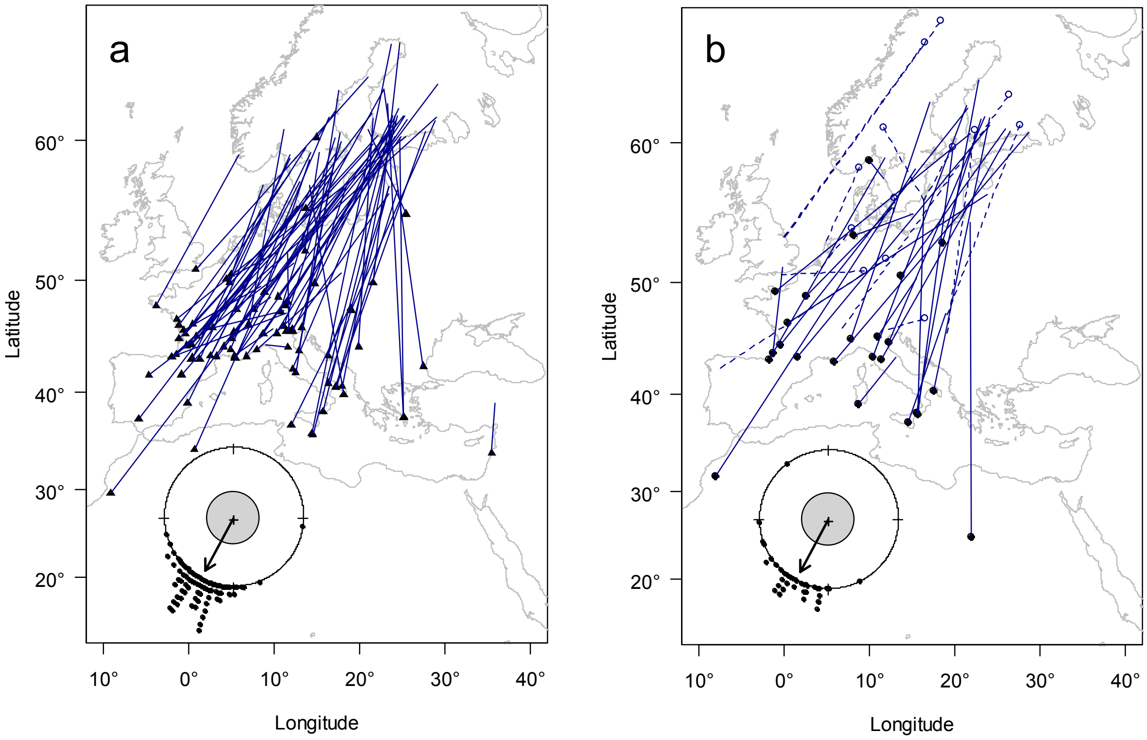

Figure 4 Recoveries of Wryneck (*Jynx torquilla*) on autumn migration: a) ringed and recovered in the same season (*n* = 83); b) ringed and recovered in different seasons (*n* = 38). *Filled circle* birds ringed and recovered in a later season are depicted with *solid lines* (*n* = 25); *open circle* birds recovered in a later season, yet attributed to inverse autumn migration are indicated with *dashed lines* (*n* = 13). *Symbols* indicate the recovery site. Test statistics of Rayleigh test 0.94 and 0.90, respectively, p < 0.001.

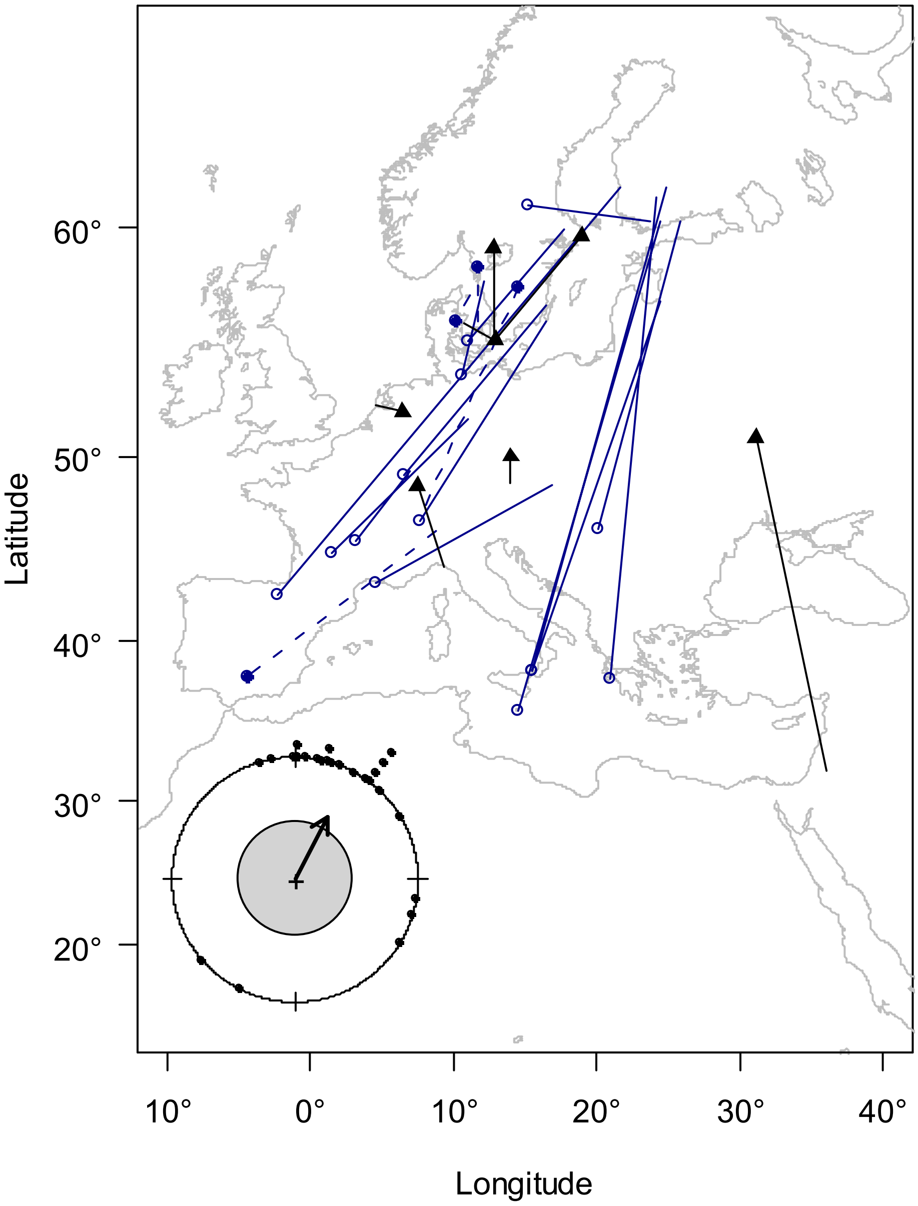

Figure 5 Recoveries of Wryneck on spring migration. *Filled triangle* birds ringed and recovered in the same season (n = 7, *solid lines*); *filled circle* birds ringed and recovered in a later season (n = 4, *dashed lines*); *open circle* birds recovered in a later season, yet attributed to inverse spring migration (only recoveries with > 400 km between ringing and recovery site, n = 14, *solid lines*). *Symbols* indicate the recovery site. Test statistics of Rayleigh test 0.69, p < 0.001.

3

Stable isotopes unexpectedly locate wintering grounds of a Western European trans-Sahara migrant in East Africa

Stable isotopes unexpectedly locate wintering grounds of a Western European trans-Sahara migrant in East Africa

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3.1 Abstract

Tracking endangered migratory animals during their whole life cycle is crucial to determine both their whereabouts and seasonal survival, a prerequisite to develop sound conservation programmes. Ringing has traditionally been used to assess migratory connectivity between breeding and wintering areas, but this exogenous marking technique suffers from low recovery rates scattered over wide areas. Stable isotope abundance measured in tissues of migratory animals represent an alternative (endogenous) means for tracking migrants, especially problematic organism such as insects and passerines. Bird feathers reflect the isotopic composition of the environment where feathers were grown. When several generations of feathers are simultaneously available on the same individual, information about a bird's breeding and wintering grounds can be gathered at a single capture event, allowing inferences about migratory connectivity. We analyzed deuterium (δD), stable nitrogen ($\delta^{15}N$) and stable carbon ($\delta^{13}C$) isotopes in the feathers of two European Hoopoe (*Upupa epops)* populations (Switzerland and Spain) in 2005 and 2006. Our goal was to establish migratory connectivity between breeding and wintering grounds, while assessing the relative effects of age, sex and year. A validation of predicted wintering areas was obtained through the comparison of isotopic values from museum specimens collected across northern subtropical Africa. All three stable isotopes in winter feathers (feathers grown on the wintering grounds) suggest that Swiss birds may moult in winter in east Africa south of the Sahara, while parts of the Spanish Hoopoes winter in southern Spain. A year effect was discernable for all three isotopes in winter feathers, which may hamper any assessments of migratory connectivity. A year effect was also found for δD in summer-grown feathers and departures of measured feather δD from values predicted based on long-term precipitation δD models need to be considered in isotope applications. This can best be accomplished by sampling known origin birds during the year of interest. Marked individuals captured in both years showed a significant effect of age on all three isotopes, which could be due to differences in timing and location of winter-moult in first-year birds compared with older Hoopoes. The unexpected predicted wintering moult location of Swiss Hoopoes, mostly in eastern Africa, now requires confirmation by complementary techniques (e.g. geolocators). Population dynamical models accounting for seasonal components of survival can then be developed for orienting conservation action.

Keywords: Hoopoe • Isoscapes • Isotopic variation • Migratory connectivity • Timing of moult

3.2 Introduction

A thorough understanding of population dynamics of migrating animals calls for estimates of seasonal survival, which requires knowledge of an animal's whereabouts during the different stages of its life cycle (Hobson 1999). Defining links between breeding and wintering grounds in a migratory species (i.e. establishing migratory connectivity) is hence prerequisite to any integrated population biological studies aiming at promoting sensible conservation action for endangered species and populations (Webster et al. 2002; Rubenstein & Hobson 2004; Webster & Marra 2005). In migratory birds, it has been shown that conditions experienced on wintering grounds may impact demographic parameters (e.g. fecundity) in the next breeding season (so called carry-over effects; Marra et al. 1998; Norris 2005). In order to establish such subtle links, individuals need to be tracked. Large animals can be satellite or GPS tracked, yet for smaller animals (e.g. passerine birds) large transmitter size remains a constraint (Webster et al. 2002; Hobson 2003; Hobson & Norris 2008). That is why passerines are traditionally tracked through ringing, although inferences about origins remain extremely limited due to poor recovery rates over wide areas, especially from wintering quarters (Hobson & Wassenaar 2001; Hobson 2003). In recent years, researchers circumvented these limitations by analyzing the relative abundance of stable isotopes in animal tissues, which may provide invaluable information about previous locations (Hobson 1999; Rubenstein et al. 2002; Hobson & Norris 2008). Hydrogen isotopes (δD) are especially promising intrinsic markers because large-scale patterns in precipitation δD have been described and these "isoscape" patterns are transferred to tissues of animals through the foodweb (Hobson et al. 2004). Other naturally occurring stable isotopes, such as nitrogen ($\delta^{15}N$), carbon ($\delta^{13}C$), and sulphur ($\delta^{34}S$) show spatial pattern often related to climate and biological processes but are generally less predictable compared to δD isoscapes (Hobson 1999; Rubenstein & Hobson 2004).

In bird studies, isotopic values in feathers are often used as geographic markers for tracking migration (Hobson 2005; Norris et al. 2006). Unlike metabolically active tissues, feathers are isotopically inert after growth, hence indefinitely retain isotopic information about origins. Combining knowledge of isoscapes and the way in which isotopic values change or fractionate between diet and feathers can assist in assigning birds to moult origin. Deuterium (δD), $\delta^{15}N$ and $\delta^{13}C$ measurements have been used successfully to assess migratory connectivity (e.g. Chamberlain et al. 1997; Evans et al. 2003; Mazerolle et al. 2005; Norris et al. 2006; Boulet & Norris 2006), for identifying either stop-over sites (e.g. Yohannes et al. 2007), wintering grounds (e.g. Møller & Hobson 2004; Greenberg et al. 2007), or breeding areas (Hobson et al. 2006). Bearhop et al. (2005) could even establish that sympatrically breeding European blackcaps (*Sylvia atricapilla*) winter in well-separated, distant areas, while maintaining a pattern of assortative mating that actually mirrors the winter spatial segregation.

Information about wintering grounds for many Palaearctic-Afrotropic migrants is scarce due to a lack of ring recoveries in Africa. So far, only a few studies have used stable isotopes to identify African wintering grounds of Eurasian breeding birds (e.g. Evans et al. 2003; Pain et al. 2004; Yohannes et al. 2008). In this study, we used stable isotopes to delineate the wintering grounds of a Swiss and a Spanish population of a non-passerine, European long-distance migratory bird, the European Hoopoe (*Upupa epops*). Hoopoe wintering quarters are assumed to be mostly in the Sahel in sub-Saharan Africa, but occasionally also in the Mediterranean, yet no ring recoveries are so far available from subtropical and tropical Africa (Reichlin et al. *in press*). Our objectives were to create predicted isoscapes for feathers grown in Africa and to evaluate which regions of Africa were isotopically consistent with African grown feathers of Hoopoes. However, isoscapes for Africa are generally poorly known and so we also were interested in evaluating and considering sources of variance in isoscapes and assumptions inherent in the isotope approach in general.

3.3 Material and Methods

The basis for the use of stable isotopes to identify the geographical origins of birds from their feathers is the existence of valid isoscapes or predictable clinal geographical variation in tissue or foodweb stable isotope ratios (Hobson & Wassenaar 1997; Bowen et al. 2005). When assigning feathers to a place of origin, i.e. linking isotopic feather values to modelled surfaces of different isotopes, it is also essential to account for discrimination factors linking tissues isotopically to the food chain (DeNiro & Epstein 1981; Hobson & Clark 1992; Lott & Smith 2006; Wunder & Norris 2008b). By applying appropriate discrimination factors, feather isotopic values can be directly compared with environmental, reference isotopic values.

There are several issues which have to be considered when using stable isotopes as geographic markers, i.e. concerning isotopic variance due to various reasons (Hobson 2008). First, feathers originating from sympatrically living birds, hence which were grown at the same geographical location could show variance in isotopic values due to sex, age, year and the type of feather being produced. Second, inter-annual variation of isotopic values of feathers from a single bird that were grown at the same location should be known. In addition, there remains the issue of isotopic fractionation between the local isotopic values and tissue isotopic values (e.g. relationship between δD_{precip} and $\delta D_{feather}$), which could differ between species, as well as between locations (Lott & Smith 2006; Wunder & Norris 2008b). We evaluated the discrimination factor published in the literature (summarized in Hobson 2008) by comparing isotopic values of feathers grown on the breeding grounds (hereafter ‘summer feathers’) with the expected modelled isotopic values of these sites. In the case of the discrimination factor for deuterium, we further cross-validated the results obtained from Swiss feathers by applying this discrimination factor to Spanish summer feathers.

We approached the first two issues from above by examining variations in feather δD, δ^{15}N and δ^{13}C values as a function of sex, age, and collection year in feathers of known (breeding ground) and unknown (wintering ground) origin in the Swiss Hoopoe population. In a subset of Swiss individuals, we could also examine the inter-annual isotopic variation in feathers grown in the winter quarters (hereafter 'winter feathers'). Referring to available isoscapes of deuterium (Bowen et al. 2005) and stable nitrogen (Bowen & West 2008), we then compared Swiss vs. Spanish summer and winter feathers. For summer feathers, we expected differences in deuterium and δ^{15}N values due to the different predicted surfaces (isoscapes) between Switzerland and Spain. Afterwards, we performed a comparison of the isotopic values of winter feathers to assess the degree of migratory connectivity in these two populations. Lastly, we matched winter feather isotopic values with wintering grounds isoscapes from Bowen et al. (2005) and Bowen and West (2008) to delineate wintering areas ('map lookup', Wunder & Norris 2008a). The latter operation was validated by comparing isotopic values of Swiss and Spanish winter feathers with values measured in Hoopoe museum specimens collected on the presumed wintering range in subtropical and northern tropical Africa.

3.3.1 Study species and study sites

European Hoopoes (ca 75 g) winter mostly in sub-Saharan Africa (between 7° and 16° latitude) although some individuals are resident in southern Mediterranean Europe. The wintering areas of specific populations remain unknown (Cramp 1985; del Hoyo et al. 2001; Reichlin et al. in press). We measured stable isotope values in Hoopoe feathers from a Swiss population (Canton of Valais, SW Switzerland, 46° 14'N, 7° 22'E, 460-520 m a.s.l.) and a Spanish population (Province of Granada, Spain, 37° 18' N, 3° 02' W, 800-1100 m a.s.l.). The Swiss study area is situated on the plain of a deep Alpine valley dominated by intensive agriculture (mostly fruit tree plantations and vineyards; Arlettaz 1984), whilst the Spanish site is in a middle altitude basin dominated by dryland cereals and irrigated crops (Martín-Vivaldi et al. 1999a; Martín-Vivaldi et al. 1999b).

3.3.2 Feather sampling

Feather samples from the Swiss birds were collected during the breeding season, in May - August 2005 and 2006 (143 and 162 individuals, respectively; 48 birds from 2006 were recaptures from the 2005 sample). From the Spanish population, 29 individuals (of which 15 were nestlings from different nests) were sampled in 2006. Birds were taken by hand directly from the nestbox or caught with mist nets or traps placed close to nest entrance. All birds were thus breeding. From primary (P) or secondary (S) wing feathers, we clipped a central piece of 2.5 to 3 cm of the vane and stored it in a paper envelope until further analysis. Sex was determined from the size of the uropygial gland, which is very conspicuous and filled with a dark and odorous liquid in females, but small and apparently empty in males. Second year birds (SY birds, i.e. birds in their 2nd calendar year) were distinguished from adults (AD, i.e. birds older than SY) from the available ring information or based on age-specific moulting patterns. First-year birds undergo only a partial moult in the wintering areas, which includes body feathers, wing coverts and inner secondary wing feathers, but not primaries. Adult birds undergo a complete moult and all primaries are renewed in the wintering area. From SY birds, we collected a piece of a primary flight feather (P4 or P5; feathers are counted from the distal side), which was not moulted during winter and hence carried the isotopic value of the site of birth ($n_{\mathrm{Switzerland}}$ = 115, n_{Spain} = 4). Among the Swiss SY birds (n = 115), 37% had been ringed as nestlings in the study area, whereas the others were of unknown origin. In addition, tail feathers of fifteen Spanish nestlings were sampled in order to compare Spanish and Swiss (the above SY P4 or P5 samples) summer feather values. To obtain isotopic values of the wintering areas from SY birds ($n_{\mathrm{Switzerland}}$ = 177), we sampled a piece of a secondary wing feather, which was usually moulted during winter (S6, or if not renewed in winter, the renewed S4 or S5 which were clearly recognizable based on their "fresh" colouration), and from AD birds ($n_{\mathrm{Switzerland}}$ = 125, n_{Spain} = 10) a piece of P4.

We finally collected contour feathers from Hoopoe museum specimens originating from 14 African countries (n = 59, Appendix 1), in order to obtain isotopic reference values across the expected Hoopoe wintering range on the African continent. Most of these specimens had been attributed to various African Hoopoe subspecies. Despite the possibility that some African Hoopoes migrate, such movements are of limited extent.

3.3.3 Stable isotope analysis

Feather samples (n = 505) were cleaned of surface oils with a 2:1 chloroform-methanol solvent, and prepared for stable isotope analysis at the Environment Canada stable isotope laboratory in Saskatoon (Saskatchewan, Canada). Approximately 350 µg of feather material were weighed into small silver cups, and the relative abundance of deuterium ($^{2}H/^{1}H$) was measured with the comparative equilibrium method (H_2 derived from high temperature flash-pyrolysis and CF-IRMS; described in detail by Wassenaar & Hobson 2003) which was referenced with calibrated keratin isotope materials. The keratin standards were used to control for the isotopic exchange between samples and ambient water vapor (Wassenaar & Hobson 2000). All results are expressed in the usual delta (δ) notation, in units of per mil (‰), and normalized on the Vienna Standard Mean Ocean Water – Standard Light Antarctic

Precipitation (VSMOW-SLAP) standard scale (Wassenaar & Hobson 2003). Measurement error, based on replicates of IAEA-CH-7 (-100%) and keratin references was smaller than ± 3‰.

Stable carbon and nitrogen isotope ratios (relative abundance of $^{13}C/^{12}C$ and $^{15}N/^{14}N$, respectively) were measured from 500 µg feather material weighed into small tin cups using standard flash combustion elemental analyses (Elemental Analyzer, Euro EA, EuroVector Instruments). The results are presented in delta notation relative to Vienna Peedee Belemnite Standard (VPDB) for $\delta^{13}C$ and relative to atmospheric N_2 (air) for $\delta^{15}N$, respectively. Measurement errors were estimated at ± 0.1‰ for $\delta^{13}C$ and ± 0.3‰ $\delta^{15}N$. Further information on mass spectrometric analyses can be found in Evans-Ogden et al. (2004).

3.3.4 Statistical analysis of feather isotope values

Feather samples were grouped into summer and winter feathers (for definitions see Introduction). For Swiss Hoopoes, we tested the influence of sex and collection year on the isotopic values of summer feathers by fitting a fixed-effects model for each stable isotope separately (age was not included as factor since all individuals in this group were of the second year). In winter feathers, the influence of age, sex, and collection year on isotopic values was examined by similarly applying a linear mixed-effects model (lme with restricted maximum likelihood, R Development Core Team 2008). Individual was treated as a random factor in this second model because some individuals were measured in two years. The inter-annual difference in isotopic values of winter feathers in individuals measured twice ($n = 48$) was tested by paired Student's t-tests, for SY and AD birds separately. Student's t-tests were also applied to compare the mean isotopic values of SY vs. AD birds within one year. This allowed us to test whether the isotopic values of an individual remained constant between years, and whether the isotopic values differed with respect to age.

To study differences in isotopic values between the Swiss and the Spanish Hoopoe populations, we also fitted fixed-effects models for each stable isotope from summer and winter feathers separately, using only feathers collected in 2006, with population being the independent variable. All analyses were performed with the statistical software R (R Development Core Team 2008, Version R 2.6.2).

3.3.5 Isoscapes

For the modelled surface of deuterium, we used the Online Isotopes in Precipitation Calculator (OIPC, www.waterisotope.org, Bowen 2007), which estimates kriged monthly and annual values for δD_{precip}. With the annual value of δD_{precip} for the study site in Switzerland

(Appendix 2) and $\delta D_{feather}$ values of Swiss summer feathers, we obtained a mean (± SD) isotopic discrimination factor of -21.3 ± 9.8‰. The calculation of this discrimination factor was restricted to SY birds which were certainly born in Switzerland (*n* = 43 individuals ringed as nestlings), even though there was no difference in δD between SY birds from Switzerland and SY "potential immigrants" (mean ± SD: -74.64 ± 9.80‰ vs. -73.33 ± 16.93‰; t = 0.52, df = 109.5, p = 0.60). The calculated discrimination factor lies between the values proposed by Bowen et al. (-19‰, 2005) and Wassenaar & Hobson (-25‰, 2001). Based on this factor, the expected feather values for the study site in Spain (δD_{Spain}) should be -62.3‰ (= -41‰ to -21.3‰).

Accurate isoscapes for environmental $\delta^{15}N$ and $\delta^{13}C$ are still difficult to obtain but Amundson et al. (2003) and Still et al. (2003) provided rough estimates of global distributions of $\delta^{15}N$ and $\delta^{13}C$ based on plant physiology and climate models, recently reanalyzed and redrawn by Bowen & West (2008). The discrimination factors between plant and feather were assumed to be +2‰ for ^{13}C and +5‰ for ^{15}N (Hood-Nowotny & Knols 2007). Generally, on a broad geographic scale, we are able to differentiate between landscapes dominated by C3- (mean $\delta^{13}C$ ± SD: -27 ± 2‰), C4- (-13.1 ± 1.2‰) and CAM-plants (-10‰ to -20‰; Smith & Epstein 1971; Koch et al. 1995; Codron et al. 2007; Hood-Nowotny & Knols 2007). For $\delta^{15}N$, environmental gradients exist between different biomes/habitats (reviewed in Rubenstein & Hobson 2004). The approximate expected ranges of $\delta^{15}N_{feather}$ values (based on the plant $\delta^{15}N$ map of Bowen & West 2008) is 3.4 to 3.9‰ for the study site in Switzerland, and 6.7 to 7.2‰ for the study site in Spain.

We explored the use of δD to make predictions of wintering grounds by matching winter $\delta D_{feather}$ values (10 - 90% percentiles) of the Swiss and the Spanish populations with interpolated δD maps of southern Europe and Africa. Maps were generated with ArcGIS based on mean δD_{precip} values for October-January (data available on www.waterisotopes.org, Bowen 2007). These months were chosen, as they reflect i) the time window of feather renewal, and ii) likely the isotopic values of recent rainfall which would then be incorporated into the renewed feather. We explored the potential of $\delta^{13}C$ and $\delta^{15}N$ for drawing wintering-ground predictions of origin by matching mean $\delta^{13}C_{feather}$ values with the global mean annual $\delta^{13}C$ isoscape and mean $\delta^{15}N_{feather}$ values with the global plant $\delta^{15}N$ isoscape, both provided by Bowen & West (2008). In all comparisons, we accounted for the above described discrimination factors.

Feather isotopic values of museum Hoopoe specimens were grouped and averaged into geographic regions (Northwest Africa, West Africa, Central Africa, and East Africa, Table 3). They presumably reflect isoscapes across the African wintering range of Hoopoes, and thus function as a local control for the modelled surfaces of δD. Additionally, they are compared to the isotopic values of the winter feathers in a further attempt to delineate the wintering range of Swiss and Spanish Hoopoes.

3.4 Results

3.4.1 Measured vs. expected isotopic values

Deuterium values of Spanish summer feathers (Table 2) were, on average, slightly lower than expected based on the OIPC (expected value -62.3‰ vs. -56.58 ± 15.1‰). Summer $\delta^{13}C_{feather}$ values for Swiss and Spanish Hoopoes corresponded to values of C3-plant dominated landscapes (approximate expected value -23.3 to -23.0‰ vs. -23.85 ± 1.1‰; and -23.7 to -23.2‰ vs. -23.19 ± 1.1‰, respectively). Furthermore, summer $\delta^{15}N_{feather}$ values were higher than expected for Switzerland (approximate expected value 3.4 to 3.9‰ vs. 8.41 ± 1.8‰), and Spain (6.7 to 7.2‰ versus 8.54 ± 2.7‰).

3.4.2 Variation in feather isotopic values between years, sexes, age classes and populations

For summer feathers of Swiss birds, δD differed significantly with respect to year only, $\delta^{13}C$ in relation to sex only, and $\delta^{15}N$ values differed significantly neither between years nor sexes (Table 1a). Feather δD values were significantly higher in 2006 than in 2005 (means ± SD: -71.10 ± 2.15‰ vs. -77.32 ± 2.52‰, respectively). Male Hoopoes had lower $\delta^{13}C$ values than females (-24.14 ± 0.19‰ vs. -23.72 ± 0.17‰, respectively). For winter feathers from Swiss birds, isotopic values differed between years for all three stable isotopes (mean ± SD 2005 vs. 2006: δD: 0.18 ± 2.76‰ vs. -8.61 ± 2.44; $\delta^{15}N$: 10.07 ± 0.30‰ vs. 10.97 ± 0.26‰; $\delta^{13}C$: -16.16 ± 0.48‰ vs. -17.19 ± 0.45‰). SY birds had significantly higher δD values in winter feathers compared to AD (5.54 ± 2.20‰ vs. 0.18 ± 2.76‰), while there was no difference due to sex (Table 1b).

In winter feathers of Swiss individuals caught as adults in both years, isotopic values for all three analyzed isotopes were similar between years. However, SY birds caught in 2005 showed significantly different δD, $\delta^{15}N$ and $\delta^{13}C$ values in the year 2006 (Fig. 1). Within the same collection year, isotopic values differed between SY and AD birds only for δD in 2005 (δD: $t = -2.57$, $df = 46$, $p = 0.0135$; Fig. 1).

Summer and winter feathers both differed significantly between the Swiss and the Spanish population for δD and $\delta^{13}C$, but not for $\delta^{15}N$ (Fig. 2). δD and $\delta^{13}C$ values in Swiss birds were lower in summer feathers and higher in winter feathers compared to the values measured in Spanish birds. $\delta^{15}N$ values were lower in Swiss birds in both summer and winter feathers (Fig. 2).

3.4.3 Wintering grounds

Matching the 10 – 90% percentiles of winter $\delta D_{feather}$ values of Swiss Hoopoes ($\delta D_{Switzerland}$ = -6.4 to +46.22‰: corrected with discrimination factor) with the generated deuterium maps showed an overlap with the Sahel (Fig. 3a). The overlap of the Spanish 10 – 90% percentiles of winter $\delta D_{feather}$ values (δD_{Spain} = -46.46 to +31.75‰) included not only the whole African continent, but also the southern end of the Iberian Peninsula (Fig. 3b). Mean winter $\delta^{13}C_{feather}$ values of the Swiss and the Spanish populations are within the range of C4- and CAM-plant dominated landscapes. Based on the map by Bowen & West (2008) on plant $\delta^{13}C$, this corresponded to an area between ca 5° and 15° N latitude in Africa (Sahel). Mean winter $\delta^{15}N_{feather}$ values of both populations corresponded to an area in Africa between approx. 5° and 32° latitude, the Sahara Desert excluded (scarlet red area in Bowen & West 2008).

Isotopic values of museum specimens were averaged for different regions in Africa (Table 3). Mean $\delta D_{feather}$ values of museum birds from East Africa corresponded to the values obtained for Swiss birds, while mean $\delta D_{feather}$ values for Spanish birds show similar isotopic values as found in museum specimens collected in West Africa.

3.5 Discussion

3.5.1 Exploring the variation in feather isotopic values

We found differences in isotopic values between the sexes (lower $\delta^{13}C$ values for male birds) and collection year (enriched δD values in 2006) in summer feathers, and between age classes (enriched δD values in SY birds) and collection years in winter feathers of Swiss Hoopoes. Fortunately, our sampling design further enabled us to disentangle any year and age effects as regards winter feathers: this is because some individuals belonging to the two age classes were measured twice in two successive years. Isotopic values measured on SY birds significantly differed from a second series of measurements operated on the same birds one year later, i.e. when they were recaptured as AD. In contrast, such a year effect was not apparent for birds caught twice as adults (Fig. 1).

Based on own observations of feeding behaviour (nestlings diet consisted up to 97% of molecrickets, Fournier & Arlettaz 2001), we could assume that individuals feeding on the same prey type at the same location incorporate similar isotopic values into their tissues, regardless of sex. Moreover, as the male breeding bird usually delivers the major part of prey items to nestlings (breeding female stays in the nestbox during the first 5-10 days after nestlings hatched), we do not assume any differential feeding according to the sexes. Nevertheless, $\delta^{13}C$ values were, on average, 0.42‰ (SE = 0.19) lower for male than female birds in Swiss summer feathers (Table 1). The difference and effect size are so small, however, that it is questionable whether they bear any biological relevance.

Age specific isotopic values could be species dependent, as some previous studies found such differences (e.g. Meehan et al. 2003), but others not (e.g. Yohannes et al. 2008). For Hoopoes, we found a significant difference in δD values in winter feathers between SY and AD birds. This could basically be due to various confounding factors (if not a combination of them) such as age-specific difference in 1) food (e.g. Meehan et al. 2003), 2) heat stress (Powell & Hobson 2006), 3) wintering locations (e.g. Chamberlain et al. 2000), 4) timing of moult (Kelly et al. 2008), or 5) the metabolism of stable isotope incorporation (e.g. Meehan et al. 2003). The comparison of the isotopic values recorded from the same individuals measured in two successive years showed that birds captured as SY have significantly more enriched δD values and significantly more depleted $\delta^{13}C$ and $\delta^{15}N$ values than birds subsequently measured as AD (Fig. 1). On the contrary, isotopic values of the same birds captured twice as AD (2005 and 2006) were highly repeatable between the two years (see also Yohannes et al. 2008). Although there is no thorough analysis of winter diet in this species, there is no reason to believe that Hoopoes of different ages have distinct trophic niches. Heat stress should affect all birds equally (but see McKechnie et al. 2004); it may explain the observed highly enriched $\delta D_{feather}$ values (Powell & Hobson 2006), but not the age-specific difference. It is furthermore unlikely that SY and AD birds winter in different areas. Although it has been documented that nestlings may have a different metabolism than adults (Meehan et al. 2003), and thus exhibit different isotopic values, the two age categories considered here both renewed their feathers in winter. A delayed winter moult in SY birds (shortly before the onset of the return, spring migration) seems hence to be the most likely explanation for an age effect. It could result in more enriched $\delta D_{feather}$, as δD_{precip} is more enriched at the beginning of the year (annual variation in δD in Africa: enriched δD_{precip} values for January and February, see www.waterisotopes.org). As ambient temperatures are generally lower during that time of the year in northern subtropical Africa, heat, water and/or nutritional stress could be diminished, resulting in reduced $\delta^{15}N_{feather}$ values (reviewed in Kelly 2000), which would precisely yield the pattern observed between SY and AD birds (Fig. 1). This delayed winter moult in yearlings could be attributed to less energy reserves compared to adults. The same line of argumentation could explain why SY birds undergo only a partial moult during their first visit to the wintering quarters (see Material and Methods).

Earlier studies have shown that feathers grown in the same geographic location should bear similar isotopic values over years (e.g. Rubenstein et al. 2002). This means highly predictable isotopic values for common geographical origins (Hobson 2004), as in the case of summer feathers. However, summer feathers from 2006 exhibited significantly enriched δD values compared to summer feathers from 2005. As our sample size is reasonably large, this reflects real annual variation in $\delta D_{feather}$ values and cannot be referred to background noise in the data (Inger & Bearhop 2008). Our data thus suggests that annual environmental variation of δD on a local scale might not be negligible, especially when the primary water source is not primarily from natural rainfall but from irrigation with sprinklers, as it is the case in the Hoopoe's main habitat in Valais (fruit plantations). The same may happen when there is a considerable amount of surface water evaporation (Inger & Bearhop 2008), which was definitely the case during the warmer summer of 2006 compared to 2005.

For winter feathers, there was an obvious between-year variation in isotopic values: in 2006, feather isotopic values were significantly depleted in δD and δ^{13}C, whilst they were significantly enriched in δ^{15}N, compared to winter feathers from 2005. In addition to a natural, annual environmental isotopic variation (as shown for δD by Koch et al. 1995; and for δ^{13}C and δ^{15}N by Bowen 2008), a year effect in winter feathers could be explained by birds visiting distinct wintering locations in the two years. These two scenarios can unfortunately not be disentangled. Yet, as winter feathers differed between the years not only for δD (which could easily be explained by varying amount of precipitation and surface waters; Dansgaard 1964), but also for δ^{13}C and δ^{15}N, it is likely that birds moulted their wing feathers at different locations. This may happen if birds track spatial food resource availability over wide areas, with foraging opportunities highly dependent on local vegetation productivity, i.e. rainfall.

3.5.2 *Differences among populations and expected feather values*

Several earlier studies have shown that geographically separated breeding populations could be distinguished from their isotopic values (e.g. Evans et al. 2003; Møller & Hobson 2004; Bearhop et al. 2005). Our expectations about differing isotopic values of deuterium and stable nitrogen in summer feathers between the Swiss and the Spanish populations were only partially met, however. We first found lower $\delta D_{feather}$ values in Swiss Hoopoes, which reflect the gradient of δD_{precip} across Europe, with more depleted values at higher latitudes (Bowen et al. 2005). Despite the fact that the expected δ^{15}N values for Swiss and Spanish feathers were different ($\delta^{15}N_{Switzerland}$ = 3.4 – 3.9‰; $\delta^{15}N_{Spain}$ = 6.7 – 7.2‰), we found no significant differences in $\delta^{15}N_{feather}$ values between the two populations. We explain this by either inaccurate estimates of local isotopic values (basemaps not detailed enough) or by insufficiently discernible geographic variation in δ^{15}N (also in Kelly et al. 2008). We thus conclude that δ^{15}N is a poor geographic marker at our study scale, although it is generally a good indicator of aridity (Koch et al. 1995 and references therein). Moreover, δ^{15}N might be strongly affected (i.e. large differences between expected vs. obtained isotopic values) by the intensive agricultural landscape and complex anthropogenically driven nitrogen fluxes (e.g. Hebert & Wassenaar 2001). The small, significant population difference for δ^{13}C suggests that the plant communities in the two study areas produce similar $\delta^{13}C$ values within the range expected for C3-plants (-25 ± 2‰) typical of temperate, irrigated agro-ecosystems.

3.5.3 Predicting wintering areas

A comparison of the feather isotopic values for δD, $\delta^{15}N$ and $\delta^{13}C$ with the reference isoscapes suggests that Swiss Hoopoes winter in the Sahel belt, while some of the Spanish Hoopoes spend the winter in southern Spain. This is supported by frequent observations of a fraction of colour-ringed Hoopoes from our Spanish breeding population wintering in the southern part of the Iberian Peninsula (Martín-Vivaldi unpublished data). Assuming a δD_{precip} threshold between Europe and Africa close to ca -30‰ (Fig. 3), we predict three out of ten birds from our Spanish study area to be residents (Fig. 2, δD: lower three tick marks). These sedentary Spanish birds would introduce a shift in the geographic location of their winter grounds towards Spain. This could result in an artifactual spatial separation of the Swiss and Spanish Hoopoes in their winter quarters, whilst they may actually share the same wintering areas.

The analysis of Hoopoe museum specimens showed a gradient of depletion in $\delta D_{feather}$ values from East to West, and then from West to North (Table 3), which is partially in line with the OIPC estimates for deuterium in precipitation (strong south-north gradient, weak east-west gradient, Fig. 3). Mean isotopic values of eastern African museum specimens correspond well to the mean of Swiss winter feathers, while the mean of all Spanish winter feathers more closely matches western African museum specimens. Note, however, that excluding the above three potential residents from the Spanish sample would similarly have resulted in a match with eastern African museum specimens (i.e. δD_{Spain} -8.18 ± 15.6‰ vs. $\delta D_{AfricaEast}$ -5.05 ± 26.71). Actually, the use of mean values for geographic attribution of samples is highly problematic as it can lead to false inferences. Notwithstanding this and further limitations associated with museum specimens (e.g. age of skins, provenance, preservation, etc., Bugoni et al. 2008), the values measured from African specimens seem to corroborate our hypothesis that Swiss Hoopoes winter primarily in northern subtropical East Africa.

3.5.4 Conclusion

The high variation induced by year, individual and age, as well an apparent low regional resolution of the current isoscapes (especially for Africa) raises numerous questions about how to assign feather samples to definite places of origin. This problem is a serious handicap to an appropriate delineation of actual wintering ranges, which hampers proper assessments of migratory connectivity. Another key methodological issue remains the isotopic fractionation between the environment and animal tissue: wrongly determined discrimination factors and incomplete knowledge on basemaps can largely offset the place of origin. This is why we (successfully) validated the published discrimination factors based on our own calculations (as suggested by Hobson 2005). Fortunately, stable isotopes provided a conclusive outcome regarding the spatial segregation of our two breeding populations, which is also to refer to a good spatial resolution of stable isotopes on a European scale.

In spite of all the potential biases and uncertainties mentioned above, it seems that the wintering area of the Swiss Hoopoes is located mostly in subtropical and northern tropical eastern Africa. Future population dynamical modelling which will attempt to estimate seasonal components of survival will thus have to account for fluctuations in environmental conditions prevailing in that part of the world. Beforehand, however, the location of these wintering quarters should be confirmed by other sources: the use of geolocators (Phillips et al. 2007) is probably the most promising technique in that respect. Overall, the combination of several independent methods (summarized in Hobson & Norris 2008) may be necessary to provide decisive insights into migratory connectivity, thus allowing the development of sound conservation programmes for endangered migrants.

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Table 1 Estimates and ANOVA tables showing for Swiss Hoopoes (a) the influence of year and sex on stable isotopes retrieved from summer feathers of SY birds; (b) the influence of year, sex and age on stable isotopes retrieved from winter feathers. Estimates (year = 2006; sex = male; age = SY) are taken from the linear fixed effects model for summer feathers, and from the linear mixed effects model with individual as random factor for winter feathers. Degrees of freedom are given for the numerator, followed by the denominator in the linear mixed effects model. Definitions of summer and winter feather samples in *Material and Methods*.

a)

Summer		Estimate	SE	DF	F-value	P-value
δD	Intercept	-77.32	2.52	1	2985.03	<0.0001
(*n* = 113)	Year	6.22	2.83	1	4.71	0.032
	Sex	-0.98	2.72	1	0.13	0.719
δ^{15}N	Intercept	8.70	0.32	1	2488.27	<0.0001
(*n* = 115)	Year	-0.34	0.35	1	0.99	0.322
	Sex	-0.16	0.34	1	0.22	0.642
δ^{13}C	Intercept	-23.72	0.17	1	66281.56	<0.0001
(*n* = 115)	Year	0.11	0.19	1	0.17	0.685
	Sex	-0.42	0.19	1	5.08	0.026

b)

Winter						
δD	Intercept	0.18	2.76	1,248	5.69	0.018
	Year	-8.79	2.15	1,49	21.89	<0.0001
(*n* = 301)	Sex	-3.80	2.57	1,49	2.56	0.116
	Age	5.36	2.37	1,49	5.12	0.028
δ^{15}N	Intercept	10.07	0.30	1,249	5277.18	<0.0001
	Year	0.91	0.23	1,49	18.11	0.0001
(*n* = 302	Sex	-0.30	0.28	1,49	1.00	0.322
	Age	-0.34	0.26	1,49	1.73	0.194
δ^{13}C	Intercept	-16.16	0.48	1,249	5356.73	<0.0001
(*n* = 302)	Year	-1.03	0.41	1,49	7.05	0.011
	Sex	-0.09	0.45	1,49	0.07	0.791
	Age	0.56	0.44	1,49	1.67	0.202

Table 2 Deuterium, stable nitrogen, and stable carbon compositions of Hoopoe summer and winter feathers. For Swiss birds, values are averaged over the years 2005 and 2006, while Spanish feathers only include feathers of 2006 (mean ± SD in ‰, sample size in brackets). Definitions of summer and winter feather samples in *Material and Methods*.

Feathers	Population	δD			$\delta^{15}N$			$\delta^{13}C$		
Summer	Swiss	-73.75	± 14.5	(113)	8.41	± 1.8	(115)	-23.85	± 1.1	(115)
	Spanish	-56.58	± 15.1	(19)	8.54	± 2.7	(17)	-23.19	± 1.1	(19)
Winter	Swiss	-2.57	± 21.7	(301)	10.23	± 2.3	(302)	-16.38	± 3.8	(302)
	Spanish	-24.42	± 29.7	(10)	11.88	± 2.8	(10)	-19.14	± 4.5	(10)

Table 3 Deuterium compositions of museum Hoopoe specimens from 14 African countries (mean ± SD in ‰), grouped into and averaged within geographic regions. The countries were chosen to span the whole potential wintering area of European Hoopoes from West to East Africa.

Country	*n*	δD	SD
North-West	2	-44.67	34.46
Algeria	1	-20.30	
Morocco	1	-69.03	
West	16	-29.80	29.68
Mali	9	-21.07	31.62
Senegal	4	-42.21	23.47
Gambia	3	-39.41	31.52
Central	11	-10.61	19.19
Chad	5	-9.01	25.17
Cameroon	3	-21.57	10.77
Nigeria	3	-2.32	12.98
East	28	-5.05	26.71
Sudan	7	1.62	21.34
Ethiopia	6	-7.09	42.63
Somalia	5	-5.40	15.13
Kenya	5	-18.50	34.90
Uganda	3	3.85	8.29
Tanzania	2	-1.11	3.24

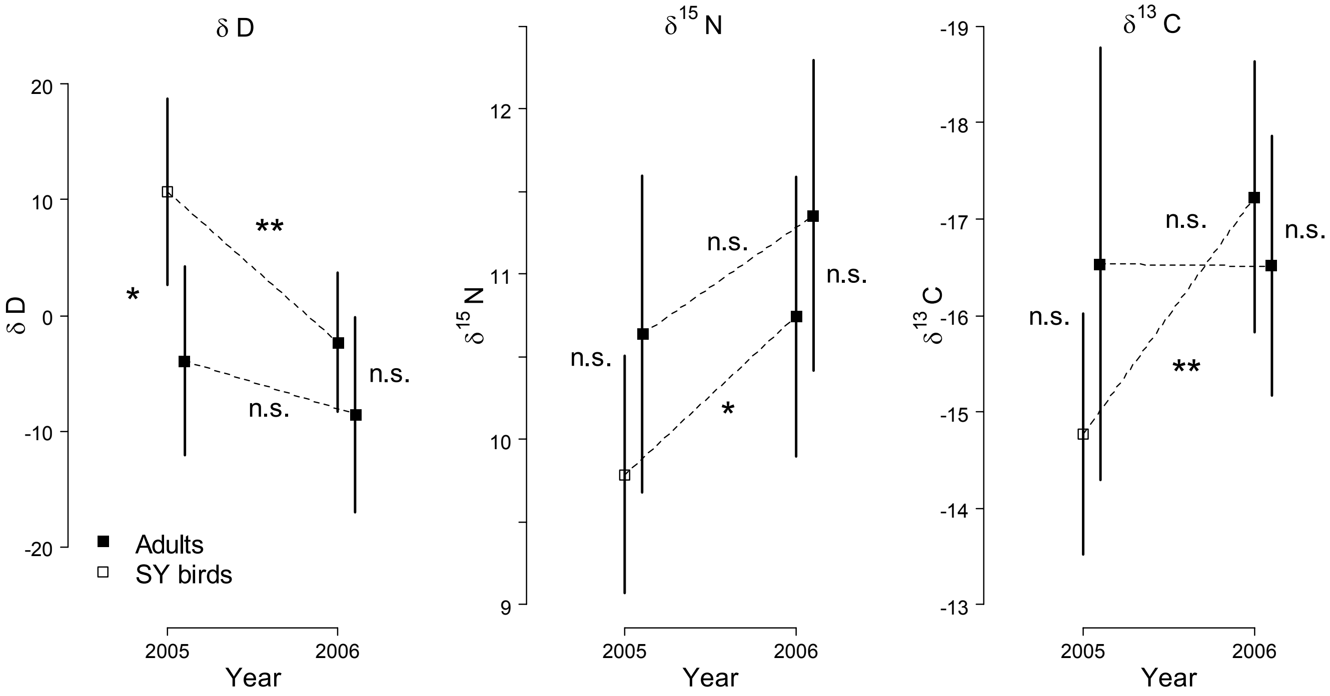

Figure 1 Deuterium, stable nitrogen and stable carbon isotopic values (means ± 95% CI) of winter feathers of Swiss Hoopoes caught in both years (*n* = 48). *Dotted lines* indicate the mean change in isotopic values in the same individuals. *Stars* indicate significant differences (* = $p < 0.05$, ** = $p < 0.01$), whereas *n.s.* indicates no difference at a significance level of $p = 0.05$. Paired t-test of birds caught as SY in 2005: δD: $t = 3.63$, $df = 27$, $p = 0.0012$; δ^{15}N: $t = -2.21$, $df = 27$, $p = 0.0357$; δ^{13}C: $t = 2.81$, $df = 27$, $p = 0.0091$.

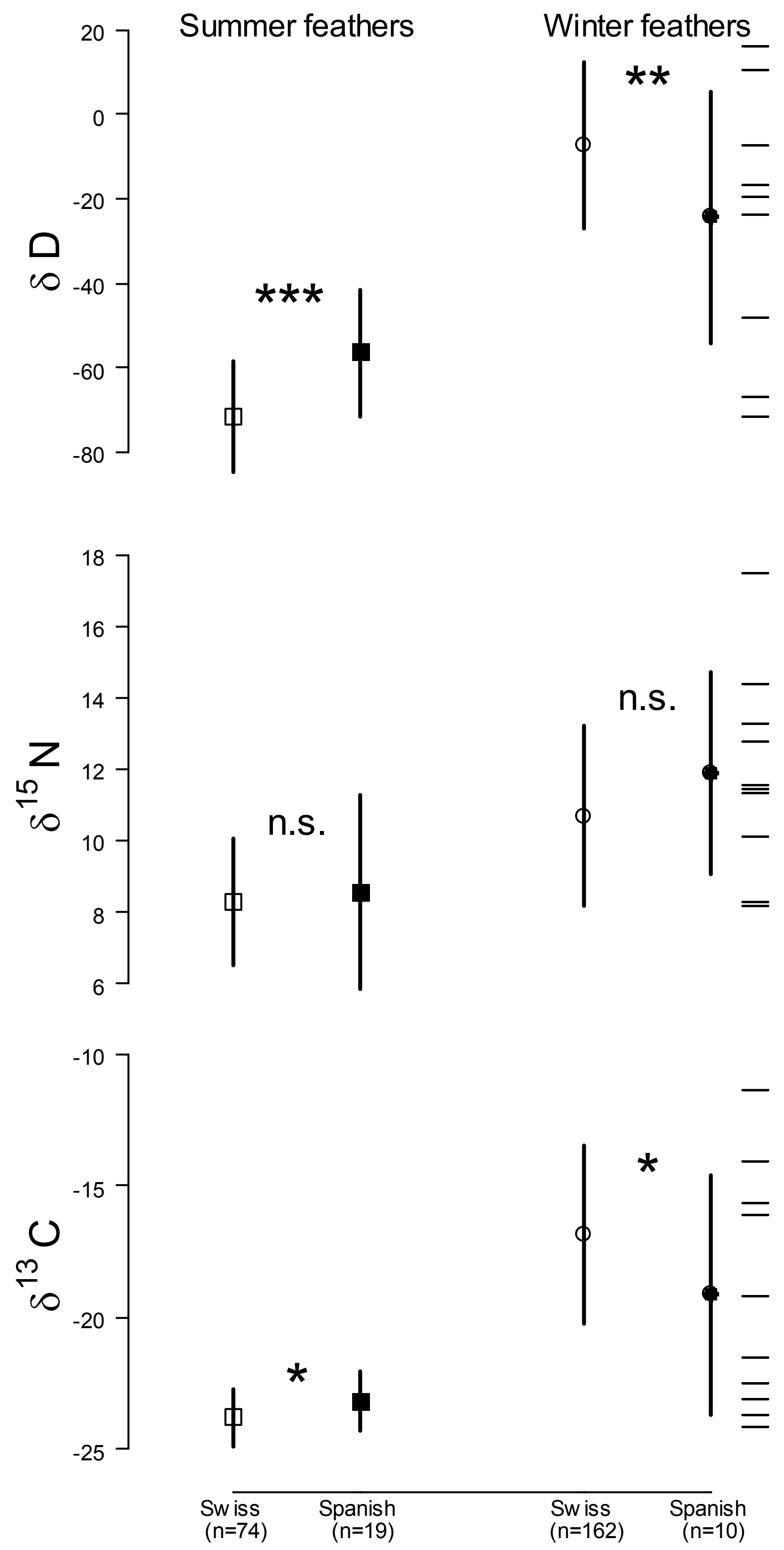

Figure 2 Comparison of Swiss and Spanish summer and winter feather isotopic values of 2006 for deuterium, stable nitrogen and stable carbon (means ± SD). *Stars* indicate significant differences between the two populations (* = $p < 0.05$; ** = $p < 0.01$, *** = $p < 0.0001$). *Vertical lines* (ticks) indicate absolute values of Spanish winter isotopic values.

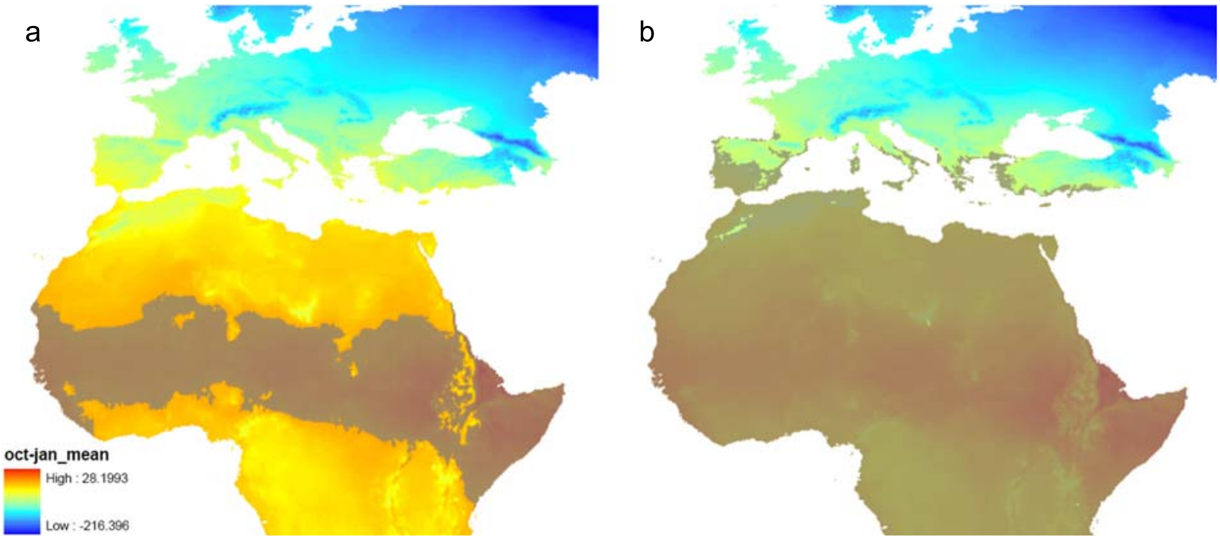

Figure 3 Deuterium (δD) distribution for the months October-January. *Areas in brown* (10 – 90 percentiles of deuterium isotopic values) indicate the presumed wintering areas of (a) Swiss and (b) Spanish Hoopoes. Feather values were previously converted to precipitation values with a discrimination factor of +21.3‰ (feather to precipitation) to match the basemaps.

Appendix 1 Deuterium values (in ‰) of Hoopoe museum specimens from the collections of: the Natural History Museum at Tring (T), London, UK; the Muséum National d'Histoire Naturelle in Paris (P), France; and from the Natural History Museum of Basel (B) in Switzerland.

Country	Coordinates		Subspecies	Collection		δD
	x	y	(as given on the museum label)		Date	
Algeria	32° 06'N	1° 14'W	*U. epops*	T	16.03.1924	-20.30
Cameroon	5° 54'N	10° 30'E	*U. e. senegalensis*	T	10.11.1956	-27.49
Cameroon	10° 35'N	14° 19'E	*U. e. somaliensis*	T	06.12.1922	-9.14
Cameroon	11° 02'N	14° 19'E	*U. e. somaliensis*	T	28.04.1925	-28.09
Chad	21° 34'N	19° 13'E	*U. e. senegalensis*	P	29.09.1958	-36.00
Chad	7° 39'N	15° 52'E	*U. e. senegalensis*	P	10.04.1973	-14.96
Chad	12° 06'N	15° 04'E	*U. e. senegalensis*	P	10.1933	-18.06
Chad	12° 06'N	15° 04'E	*U. e. senegalensis*	P	10.1933	32.07
Chad	21° 34'N	19° 13'E	*U. e. senegalensis*	P	13.07.1959	-8.08
Ethiopia	8° 24'N	39° 00'E	*U. epops*	T	18.12.1904	-34.24
Ethiopia	8° 28'N	38° 50'E	*U. epops*	T	10.02.1905	NA
Ethiopia	9° 19′N	42 70'E	*U. epops*	T	08.01.1902	-81.30
Ethiopia	14° 00'N	40° 30'E	*U. epops*	T	02.02.1902	16.28
Ethiopia	–	–	*U. epops*	T	12.01.1899	6.66
Ethiopia	8° 11'N	34° 51'E	*U. e. senegalensis*	T	26.12.1916	20.38
Ethiopia	–	–	*U. epops*	T	12.01.1900	29.70
Gambia	13° 29'N	14° 11'W	*U. e. somaliensis*	T	19.01.1929	-9.63
Gambia	13° 29'N	14° 11'W	*U. epops*	T	19.01.1929	-36.18
Gambia	13° 38'N	14° 58'W	*U. e. senegalensis*	T	–	-72.43
Kenya	1° 00'S	39° 56'E	*U. e. africana*	T	28.02.1928	-58.12
Kenya	0° 40'N	36° 06'E	*U. e. africana*	T	10.01.1900	25.02
Kenya	1° 27'S	36° 58'E	*U. e. africana*	T	01.11.1899	7.44
Kenya	–	–	*U. e. africana*	T	18.02.1912	-21.40
Kenya	–	–	*U. e. africana*	T	20.02.1935	-45.44
Mali	13° 26'N	6° 16'W	*U. e. somaliensis*	T	30.01.1932	-10.10
Mali	13° 26'N	6° 16'W	*U. e. somaliensis*	T	24.01.1932	-3.24
Mali	16° 46'N	3° 00'W	*U. e. somaliensis*	T	16.11.1931	-45.23
Mali	16° 46'N	3° 00'W	*U. e. somaliensis*	T	18.11.1931	6.76
Mali	12° 52'N	7° 33'W	*U. epops*	P	11.1956	-88.46
Mali	12° 17'N	10° 58'W	*U. e. senegalensis*	P	01.1959	-23.37
Mali	14° 28'N	4° 12'W	*U. e. senegalensis*	P	1957	-34.96
Mali	14° 28'N	4° 12'W	*U. e. senegalensis*	P	1957	-4.40
Mali	15° 54'N	3° 55'W	*U. e. senegalensis*	P	22.04.1957	13.34
Morocco	35° 45'N	5° 48'W	*U. epops*	T	23.02.1936	-69.03
Nigeria	13° 28'N	12° 57'E	*U. e. africana*	T	10.01.1905	10.19
Nigeria	6° 26'N	7° 30'E	*U. e. senegalensis*	T	31.03.1954	-1.43
Nigeria	7° 40'N	11° 05'E	*U. e. somaliensis*	T	28.05.1925	-15.73
Senegal	14° 21'N	16° 56'W	*U. e. somaliensis*	T	-	-13.60
Senegal	15° 24'N	15° 24'W	*U. epops*	P	26.09.1967	-69.28
Senegal	14°' 48'N	16° 31'E	*U. e. senegalensis*	P	01.1909	-35.89

Senegal	–	–	*U. e. senegalensis*	P	1836	-50.07
Somalia	9° 30'N	44° 00'E	*U. e. senegalensis*	T	26.02.1949	17.63
Somalia	9° 31'N	45° 32'E	*U. epops*	T	12.01.1919	NA
Somalia	10° 01'N	45° 12'E	*U. e. somaliensis*	T	17.12.1918	2.29
Somalia	6° 15'N	47° 58'E	*U. epops*	T	14.11.1894	-12.89
Somalia	–	–	*U. e. somaliensis*	T	14.11.1897	-16.72
Somalia	–	–	*U. epops*	T	11.11.1918	-17.30
Sudan	9° 70'N	31° 40'E	*U. e. senegalensis*	T	18.02.1908	-10.75
Sudan	13° 05'N	30° 21'E	*U. e. somaliensis*	T	17.01.1921	-0.16
Sudan	6° 30'N	31° 14'E	*U. epops*	T	19.01.1914	45.09
Sudan	13 33′N	33° 36′E	*U. epops*	T	18.12.1913	-14.62
Sudan	15° 16'N	26° 30'E	*U. epops*	T	18.02.1922	9.06
Sudan	21° 55'N	31° 18'E	*U. e. major*	T	11.02.1928	-17.50
Sudan	21° 55'N	31° 18'E	*U. e. major*	T	11.02.1928	0.22
Tanzania	5° 06'S	30° 23'E	*U. e. africana*	B	01.01.1937	-3.40
Tanzania	6° 49'S	38° 52'E	*U. e. africana*	B	22.01.1962	1.18
Uganda	2° 20'N	32° 35'E	*U. e. somaliensis*	T	01.01.1910	3.91
Uganda	–	–	*U. e. senegalensis*	T	23.02.1913	12.11
Uganda	–	–	*U. e. senegalensis*	T	01.02.1913	-4.47

Appendix 2 Monthly precipitation values for δD (in ‰, V-SMOW; www.waterisotopes.org, accessed 10.09.2008), for the study site in Switzerland (Canton Valais, δD_{precip} estimates for latitude 46.228°, longitude 7.349°, approx. altitude 480 m) and the study site in Spain (Province of Granada, δD_{precip} estimates for latitude 37.328°, longitude -3.059°, approximate altitude 1061 m).

	Annual	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec
Switzerland	-53	-71	-70	-62	-61	-49	-44	-35	-35	-45	-52	-65	-74
Spain	-41	-45	-43	-47	-42	-35	-28	-25	-22	-29	-39	-44	-47

4

Feather stable isotopes reveal migratory connectivity in endangered populations of the European Wryneck

Feather stable isotopes reveal migratory connectivity in endangered populations of the European Wryneck

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4.1 Abstract

1. Integrated conservation programmes for endangered migratory animal species or populations require locating and evaluating both breeding, stopover, and wintering areas. Stable isotopes in bird feathers indicate the geographical area where feathers have been grown. The source region assignment hinges on 1) wide-scale geographic variation in these isotopes; 2) relatively little between-bird variation in the isotopic value of feathers stemming from the same area; 3) documented temporal and age patterns of moult for individual feathers.

2. We analyzed stable nitrogen ($\delta^{15}N$), carbon ($\delta^{13}C$) and hydrogen (δD) isotopes from wing feathers of two endangered European populations (Switzerland and Germany) of the Wryneck, *Jynx torquilla,* in order to locate wintering grounds and assess the degree of migratory connectivity between breeding and wintering populations. Some basic assumptions of isotope theory were tested beforehand. First, we examined whether feather isotopic values of birds on the breeding grounds matched expected local (reference) feather values. We then tested whether variation in feather isotopic values within the Swiss population was affected by bird age and collection year and investigated differences in isotopic values between the two breeding populations. Finally, the variation in feather isotopic values between breeding and wintering grounds was used to estimate the geographical extension of the winter distribution.

3. Deuterium values of feathers grown on the breeding grounds by hatching year (first year) birds closely matched the expected local values of mean annual δD_{precip}. Bird age and collection year caused substantial isotopic variation in feathers grown in winter, which may be due to annual variability in weather conditions, movements of birds among wintering sites, and/or reflect more asynchronous moulting than previously assumed. The large isotopic variance in winter feathers nevertheless suggests low migratory connectivity for each breeding population, with wintering quarters of the two populations overlapping only slightly.

4. *Synthesis and application*. Our isotope results suggest that a leapfrog migration occurs in Wrynecks, with the northern population (Germany) wintering farther south than the more meridional, Swiss breeding population. A geographical separation of wintering grounds implies that demographic analyses seeking causality for the negative population trends observed in different European Wryneck populations should account for local wintering conditions while estimating seasonal survival.

Keywords: Africa • Annual climatic variation • Isotopic variation • Leapfrog migration • Long-distance migrant

4.2 Introduction

Naturally occurring geographic variation in the stable isotope composition of abiotic and biotic substrates can be used to place animals approximately to their origins. This is because some stable isotopes show a clinal change across continents, hence forming isotopic landscapes or “isoscapes” (isotopic landscapes; Rubenstein & Hobson 2004; Hobson 2005). Site-specific isotopic values are passed on through the food web (DeNiro & Epstein 1981) and are finally incorporated into animal tissues. Stable isotopes measurements of feathers of migratory birds are often used as geographic markers for tracking their wide-scale movements (Hobson & Wassenaar 1997; Chamberlain et al. 1997; Hobson 2005; Norris et al. 2006; Hobson & Wassenaar 2008).

As most stable isotope values remain constant in feathers after their formation (e.g. Pain et al. 2004; but δD, see Chamberlain et al. 1997), these intrinsic markers can provide information about a bird's previous origins. Moreover, such information can be obtained non-invasively and without the bias and costs associated with conventional mark-recapture methods (Wassenaar & Hobson 2001; Hobson 2008). Finally, provided that the moulting pattern of a bird species is known, simultaneous sampling of several generations of feathers from the same individual offers the opportunity to collect, on a single capture event, information on previous locations (the number of potential places basically depending on the number of feather generations available on an individual).

In bird studies, the stable isotopes of hydrogen (δD), nitrogen ($\delta^{15}N$), and carbon ($\delta^{13}C$) have been used to investigate migratory connectivity (e.g. Chamberlain et al. 1997; Evans et al. 2003; Mazerolle et al. 2005; Procházka et al. 2008), metapopulation structure (e.g. Chamberlain et al. 2000), and even to determine location of stop-over sites (e.g. Yohannes et al. 2007). With the help of good species specific isotopic reference basemaps and well-established isotope-specific diet-tissue discrimination factors, feathers can be assigned approximately to origin (e.g. Greenberg et al. 2007). Discrimination factors account for the difference between environmental and tissue isotopic values due to metabolic enrichment or depletion which occur during transfer along the food chain (Hobson & Clark 1992; Hood-Nowotny & Knols 2007).

Successful application of stable isotope measurements to place individuals to isoscapes has typically assumed that annual variation in these isoscape patterns is fairly small. For deuterium, this has been illustrated in both North America and Europe where feather δD values correlate well with weighted average growing season δD values derived from the International Atomic Energy Agency (IAEA) Global Network of Isotopes in Precipitation (GNIP) (Hobson & Wassenaar 1997; Hobson 2004; Bowen et al. 2005; summarized in Hobson 2008). However, there remains intra-annual variation in isotopic δD values, which is mainly driven by temperature and amount of precipitation (Bowen 2008). Intra-annual variation, on the other hand, might again be attenuated due to averaging that takes place in food webs. Variation in $\delta^{13}C$ depends on the different photosynthetic pathways (C3-, C4- and CAM-plants) and hence is dictated by the type of vegetation. Temperate climatic regions with predominant C3 vegetation show more depleted $\delta^{13}C$ values (-27 ± 2‰) compared to high light intensity C4 dominated environments (-13 ± 1.2‰), whereas CAM dominated areas with succulent/desert plants show intermediate values (-10 to -20‰, O'Leary 1988). Variation in $\delta^{15}N$ values is dependent on the type of biome: values are enriched in arid regions and lower in wet regions (Koch et al. 1995 and references therein). Yet, this variation can be strongly influenced by the agricultural landscape and complex nitrogen fluxes in general (N-fixation, atmospheric and anthropogenic N). Moreover, isotopic values in bird tissues could be associated with the age (Yohannes et al. 2008) and/or sex of birds. Adult birds in Cooper's Hawks showed heavier δD values than nestlings in feathers from the same origin (Meehan et al. 2003), whereas Yohannes et al (2008) found no age-specific isotopic feather values (δD, $\delta^{13}C$, $\delta^{15}N$) in Great Reed Warblers. Sex-specific isotopic $\delta^{15}N$ values in diving seabirds (Bearhop et al. 2006) and albatrosses (Awkerman et al. 2007) could indicate different trophic niche use between the sexes.

We investigated the use of multi-isotope geographic variation in δD, $\delta^{13}C$, $\delta^{15}N$ values in feathers collected from two populations of a Palaearctic-African long-distance migratory bird, the Wryneck *Jynx torquilla,* to establish migratory connectivity between breeding and wintering grounds. We define connectivity as the degree to which two or more periods of the annual cycle are geographically linked (Boulet & Norris 2006). Winter ranges of different Wryneck populations are poorly understood as extant data refer only to scarce ring recoveries, mostly from within Europe (Reichlin et al. in press). Rarely has the joint information from three isotopes been used to that purpose in European birds (Pain et al. 2004; Yohannes et al. 2008).

The isotopic values of summer-grown feathers (i.e. feathers grown on the breeding grounds) were compared with the predicted, interpolated isotopic values of deuterium in the environment drawn from reference basemaps (isoscapes). We then evaluated the effect of collection year and bird age on the isotopic values of both summer and winter-grown feathers. Thirdly, we studied the isotopic variation between two geographically distinct breeding populations in order to evaluate isotopic evidence for migratory connectivity. Finally, we compared the magnitude of isotopic variation between feathers grown on the breeding and the wintering grounds to get a relative measure of the extent of the summer and winter distribution range of the two populations (Bearhop et al. 2004).

Information about wintering grounds and migratory connectivity is an essential step to build realistic demographic models that incorporate seasonal variation of survival and link temporal mortality patterns to local environmental conditions (Norris et al. 2004; Norris & Marra 2007). Such integrative population dynamical modelling would pave the way for a clear recognition of the mechanisms beyond species' decline, i.e. lead to the formulation of sound conservation guidelines (Esler 2000; Webster & Marra 2005).

4.3 Material and Methods

4.3.1 Study species and study sites

The Wryneck, a small (ca 35 g) long-distance migrant, feeding almost exclusively on ground-dwelling ants (Freitag 1996), is the only migratory woodpecker of Europe. Wrynecks from the western Palaearctic breed from boreal to Mediterranean zones, and winter in the Mediterranean basin as well as south of the Sahara in Africa (Cramp 1985). Connectivity between breeding and wintering areas, as well as exact wintering locations for specific breeding populations are largely unknown. A recent ring recovery analysis has shown that the main migratory directions are towards southwest for individuals breeding in the western part of Europe, and then gradually change to a south-eastern direction for individuals breeding more in the east (Reichlin et al. 2009). In this study, we collected feathers from a Swiss and a German Wryneck population. The study area (62 km^2) in south-western Switzerland (Canton of Valais, 46°14’N, 7°22’E, 450–520 m a.s.l.) is situated on the plain of the lower Rhône valley which is characterized by intensive agriculture (predominantly fruit tree plantations and vineyards), and warm and dry summers. The study area (4.5 km^2) in north-eastern Germany (Saxony-Anhalt, 52°01’N, 13°04’E, 140–175 m a.s.l.) is a former military training area, now used as sheep and goat pasture, dominated by dry grassland with a rather continental climate on the lee side of the Harz mountains (for details see Becker & Tolkmitt 2007). In both study areas, Wrynecks frequently breed in nestboxes.

4.3.2 Feather sampling

In April 2005 and 2006, birds in the pre-breeding phase or still on passage were mist-netted using tape-luring of their territorial song. Later on in May–July, breeding birds were either directly taken off the brood (but never from the clutch), or caught with mistnets or traps at the nestbox entrance. All captured birds were aged according to the moulting pattern (see below) as second-year (SY) or older than second-year birds (adults: AD), and feather samples were collected (2005: n_{Swiss} = 66; 2006: n_{Swiss} = 73, of which nine were recaptures of 2005; n_{German} = 21). Out of 130 Swiss and 21 German birds, 20.8% and 14.3%, respectively were ringed as nestlings in the study areas, 39.2% and 33.3%, respectively were ringed as adults in another than the collection year, and 40% and 52%, respectively were newly ringed in the study areas.

The moulting pattern of the Eurasian Wryneck differs between SY and AD (Glutz von Blotzheim & Bauer 1980). In the breeding area, SY birds usually carry feathers of three generations: 1) juvenile feathers, usually the secondary feathers S3 and S4 (counted in ascending order) as well as primary coverts (hereafter 'summer feathers'); 2) feathers from the post-juvenile moult of the previous summer (primaries and contour feathers); and 3) winter grown (hereafter 'winter feathers') secondaries S5-S6 and tertials S7-S9. A reliable aging criterion for SY birds are thus the presence of S3 or S4 from the juvenile plumage, two feathers which are longer and more pointed compared to adjacent secondaries which are moulted in winter. Adults undergo a complete post-breeding moult in the breeding area, whereas in the wintering quarters, they perform a partial moult including body feathers, wing coverts including part of the primary coverts, and usually secondaries. On the breeding grounds, the partially moulted primary coverts are a reliable aging criterion for AD. In both age categories, we clipped either a piece of the inner vane (2.5 to 3 cm) or the whole feather tip (2 cm) of S6 (or alternatively S5) as this feather has an isotopic value of the winter moulting location in both age classes (n_{Swiss} = 139, n_{German} = 21). In SY Swiss birds, we additionally collected a piece of S3 or S4 which represent isotopic values of the natal area (n = 35). All feathers were stored in individually labelled paper envelopes until further analysis.

4.3.3 Stable isotope analysis

Feather samples (n = 195) were washed with 2:1 chloroform-methanol solvent (≥ 12 h) to remove surface oils, and air-dried under a fume hood for ≥ 12 h. Approximately 0.35 mg of feather material were weighed into small silver cups, and the relative abundance of deuterium ($D/^1H$) was measured with the comparative equilibrium method (H_2 derived from high temperature flash-pyrolysis and CF-IRMS; described in detail by Wassenaar & Hobson 2003), which was referenced with calibrated keratin isotope materials. Keratin standards are used to control for the isotopic exchange between samples and ambient water vapour (Wassenaar & Hobson 2000). All results are expressed in the usual delta (δ) notation, in units of per mil (‰):

$$\delta_{\mathrm{sample}} = \left[\left(\frac{R_{\mathrm{sample}}}{R_{\mathrm{standard}}}\right) - 1\right] \times 1000 \qquad (1)$$

where δ_{sample} is the isotope ratio of the sample relative to a standard, R_{sample} and R_{standard} are the proportions of heavy to light isotopes in the sample and standard, respectively. Deuterium measurements were normalized on the Vienna Standard Mean Ocean Water – Standard Light Antarctic Precipitation (VSMOW-SLAP) standard scale (Wassenaar & Hobson 2003). Measurement error, based on replicates of IAEA-CH-7 (-100%) and keratin references, was smaller than ± 2‰.

Stable carbon and nitrogen isotope ratios were measured from 0.5 mg feather material weighed into small tin cups using standard flash combustion elemental analysis (Elemental Analyzer, Euro EA, EuroVector Instruments). The results are presented in delta notation relative to Vienna Peedee Belemnite Standard (VPDB) for $\delta^{13}C$ and relative to atmospheric N_2 (air) for $\delta^{15}N$. Measurement errors were estimated at ± 0.1‰ for $\delta^{13}C$ and ± 0.3‰ for $\delta^{15}N$. All feather samples were prepared and analyzed at the Environment Canada stable isotope laboratory in Saskatoon (Saskatchewan, Canada).

4.3.4 Statistical analyses

Regarding the causes of isotopic variation in winter feathers collected from Swiss Wrynecks, we had the following *a priori* hypotheses: (1) Annual variation: a) variation in weather (mainly amount and pattern of precipitation) could cause δD, $\delta^{13}C$ and $\delta^{15}N$ values to vary between years, or b) different geographic wintering locations could lead to interannual isotopic variation. (2) Age-related variation: isotopic values could vary between age categories because SY and AD birds could migrate to different wintering areas, feed on different prey, and/or moult at different times.

We used an information-theoretic approach to check whether inter-year differences or bird age contributed more to the observed isotopic variance (Burnham & Anderson 2002). We applied linear mixed effects models (with individual as random factor) to evaluate the influence of collection year and bird age on each stable isotope separately, and tested all five possible models (including two-way interactions and the null model) resulting from these factors. Based on the Akaike Information Criterion for small sample sizes (AIC_c; Burnham & Anderson 2002) we selected the models which best described the variation in the isotopic values. Regarding the summer feathers of Swiss Wrynecks, we could only test for a year effect, as sufficient data was available only for SY birds. Furthermore, due to too little feather material in this particular sample, we could only analyze the proportion of deuterium in these feathers.

Differences in isotopic values of winter-grown feathers between the Swiss (n = 52) and the German (n =21) populations were analyzed for each stable isotope with a two-sample Student's t-test. We only used data from AD caught in 2006 as the German data set contained data neither from 2005 nor for SY birds from 2006.

To estimate the relative geographical extent of breeding vs. wintering ranges, we compared (F-Test) the isotopic variances between summer and winter feathers in Swiss SY birds from 2006 (only this sample was large enough for this purpose). We expected the variation in isotopic values within breeding areas to be comparatively smaller than in wintering areas, despite the potential diluting effect of natal dispersal into breeding populations. Eight out of 35 individuals from which summer feathers were available, were born at the study site (ring information). The remaining 27 individuals (potential immigrants) had isotopic values comparable to the former eight birds (statistically non-significant difference for all three isotopes with an α rejection value of 0.05).We hence assumed this diluting effect to be marginal, because potential immigrants into the Swiss breeding population were likely to come from nearby populations, which should cause little variation in isotopic values. In contrast, the variation in isotopic values of feathers grown in wintering areas was expected to be much larger merely due to an *a priori* wide geographical extension of the winter range. It must be pointed out, however, that the resolution of the reference isoscapes (i.e. isotopic variance in the environment) may *per se* affect the outcome. For instance, a currently low resolution of the African isoscapes for deuterium, compared to the fine-grained isoscapes available from Europe, may bias the interpretation (Bowen et al. 2005).

4.3.5 Isoscapes

Deuterium (mean annual, as well as mean growing season) in precipitation in Europe shows a gradual change from negative values in the north to more positive values in the south and at lower altitudes (Bowen et al. 2005). There is a continuation of this cline in Africa, although the N-S gradient is less marked across the African continent and it shows an additional increase in deuterium values from west to east (see Fig. 6 in Bowen et al. 2005). To compare δD values obtained from summer feathers of SY Swiss Wrynecks with the local isotopic values at the Swiss study site, we used the Online Isotopes in Precipitation Calculator (OIPC, www.waterisotopes.org, Bowen 2007). The OIPC estimates local deuterium values in precipitation (δD_{precip}) based on the long-term IAEA GNIP data. We referred to the annual mean δD_{precip} value, as well as to an average value for May-July (Appendix 1), as this second value represents the time-window when feathers are grown in nestlings. Applying two frequently used discrimination factors (-25‰ in Wassenaar & Hobson 2001; -19‰ in Bowen et al. 2005) to account for the depletion of deuterium from precipitation (δD_{precip}) throughout the food chain to feather ($\delta D_{feather}$) resulted in an expected $\delta D_{feather}$ range of -80.8 -74.8‰ based on the annual mean δD_{precip} and -62 to -68‰ based on the mean δD_{precip} value for May-July.

We did not predict a value for $\delta^{15}N$ for the Swiss study site as this is difficult due to complex anthropogenic nitrogen fluxes. The mean $\delta^{15}N$ value of the Swiss birds might however be indicative of the trophic position of the birds (i.e. ^{15}N enrichment increases with trophic level by an average of +2.3‰ per consumer; Hood-Nowotny & Knols 2007). Nor did we predict a value for $\delta^{13}C$ as ^{13}C is mostly driven by the different photosynthetic pathways (C3-, C4- and CAM-plants) and hence dictated by the type of vegetation. Temperate climatic regions with predominant C3 vegetation show more depleted stable carbon values (-27

± 2‰) compared to high light intensity C4 dominated environments (-13 ± 1.2‰), whereas CAM dominated areas with succulent/desert plants show intermediate values (-10 to -20‰, O'Leary 1988; Hood-Nowotny & Knols 2007).

We visually matched winter $\delta D_{feather}$ values (10 – 90% percentile, corrected with fractionation factor -19‰) of the Swiss and the German population with interpolated δD maps of southern Europe and Africa in an attempt to depict the origin of these feathers. Maps were generated with ArcGIS based on mean δD_{precip} values for October-February (data available on www.waterisotopes.org, Bowen 2007). These particular months are chosen, as they reflect i) the time window of feather renewal, and ii) likely the isotopic signatures of recent rainfalls which would then be incorporated into the renewed feather.

4.4 Results

Mean deuterium isotopic values in summer feathers of Swiss SY birds (*n* = 35) matched the expected values from the mean annual δD_{precip} calculation (-80.3 vs. -80.8 – -74.8). However, they were much lower than expected from the mean δD_{precip} values form the time window of feather growth (80.3 vs. -62 – -68‰). There was no overlap between feather δD values and the ranges of deuterium values on the Swiss study site for the period May-July (Table 1 and Appendix 1).

The model best explaining the variation in δD from winter feathers included the factors collection year and age (Table 2). δD values were more depleted in 2006 compared to 2005, and SY birds showed more enriched values compared to AD. The variation in $\delta^{15}N$ of winter feathers was best explained by year, with lower values in 2006 than in 2005. The second-best model performed almost as well as the best one, and included the two factors as well as the interaction term. The best model explaining the variation in $\delta^{13}C$ included year, age and the interaction year*age. Adults showed higher $\delta^{13}C$ values in 2005 than in 2006, whereas SY birds showed lower values in the year 2005 than in 2006. The best model explaining the variation in summer feather δD values in Swiss Wrynecks was the null model. However, the second best model showed, that δD values were lower in 2006 compared to 2005 (Table 3).

There was no significant difference in $\delta^{15}N$ between Swiss and German winter feathers ($t = -1.31$, $df = 71$, $p = 0.193$), whereas deuterium and stable carbon showed higher isotopic values in Germany than in Switzerland (δD: $t = -5.71$, $df = 71$, $p < 0.001$; $\delta^{13}C$ $t = -4.17$, $df = 71$, $p < 0.001$, respectively; Fig. 1). In the two populations, variances were equal for deuterium and stable nitrogen ($F = 0.99$, $df = 51, 20$, $p = 0.928$; $F = 0.78$, $df = 51, 20$, $p = 0.463$, respectively), but not for stable carbon ($F = 0.20$, $df = 51, 20$, $p < 0.001$).

The variances of isotopic values of Swiss SY birds caught in 2006 were generally smaller in summer than in winter feathers for all three isotopes, but differed significantly only in stable nitrogen and stable carbon, pointing to a wider winter than summer range (Table 4).

Visual inspection of deuterium isoscapes for Africa with the 10 – 90% percentile of winter $\delta D_{feather}$ values of Swiss ($\delta D_{Switzerland}$ = -35.4 to 20‰) and German ($\delta D_{Germany}$ = -14.1 to 44.1‰) Wryneck populations suggests that the wintering grounds of the German population are situated probably to the south of the Sahara desert (Sahel zone, higher δD values), while the 10 – 90% percentile of δD values of the Swiss breeding population also include southern European areas (south-western Spain and Portugal, lower δD values; Fig. 2) (but see comments on the limits of African isoscapes in Material and Methods).

4.5 Discussion

4.5.1 Applicability of the method

This study suggests that stable isotopes are in general an appropriate method to roughly delineate wintering grounds and investigate migratory connectivity of European migratory birds provided that crucial information about moulting patterns are available. It points out, however, discrepancies between some *ad hoc* formulated premises, and possible biases in reference isoscapes for a specific isotope. This calls for further methodological improvements, especially with regard to the resolution of the species specific reference maps.

When using stable isotopes to approach questions of migratory connectivity, Hobson (2005) suggested calibrating the method by matching local isotopic values against locally grown feathers of the species in question. Exact matches are obtained only seldom, however, due to uncertainties such as analytical or spatial interpolation errors (discussed in Wunder & Norris 2008), or due to inter-individual differences in physiology (Powell & Hobson 2006). The match of summer-grown feathers in Swiss Wrynecks with the local values was good for δD_{precip} mean annual values (expected value -80.8 -74.8‰ vs. -80.3 ± 9.22‰). The large deviation from the mean values of May-July with the obtained $\delta D_{feather}$ values (-62 to -68‰ vs. -80.3 ± 9.22‰) clearly illustrates that deuterium in precipitation is not integrated in the food web immediately. There was not even an overlap of values ranges between the observed and the reference samples during breeding months (May-July). In addition to the uncertainty of the time period over which deuterium in precipitation is integrated into the food web, the peculiar topography and climate of the Swiss study site could further add to a mismatch of expected vs. obtained δD values. The plain of the upper Rhône is flanked on both sides by high mountain ranges culminating at more than 4000 m altitude. This implies particular precipitation patterns, namely a very dry and relatively warm climate in summer, which could hamper correct calculations in the detrended interpolation of deuterium in precipitation. Reference isoscapes with a finer-grained resolution are therefore needed.

4.5.2 Variation of isotopic values within population

We showed that bird age and collection year both influenced isotopic values of winter feathers within the Swiss breeding population, although this effect was marginal for $\delta^{15}N$ measurements regarding bird age (Table 2). The model selection approach used did not enable us to disentangle these two effects; a bigger sample size would be needed to directly test for this (Reichlin et al. in prep.). Regarding summer feathers, collection year had no effect on deuterium. These results are in line with the very general expectation that deuterium isotopic values are predictable and repeatable between years at a given location (small interyear variation in δD_{precip} in Europe, Hobson 2004). Regarding winter feathers, we found a collection year effect in all three isotopes. Annual variation in precipitation in the wintering area could, at least partly, account for the variation in isotopic values. More rainfall in areas where birds have grown their feathers would result in more depleted deuterium values (Dansgaard 1964) (what we observed for feathers in 2006). In addition, more mesic environments would lead to more depleted $\delta^{15}N$ values (this study: feathers of 2006). Actually, precipitation in Sahelian Africa was higher in 2005 compared to 2004 (NOAA/National Weather Service, Climate Prediction Center: http://www.cpc.ncep.noaa.gov/products/fews/africa/), which may provide some explanation to the observed interyear differences. Moreover, differences in moult periods between SY and AD may also affect the δD isotopic feather values (Kelly et al. 2008). As a result, enriched deuterium values (Table 2) could be associated with a comparatively late moult in SY birds corresponding to the annual variation of δD_{precip} (e.g. see δD_{precip} of January & February on www.waterisotopes.org).

However, year and age variation in the analyzed stable isotopes may be “artefactual”. First, non-fidelity to wintering sites due to diffuse migratory connectivity (see below) could be a plausible explanation. Also, age-specific feeding strategies could theoretically result in isotopic values to vary as well (e.g. Meehan et al. 2003; Bearhop et al. 2006). However, we doubt this explanation since Wrynecks are exclusive ant predators (Glutz von Blotzheim & Bauer 1980; Freitag 1996).

4.5.3 Variation of isotopic values between populations

We showed that the Swiss and the German Wryneck populations have distinct isotopic values in winter feathers for two out of three analyzed isotopes (Fig. 1). By comparing only one age class in one year, we could rule out any of the confounding effects of year and age.

This suggests that the wintering grounds do overlap only little between the two populations (see frequency distributions in Fig. 1), with wintering grounds of the German population probably situated in the Sahel zone (more positive δD, Fig. 2b), while mean isotopic values of the Swiss breeding population would also include the south-western part of the Iberian peninsula (more negative δD, Fig. 2a). We suggest a leapfrog migration system with northern breeding populations wintering further south than more meridional breeding populations. This additionally points to some "strong connectivity" for these two breeding populations. Similar findings were obtained from δD values in Wilson warblers (Kelly et al. 2002). Another indication of separate wintering grounds is that German birds seem to moult in a more C4- or CAM-plants dominated landscape, while feather values of Swiss birds may originate from regions with larger proportions of C3-plants (10-15°N upwards, Still et al. 2003).

Discrete wintering grounds could have consequences on the population dynamics of these two populations. Changing conditions, e.g. droughts perturbing some regions of the Sahel (e.g. Newton 2004), could affect demographic parameters differently within two breeding populations (Kanyamibwa et al. 1990). German Wrynecks could be more susceptible to such climatic perturbation in the Sahel, as they primarily winter in these regions and might not be genetically apt to switch to other wintering areas (i.e. Mediterranean basin) (Schaub et al. 2005). There is, however, no evidence for distinct demographic trajectories in breeding European Wryneck populations so far, although the information remains scarce (unpublished data; BirdLife International 2008). Demographic models accounting for variation in seasonal mortality could incorporate environmental fluctuations in wintering areas so as to disentangle factors operating on breeding vs. wintering grounds.

4.5.4 Isotopic variation in breeding vs. wintering range

Isotopic variances for $\delta^{15}N$ and $\delta^{13}C$ were significantly smaller in summer than in winter feathers of Swiss Wrynecks. This corroborates our assumption that the variance of isotopic values in a confined breeding area (here our study site in Switzerland) is comparatively smaller than the variance observed in an (unknown) wintering range. A wide range of geographical areas used as foraging grounds in winter is the most plausible explanation here (Møller & Hobson 2004). Actually, although Bearhop et al. (2004) have proposed that a large variance in isotopic values of winter feathers could result from a more plastic trophic niche in wintering birds, however the very specific diet of Wrynecks (ants) provides little support to this hypothesis.

4.5.5 Perspectives

This study suggests a leapfrog migration to the wintering grounds in Wrynecks. Furthermore, the fact that breeding individuals stemming from the two European populations winter in geographically distinct but rather wide areas suggest the existence of some "diffuse migratory connectivity" *sensu* Webster et al. (2002). This may have consequences when assessing population dynamics of different Wryneck breeding populations because local demographic trajectories may be impacted by factors operating at different places, i.e. affecting different components of seasonal mortality. Any future demographic analyses must account for this seasonal variation in survival and must attempt to link it to environmental fluctuations so as to understand the mechanism of population growth rate changes. Then, based on these analyses, refined population models can be built which will lead to sound, targeted conservation action plans for endangered populations.

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Table 1 Isotopic values of δD, δ^{15}N, and δ^{13}C in Wrynecks: mean, standard deviation (SD), range and sample size (*n*) of feathers representing isotopic values of the breeding (summer) and wintering areas (winter) of the populations in Switzerland (CH, 2005 and 2006) and Germany (D, 2006).

		δD (‰)				δ^{15}N (‰)				δ^{13}C (‰)			
		Mean	SD	Range	*n*	Mean	SD	Range	*n*	Mean	SD	Range	*n*
CH	Summer	-80.3	9.2	-93.6 – -56.3	35	+9.2	1.1	7.1 – 10.7	20	-22.8	0.5	-23.5 – -21.3	20
	Winter	-22.4	20.6	-66.6 – 17.4	111	+8.5	2.5	4.0 – 17.4	108	-20.9	1.3	-23.9 – -13.1	108
D	Winter	+3.6	21.8	-45.7 – 31.9	21	+9.2	2.7	2.6 – 13.5	21	-18.3	2.9	-22.7 – -12.9	21

Table 2 Influence of year, age category and their interaction on isotopic values in a) deuterium (δD), b) nitrogen ($\delta^{15}N$), and c) carbon ($\delta^{13}C$) in winter feathers of Swiss Wrynecks (*n* = 139). The three best models (out of 5 candidate models) are shown for each isotope and ranked according to the Akaike Information Criterion for small sample sizes (ΔAIC_c: difference of AIC_c to best model). AIC_c w indicates the Akaike weight.

Model	Best		2nd Best		3rd Best	
	Estimate	SE	Estimate	SE	Estimate	SE
a) δD						
Effects						
Intercept	-17.35	3.46	-18.52	3.89	-14.44	3.20
Year[1]	-11.47	3.84	-9.73	4.63	-11.92	3.88
Age[2]	8.29	4.05	11.81	6.68	–	–
Year*age[3]	–	–	-5.55	8.32	–	–
Selection criteria						
ΔAIC_c	0.00		1.73		2.05	
AIC_c w	0.55		0.23		0.20	
Deviance	971.44		970.98		975.65	
b) $\delta^{15}N$						
Effects						
Intercept	9.14	0.41	8.74	0.48	8.45	0.24
Year[1]	-0.98	0.49	-0.38	0.58	–	–
Age[2]	–	–	1.56	0.94	–	–
Year*age[3]	–	–	-2.25	1.13	–	–
Selection criteria						
ΔAIC_c	0.00		0.35		1.70	
AIC_c w	0.36		0.30		0.16	
Deviance	497.89		493.91		501.71	
b) $\delta^{13}C$						
Effects						
Intercept	-20.83	0.24	-20.89	0.13	-20.99	0.16
Year[1]	-0.22	0.27	–	–	–	–
Age[2]	-1.08	0.49	–	–	0.30	0.29
Year*age[3]	1.97	0.60	–	–	–	–
Selection criteria						
ΔAIC_c	0.00		6.64		7.69	
AIC_c w	0.92		0.03		0.02	
Deviance	353.76		366.86		365.79	

[1]estimate for 2006; [2]estimate for SY birds; [3]estimate for 2006 and SY birds

Table 3 Influence of year on deuterium isotopic values in summer feathers of Swiss Wrynecks (only SY birds, *n* = 35). The models are ranked according to the Akaike Information Criterion for small sample sizes (ΔAIC_c: difference of AIC_c to best model). AIC_c w indicates the Akaike weight.

Model	Best		2nd Best	
	Estimate	SE	Estimate	SE
Effects				
Intercept	-80.31	1.56	-78.36	2.38
Year[1]	–	–	-3.40	3.14
Selection criteria				
ΔAIC_c	0.00		1.34	
AIC_c w	0.66		0.34	
Deviance	253.83		252.61	

[1] estimate for 2006

Table 4 Variances of isotopic values in deuterium (δD), stable nitrogen ($\delta^{15}N$) and stable carbon ($\delta^{13}C$), respectively, for summer and winter feathers in Swiss SY Wrynecks in 2006 (*n* = 41). F-tests (df: degrees of freedom; num: numerator; denom: denominator).

	Variance (‰)		df		F-value	p
	Summer	Winter	num	denom		
δD	73.2	154.9	19	20	2.12	0.1081
$\delta^{15}N$	1.1	8.4	19	20	7.50	< 0.0001
$\delta^{13}C$	0.2	3.1	19	20	13.51	< 0.0001

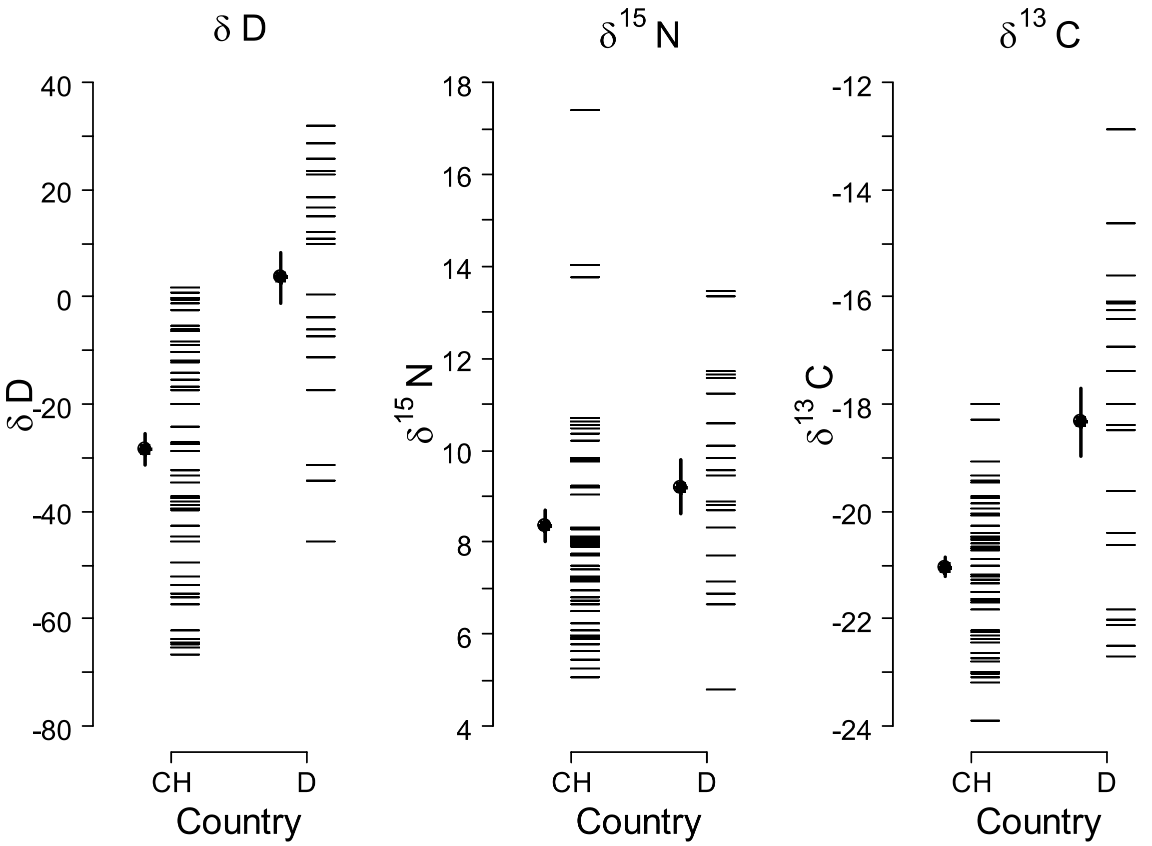

Figure 1 Individual isotopic values of winter feathers (AD birds captured in 2006) of the Swiss (CH, *n* = 52) and the German (D, *n* = 21) populations. Plotted are mean values ± SEM. *Horizontal lines* indicate the individual isotopic values.

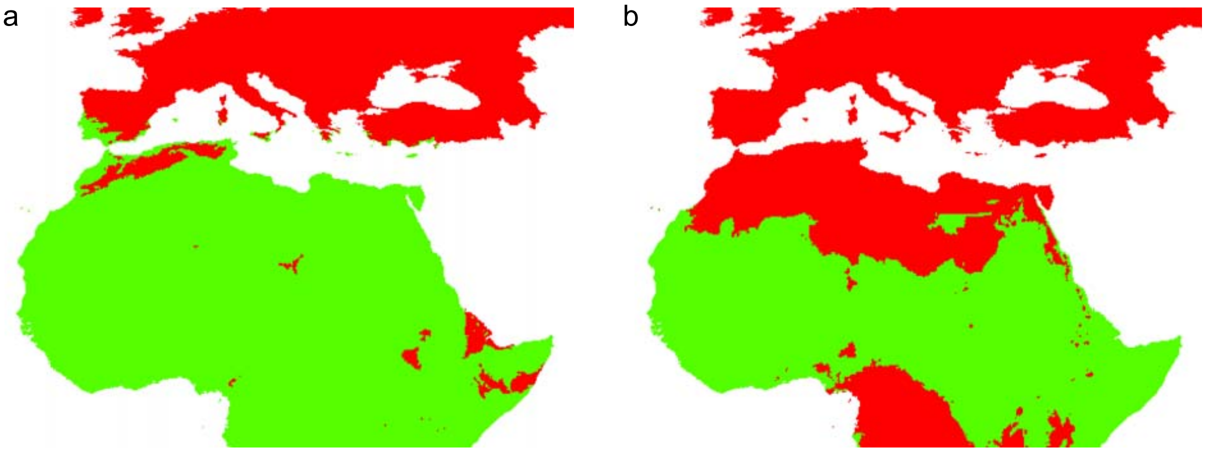

Figure 2 Distribution of δD values from winter-grown feathers of Wrynecks from the a) Swiss and b) German breeding populations. *Areas in green* indicate the overlap of the 10 – 90% percentile of $\delta D_{feather}$ values with the generated interpolated basemap for deuterium including mean values for months October-February (www.waterisotopes.org, Bowen 2007).

Appendix 1 Monthly precipitation δD values (in ‰, V-SMOW; www.waterisotopes.org, accessed 10.10.2008) for the study site in Switzerland (Canton Valais, Sion, δ^2H estimates for latitude 46.228°, longitude 7.349°, altitude 500 m a.s.l.).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec
δD	-72	-70	-63	-62	-49	-45	-35	-35	-45	-53	-66	-75

5

Key ecological features for the persistence of an endangered migratory woodpecker of farmland, the Wryneck *Jynx torquilla*

Key ecological features for the persistence of an endangered migratory woodpecker of farmland, the Wryneck Jynx torquilla

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5.1 Abstract

Identifying areas with high quality territories is essential to ensure the persistence of endangered populations. Based on the principle of an ideal despotic distribution, the frequency of territory occupancy is an excellent indicator of territory quality. We studied territory occupancy in a Swiss population of the Wryneck *Jynx torquilla*, a declining ant-eating woodpecker species, with the aim to identify key habitat features for conservation management. Both static and dynamic approaches were applied using data on nest site occupancy of 100 territories from six successive years. Frequently occupied territories were settled earlier in the season, suggesting that they may be of better quality. The static occupancy approach revealed that the larger the area of old pear orchards and the smaller the area of vegetable culture within a territory, the higher the probability of territory occupancy. The dynamic approach showed that both the proportion of old pear orchards and the presence of conspecifics within a territory were positively related to territory colonisation, whereas territory desertion was negatively related to habitat heterogeneity. Old pear orchards were characterized by having both the highest density of ant nests and the greatest amount of bare ground. The latter is likely to facilitate access to ant prey. To ensure persistence of Wryneck populations in farmland, it seems that heterogeneous, orchard-dominated agricultural matrices should be promoted. Finally, a sufficient offer of nesting cavities is likely to enhance social aggregation, which impacts positively on territory occupancy. Providing that these key elements are present, Wrynecks are likely to persist in even intensively farmed areas.

***Keywords*:** Ants • Colonisation and desertion probabilities • Food availability • Habitat selection • Occupancy model • Territory quality

5.2 Introduction

Individuals should establish breeding territories in high quality habitat patches that provide suitable resources such as food, breeding sites and shelter from predators. This is because reproductive output usually increases with increasing territory quality (e.g. Andrén 1990, Tye 1992, Holmes et al. 1996, Pärt 2001). Territory selection is therefore crucial to the fitness of individuals. According to the ideal despotic distribution, the highest quality territories are selected first (Fretwell & Lucas 1969). The occupancy of territories is thus a non-random process, with the best quality territories being monopolised by the fittest individuals or the first to arrive.

If individuals are distributed according to the ideal despotic distribution, the frequency of territory occupancy will be positively correlated with territory quality (Krüger 2002, Sergio & Newton 2003, Sim et al. 2007). High quality territories tend to always be occupied, whereas low quality ones are only occupied when breeding density is high. Relating the frequency of territory occupancy to territory variables may thus be a good indicator of habitat quality.

This static view of territory occupancy can be extended to a dynamic occupancy approach. Territory occupancy involves two processes: colonisation and desertion. These local processes may depend on stochastic, intrinsic or extrinsic factors (Hanski 1998), such as habitat quality or conspecific attraction (Stamps 1988, Muller et al. 1997, Danchin et al. 1998). Territory variables that are positively correlated with colonisation and negatively with desertion indicate high quality. As currently unoccupied territories may still be fundamental for ensuring the long-term persistence of a population, it is important to recognise factors involved in these processes.

A key issue in conservation ecology is the identification of territory quality gradients, to strategically prioritise conservation management. The main goal of this study was to identify which habitat features are the best indicators of habitat quality for Wrynecks *Jynx torquilla* (L.), a declining bird of European farmland.

We first mapped various habitat features in Wryneck breeding territories located at the study site between 2002-2007. We then assessed the abundance of ant nests in territories, as ant broods constitute the staple food provisioned to Wryneck nestlings (Bitz & Rohe 1993, Freitag 1998). Finally, we related habitat type, food availability, interspecific competition for nest sites and conspecific attraction to the pattern of territory occupancy. Analyses were carried out using both static (variables related to frequency of occupancy) and dynamic occupancy models (variables related to local colonisation and desertion processes of a given territory). Prior to analysis, we tested some assumptions inherent to the occupancy models, such as territory selection, settlement order and site-dependent breeding success of different territories. It is expected that in depth information on patterns of breeding habitat selection will lead to concrete management recommendations ensuring long-term stability of the farmland Wryneck population. We also aimed to identify key ecological requirements of Wrynecks in general, which may be relevant beyond the local context, especially given the precarious status of this species in several areas of its distribution.

5.3 Methods

5.3.1 Study site and study species

The study area is located in the plain of the Rhone valley, between Vernayaz and Sion (SW Switzerland, 46.2° N, 7.4° E; 482 m above sea level). The area is characterised by intensive farming, consisting mainly of dwarf fruit tree plantations and vegetable cultures. The study area harbours 351 nest boxes, which were installed in 2002 at 195 nest sites (mostly inside agricultural shacks, with most buildings having two boxes each).

In contrast to other woodpeckers, Wrynecks are secondary-cavity breeders. They also require foraging grounds offering a sparse vegetation cover, which facilitates the access to ant nests (Hölzinger 1992, Bitz & Rohe 1993, Freitag 1996, Ehrenbold 2004, Weisshaupt 2007). In our study area, 90% of the food provisioned to Wryneck nestlings comprises ant larvae and nymphs (Freitag 1998). Telemetry studies in study area revealed that Wrynecks forage mostly within 100–125 m of their nest site, having home-ranges of 2.1–4.8 ha (Freitag 1998, Weisshaupt 2007). Orchards and fallow land are the preferred foraging habitats. Optimal feeding locations typically occur where there is around 60% cover of bare ground (Weisshaupt 2007).

Between 2002-2007, all 195 nest sites were checked fortnightly during the breeding season. Once detected, a brood was monitored every 3–4 days. A brood was defined as any clutch consisting of at least one egg, irrespective of the outcome, whilst a successful brood should yield at least one fledgling.

5.3.2 Design and habitat variables

A random sample of 100 nest sites was selected from the 195 available sites in the study area. Around each nest site we delineated a circle of 111 m radius, in order to define a 3.9 ha ‘foraging territory’ (median local foraging home-range size; Weisshaupt 2007). In only three cases was there an overlap between two adjacent ‘foraging territories’ (overlap of 8.2%). The habitat characteristics of the selected territories were mapped in early summer 2007 (Appendix A). Variables recorded were Habitat type, Number of trees, and Percentage of bare ground, according to features stressed as important by Weisshaupt (2007; Tables 1 and 2). The percentage of bare ground was estimated visually for each culture parcel in the field.

Occupancy models assume that territory quality and food resources remain constant over time and that individuals are able to promptly locate the best quality territories. In our study area, territory quality was assumed to be constant over the 6-year period, since dwarf fruit tree plantations, which covered on average 48.9 ± 0.6% of foraging territories (n = 100) have a slow replacement turn-over, and because ant nests are relatively long-lived (Seifert 1996). In addition, there was excess availability of nest sites (on average of 2.03 ± 0.06 boxes per territory), so that we could assume that territory selection would operate independently of nest site availability.

The density of ant nests within a territory was also used as a potential criterion for estimating habitat quality. Perches, such as trees, poles, shacks and fences are an important habitat feature for Wrynecks, as perches enhance detectability of ant nests. We thus distinguished between ant nest availability from habitats with perches (i.e. orchards, vineyards, riverbank, and pasture) and without perches (i.e. vegetable cultures, fallow land, and meadow). Nests from woodland specific ant species (*Formica* spp. and *Camponotus* spp.) were not included in the food availability estimates, because woodland specific species are almost never eaten by Wrynecks (Seifert 1996, Freitag 1998). Ant nest accessibility was accounted for in the modelling, as this depends primarily on the area of bare ground in the vicinity of an ant nest, and because Wrynecks capture and eat prey on the ground (Weisshaupt 2007). The quadratic terms of the three discrete variables; Bare ground with perches, Bare ground without perches, and Total bare ground were also used in an attempt to identify optimal proportions of these key habitat components. Finally, an index of potential competition with Hoopoes *Upupa epops* L., which use the same nest boxes as Wrynecks, was derived from the number of years between 2002-2007 a Hoopoe pair had occupied one of the two available nest boxes within a territory.

In the dynamic occupancy analysis, we also included a variable indicating presence of conspecifics in a given year (whether there were other breeding Wrynecks within a 500 m radius of the focal nest site), which is twice the maximal foraging distance from the nest site (Freitag 1998). Conspecifics may actually influence site occupancy through patterns of social attraction and/or public information about territory quality (Danchin et al. 1998, Doligez et al. 1999, Danchin et al. 2001).

Spatial data was digitised using ArcGIS 9.1 (ESRI 2005). In total, 2589 different culture parcels were recorded and their areas calculated from the digitalised polygons. Multiple parcels of the same habitat type within a territory were summed and their proportional area was used in the analysis. Total percentage of bare ground within a territory was calculated by summing the percentage of bare ground per parcel, weighted by its proportion of the entire territory area.

5.3.3 Food availability: ant nest abundance and accessibility

To estimate overall food availability within a territory, habitat-specific ant nest densities were multiplied by their proportional area of territory and summed. Density of terrestrial ant nests was assessed in potential Wryneck territories throughout the study area in 2003 and 2004. Sampling was based on a stratified design (at least 90 randomly selected plots per main habitat type: orchards, vineyards, meadow, river bank, fallow land, and vegetable cultures). From 2005-2007, assessments were restricted to orchards (with different fruit types), as these were identified as the most important foraging habitat (Weisshaupt 2007). Sample size varied between habitat types and years, ranging from 10 to 175 samples. Each sampling location was situated in the core of a given culture type to avoid edge effects. Ant nests were surveyed in five 2 m^2, randomly defined replicates, by scraping the topsoil with a rake and counting the nests. Surveys took roughly 2-3 minutes per replicate, and were always carried out in the first half of May on 3–9 consecutive days, under similar weather conditions. Habitat type (for orchards, also age and fruit type), percentage of bare ground, grass height, and number and relative size of ant nests were recorded. An ant nest was defined by the presence of an aggregation of $\geq$ 20 imagos, or the presence of eggs or larvae. A few individuals from each nest were sampled for subsequent species identification (Della Santa 1994, Seifert 1996).

Detection probability of ant nests was estimated in an additional study in 2007. We repeatedly searched for ant nests at exactly the same five 2 m^2 plots in 19 randomly selected orchards (= 95 replicates), using the same technique as for the ant nest density assessment, as described above. All 95 replicates were recorded over a period of 3–4 days, during three recording sessions in early May, June, and July. Data for mean daytime temperature, measured 5 cm above ground were obtained from MeteoSwiss (on-line data base). A few ants were sampled from each nest for subsequent species identification.

The resulting detection histories for each of the 95 replicates were analysed with MARK (White & Burnham 1999), using occupancy models (MacKenzie et al. 2002). We did not distinguish between detection probabilities of different ant species, as sample sizes of different species were unbalanced. The covariates Vegetation height (range: 0 –110 cm), Percentage of bare ground (range: 0 – 100%), and mean hourly Temperature (range: 3.3 – 35.0°C) were used to model detection probability. All variable combinations were tested with both a constant and a time-dependent intercept, giving a total of 16 models. The occupancy probability ψ was always kept constant. Models were ranked according to Akaike's

Information Criterion adjusted for small samples (AIC$_c$) and the corresponding AIC$_c$ weights (Burnham & Anderson 1998). Model averaging was performed for the smallest subset of models with accumulated AIC$_c$ weights summing to 0.95, to account for model selection uncertainty (Burnham & Anderson 1998).

To obtain an estimate of the number of ant nests ($\hat{N}_i$) for replicate *i*, we divided the ant nest count (C_i) by the replicate-specific detection probability ($\hat{p}_i$)

$$\hat{N}_i = \frac{C_i}{\hat{p}_i} \qquad (1).$$

Replicate specific detection probability is estimated using replicate specific temperature (t_i), vegetation height (v_i), percentage of bare ground (b_i), and the model averaged parameter estimates ($\bar{\hat{\beta}}_x$)

$$\hat{p}_i = \frac{1}{1 + \exp(-\bar{\hat{\beta}}_0 - \bar{\hat{\beta}}_1 t_i - \bar{\hat{\beta}}_2 v_i - \bar{\hat{\beta}}_3 b_i)} \qquad (2).$$

Estimated detection probability from the occupancy model did not exactly match the detection probability needed to correct the ant nest counts (eq. 1). This is because the occupancy detection probability estimates the probability to detect at least one ant nest within a replicate, given that the replicate is occupied by at least one ant nest. To correct the counts, we would need to know the probability to detect one ant nest, however, as the area of replicates was small, only one ant nest was present in most occupied replicates. Consequently, the two detection probabilities were close.

The counts of ant nests of each replicate were corrected with the corresponding detection probability. The mean ant nest density for each habitat type (fallow land, meadow, vineyards, vegetable cultures, riverbank, and apple, apricot, and pear orchards) was then estimated by fitting a linear mixed model to $\hat{N}$. The random effect was plot, as there were always five replicates in each plot per year, which were not completely independent, and the fixed effects were year and habitat type. Averaged estimates and confidence intervals were obtained by using bootstrapping, with 1000 repetitions.

The accessibility of ant nests for Wrynecks is primarily determined by the amount of bare ground (Weisshaupt 2007). As an indication of food accessibility, we therefore used average amount of bare ground for each habitat, estimated with a linear mixed effects model, with territory as a random effect. Estimates and confidence intervals were again obtained by bootstrapping, with 1000 repetitions.

5.3.4 Occupancy analyses

5.3.4.1 Assumptions

To test whether Wrynecks actively selected their territories, or settled randomly, a χ^2 test was performed comparing the observed frequency of territory occupancy with an expected frequency drawn from a binomial distribution.

According to the ideal despotic distribution hypothesis (Fretwell & Lucas 1969), high quality territories are settled earlier, and thus, more frequently occupied territories should be settled earlier. We used laying date of the first egg as an index of territory settlement. To test whether settlement order depended on the year we used linear mixed models and a likelihood ratio test. We then related the median of the laying date of the first egg for each territory to the frequency of its occupancy using linear regression. Only first broods were considered (n = 108).

If breeding success is site-dependent, it should be positively correlated with frequency of territory occupancy. This prediction was tested using linear regression, with breeding success of a territory (territory specific average of clutch size, number of hatchlings, and number of fledglings, respectively) as dependent variables and frequency of territory occupancy as the independent variable. Fledgling success (number of fledglings divided by number of hatchlings) was also tested, using general linear regression, assuming a binomial error distribution. Successful first and second broods were included in this analysis (n = 85).

5.3.4.2 Static model

To model the annual probability that a territory was occupied, we used a generalised linear model, with a binomial error distribution. The nominator of the response variable was the number of times a territory was occupied, and the denominator was the number of study years (n = 6). From all recorded territory variables (Tables 1 and 2), some were excluded from this analysis, either due to their irrelevance as foraging habitat (anthropogenic habitat and water), or because they occurred in less than 20 territories (riverbank and pasture). The remaining 22 variables were tested for pair-wise correlation, using a Spearman's Rank correlation test. As a result of this, the variable Ant without perches was excluded, due to it being highly correlated ($r_s > |0.7|$) with two other variables. The remaining 21 explanatory variables were included in the following analyses. The quadratic terms of the variables Total bare ground, Bare ground with perches, and Bare ground without perches were also modelled, to test for the presence of an optimum (= 24 variables). We then fitted models containing each one of these explanatory variables singly and ranked them according to their AIC_c weights. All variables from models with a $\Delta AIC < 4$ when compared to the best model were included into the second modelling step. We built models with all possible combinations of the remaining variables (= 3 variables; 8 models) and ranked them according to their AIC$_c$ weights. Predictions were made using model averaging, including all models within the second step of the analysis that accumulated to at least 0.95 of the AIC$_c$ weight.

5.3.4.3 Dynamic model

To model colonisation and desertion probabilities, we used a dynamic occupancy model (MacKenzie et al. 2003, Royle & Dorazio 2008). Let $z_{i,t}$ denote the occupancy status of site *i* at time *t* with $z = 0$ if the site is unoccupied, and $z = 1$ if the site is occupied. To model site occupancy dynamics, a simple formulation in terms of initial (i.e. at time $t = 1$) occupancy (ψ), colonisation (γ) and desertion probabilities (ε) exists. The initial occupancy state is assumed to be a Bernoulli random variable,

$$z_{i,1} \sim Bern(\psi) \qquad (3),$$

whereas in subsequent periods,

$$z_{i,t} \mid z_{i,t\text{-}1} \sim Bern\left(\pi_{i,t}\right) \qquad (4),$$

where

$$\pi_{i,t} = z_{i,t\text{-}1}(1 - \varepsilon_{i\text{-}1}) + (1 - z_{i,t\text{-}1})\gamma_{t\text{-}1} \qquad (5).$$

This model was fitted using the program MARK (White & Burnham 1999).

The same 21 variables were used as for the static occupancy model. In addition, we also considered the variable Presence of conspecifics. The quadratic terms of the variables Total bare ground, Bare ground with perches, and Bare ground without perches were also modelled (25 variables).

Model selection was performed in multiple steps: first, all 25 variables were tested singly for ε (desertion-models) and for γ (colonisation-models), with a constant and a time-dependent intercept, whilst the probability without explanatory variable (γ or ε) remained time-dependent. All models with a ΔAIC < 4 were selected for inclusion in the desertion and colonisation modelling. In the second step, the variables from the selected desertion models were combined with the variables from the selected colonisation models. From the selected variables, at most one variable for ε and one for γ were combined, using both time-dependent and constant intercepts (= 36 models). Model averaging was performed for models accounting for 0.95 of the AIC$_c$ weight. The initial occupancy probability (ψ) was not modelled against explanatory variables.

5.3.5 Breeding success

To test whether the important territory variables identified in the static and dynamic approaches were linked to breeding success, we fitted generalised linear mixed models with Poisson error distribution. The dependent variable was Number of fledglings from successful broods (*n* = 97). Territory identity (*n* = 50) was considered as random, as some territories contributed data from more than one year. Year was considered as a fixed effect and was included in all candidate models. All possible variable combinations were tested, with models ranked based on ΔAIC_c.

All statistical analyses were performed using the program R version 2.5 (R Development Core Team 2007), unless stated otherwise.

5.4 Results

5.4.1 Food supply: ant nest abundance and accessibility

During the three visits to orchards carried out in 2007, we located 242 ant nests belonging to four species: *Lasius niger* L. (75.6%, *n* = 183) was by far the most abundant species; *L. flavus* Fabricius (14.9%, *n* = 36), *Tetramorium caespitum* L. (7.4%, *n* = 18) and *Solenopsis fugax* Latreille (2.1%, *n* = 5) were less common.

Model selection revealed that ant nest detection probability was strongly dependent on temperature, vegetation height, and that it varied across time (Table 3). The amount of bare ground also affected detection probability, but with more uncertainty around the estimate compared to the other variables. Detection probability increased with temperature (Fig. 1a), decreased with vegetation height (Fig. 1b) and increased slightly with amount of bare ground (Fig. 1c). Mean model averaged detection probabilities decreased during the course of the season (mean ± SE; May: 0.723 ± 0.058, June: 0.588 ± 0.061, July: 0.438 ± 0.059).

To calculate the detection probability of ant nests for each replicate, we used the model averaged parameter estimates and the replicate specific variables. Since most surveys were conducted in May, we used the detection probability for this month. Thus, the equation used to calculate replicate specific ant nest detection probabilities was: $p = 1/(1+\exp(-0.63206012 - 0.06966036 * \text{temperature [°C]} - 0.00300383 * \text{bare ground [\%]} + 0.04090232 * \text{vegetation height [cm]}))$.

Ant nest densities corrected for detection probability were lowest in vegetable cultures and highest in orchards, especially in pear orchards (Fig. 2).

The amount of bare ground differed strongly between habitat types (Fig. 2). It was highest in vegetable cultures, vineyards and fallow land, and lowest in meadows. Bare ground cover was moderate in orchards, with pear orchards having the highest amount compared to other orchard types. The combination of both high ant density and a large amount of bare ground (i.e. high accessibility) was highest in orchards, vineyards and fallow land.

5.4.2 Occupancy analyses

5.4.2.1 Assumptions

The frequency distribution of territory occupancy deviated significantly from a randomly generated frequency distribution (χ^2_6 = 42.22, p < 0.001; Fig. 3), indicating that Wrynecks did not settle randomly, but that they chose their territories. Territories that were occupied for 1 or 2 years were more frequent than expected, while territories occupied for more than 2 years and in particular those that were never occupied, were less frequent than expected. Non-random territory choice was also true when considering only the 100 sampled territories (χ^2_6 = 20.77, p = 0.002).

More frequently occupied territories were settled earlier in the season (estimate = -3.298 ± 0.894, p < 0.001). Settlement order was independent of year (likelihood ratio test, χ^2_1 = 1.726, p = 0.189).

Breeding success was not significantly associated with frequency of territory occupancy. Clutch size (estimate = 0.110 ± 0.120, p = 0.363), number of hatchlings (estimate = 0.259 ± 0.178, p = 0.148), and number of fledglings (estimate = 0.245 ± 0.194, p = 0.209) showed a positive trend, whereas fledgling success showed a negative trend (estimate = 0.016 ± 0.128, p = 0.903).

5.4.2.2 Static model

Firstly, we tested each of the 24 explanatory variables singly. Old pear orchard showed the strongest impact on occupancy, while the other variables did not perform as well (Appendix B). The second and third best variables, Vegetable cultures and Ant nests from area with perches, were still within 4 ΔAIC_c units, so they were also included in the second step.

The second step showed that the combination of Old pear orchard and Vegetable cultures resulted in the most parsimonious model (Table 4). The variable Ant nests in areas with perches, was not well supported by the data. Model averaged occupancy probabilities increased with the proportion of old pear orchards within a territory and decreased with the proportion of vegetable cultures (Fig. 4), while it changed very little with increasing number of ant nests in areas with perches.

5.4.2.3 Dynamic model

First, we tested the impact of each of the 25 variables on colonisation and desertion probability (Appendix C & D). The most parsimonious set of models ($\Delta AIC_c < 4$) affecting desertion probability included Number of parcels and Proportion of young apple orchards. The most parsimonious set of models affecting colonisation probability included Proportion of old pear orchards and Presence of conspecifics. In addition, colonisation probability differed across study years, while desertion probability did not.

Variables identified as potentially important in the second step were combined (Table 5). The most parsimonious model affecting desertion probability included Number of parcels, while the most parsimonious model affecting colonisation probability included Proportion of old pear orchards. There was some support for Presence of conspecifics affecting colonisation probability, while there was almost no support for an effect of Proportion of young apple orchards on desertion probability.

Model averaged probabilities of territory desertion decreased with increasing Number of parcels and increased slightly with the Proportion of young apple orchards within a territory (Fig. 5a, b). Territory colonisation probability strongly increased with increasing Proportion of old pear orchards within the territory (Fig. 5c). It was also slightly enhanced when conspecifics were present (Fig. 5d).

5.4.3 Breeding success

Based on the previous results, we considered the variables Old pear orchard and Number of parcels to test whether breeding success was a function of territory quality. The modelling revealed that breeding success did not depend on either of these two variables (Table 6).

5.5 Discussion

Wrynecks did not randomly select territories, with the most frequently occupied territories settled earlier in the season. The probability that a territory was occupied or newly colonised was positively related to the proportion of old pear orchards within the territory. The probability that a territory was deserted was negatively related with the number of cultivated parcels within the territory (i.e. a structure mosaic effect). Pear orchards had the highest density of ant nests, thus offered the highest density of food resources, and were sparsely vegetated, which enhanced ant detection/accessibility. Finally, territories where conspecifics were present in the vicinity were slightly more likely to be colonised. Reproductive success, however, was not related to any of these variables.

5.5.1 Territory selection and territory quality

The proportion of old pear orchards within a territory appears to be an important factor affecting territory colonisation and occupancy in this study. Old and middle-aged orchards, but not necessarily old pear orchards, had been determined as preferred foraging habitats of Wrynecks in a previous study on the same population (Freitag 1998, Weisshaupt 2007). In general, orchards had higher densities of ant nests than other habitat types, with pear orchards harbouring higher densities than apple or apricot orchards. Pear orchards also had higher proportion of bare ground than apple and apricot orchards. Thus, pear orchards are a favoured habitat type due to high food density and good prey accessibility. The negative impact of the proportion of vegetable cultivation is in line with the findings of Freitag (1998) and Weisshaupt (2007), who observed an avoidance of vegetable cultures by foraging Wrynecks. Although areas with vegetable cultures were sparsely vegetated, which would allow easy access to ant nests; they had a low ant nest density and were mostly devoid of perches. Thus, these areas were not suitable foraging habitats and therefore negatively affected territory occupancy.

Territory desertion probability was negatively affected by the number of parcels, which indicates a positive effect of habitat heterogeneity of the agricultural matrix. According to Dauber & Wolters (2004), most ant species can experience an edge effect, which would lead to differences in abundance between the centre and the edge of a culture parcel. This may provide a functional explanation, in contrast to the traditional view that habitat complexity itself is the main reason for favouring heterogeneity (Roth 1976, Boecklen 1986, Benton et al. 2003). Moreover, territories within a highly structured habitat matrix are more likely to be buffered against disturbance (removal of orchards, pesticide application) and may thus provide more stable food resources. This may be especially important in areas with intensively managed agriculture.

In contrast to our expectations based on a previous study of the same population (Weisshaupt 2007), the proportion of bare ground within a territory was neither important for territory occupancy, nor for desertion or colonisation, despite the fact that Wrynecks preferentially forage in areas with ca. 60% bare ground (Weisshaupt 2007). This discrepancy is most probably due to a scale effect (Orians & Wittenberger 1991, George & Zack 2001). At the micro-habitat scale, the proportion of bare ground appears to be important, whereas at a larger spatial scale, it might be not that crucial.

The presence of conspecifics positively affected colonisation probability, which is in accordance with many dispersal studies (Stamps 1988, Muller et al. 1997). While experienced birds often rely on their own reproductive success, which eventually leads to site fidelity (Switzer 1997a, Switzer 1997b), juveniles and unsuccessful breeders may either rely on reproductive success of other individuals (Doligez et al. 1999), or on the presence of conspecifics to evaluate territory quality (Muller et al. 1997). Our results show that Wrynecks preferred to colonise territories where conspecifics were present within a 500 m radius of their nest site. Since breeding success was not related to territory quality, settlement decisions were probably less influenced by public information, than by an assessment of obvious territory features (presence of old pear orchards, vegetable cultures, habitat heterogeneity) and/or by the presence of conspecifics.

Territory colonisation probability differed between years, whereas desertion probability remained constant. This indicates that colonisation also depends on time-dependent factors, such as weather-induced variation in food resource availability and/or foraging habitat accessibility (Geiser et al. 2008), or that stochasticity may play a role.

The outcomes of the static and dynamic models were mostly congruent, although slight discrepancies appeared. The advantage of the dynamic approach is that territory selection can be modelled for each year, eliminating the constraint that territory variables must remain constant across time. It is therefore a promising way of analysing habitat selection patterns, even in the context of a changing environment.

High quality territories should provide a fitness benefit for the territory holder, most likely in terms of increased reproductive success (Andrén 1990, Holmes et al. 1996, Pärt 2001). In the present study, reproductive success of Wrynecks was neither related to the frequency of territory occupancy, nor to the habitat variables identified as important, pointing towards a possible mismatch between habitat preference and fitness (Arlt & Pärt 2007). One likely reason for this result is that the reproductive success of Wrynecks has a stochastic component, because it is affected by the prevailing weather (Geiser et al. 2008). This might blur any relationship with habitat variables. Another explanation is that the number of fledglings, as considered in the current study, is not the relevant fitness component. Other components such as post-fledging or adult survival may be more strongly affected by territory quality.

5.5.2 Food resources

Ant species richness was extremely poor in the intensively farmed study area: only four species were found in the tree plantations. These four species are similar regarding habit and behaviour, and they all enter the diet of Wrynecks, which feed opportunistically on the available ant species (Freitag 1996). *Lasius* spp. are by far the most common prey, due to their high abundance and relatively large nests. A potential drawback of the dependence on one prey species is the possibility of seasonal fluctuations of food abundance. For example, the most profitable larvae of *Lasius niger* are mostly available in May and June, while later in the season the less profitable pupae prevail.

In line with the results of Freitag (1996, 1998) and after correcting for detection probability, the highest ant nest densities were observed in orchards and meadows, whilst the lowest density was found in vegetable-growing areas. In the study area, meadows were intensively cultivated areas, which can explain why ant nest density was comparative to orchards. Dwarf tree orchards appear to be similarly suitable for *Lasius niger*, most likely due to the abundance of aphids, their main food resource, on fruit trees.

5.5.3 Implications for conservation

The persistence of suitable Wryneck territories at this study site appears to depend primarily on a richly structured, orchard dominated agricultural matrix, as habitat heterogeneity enhances territory occupancy. Second, pear arboriculture seems to offer the best compromise for Wrynecks: high density of ant nests and optimal prey detectability/accessibility. Further studies are needed to determine if this link to pear trees is similar for other Wryneck populations breeding in farmland. Finally, a sufficient availability of nest cavities (nest boxes) might be crucial for facilitating conspecific attraction, which impacts positively on territory colonisation. Although the Wryneck is often viewed as a species that can only survive in traditional, low intensity, farmed areas (Hölzinger 1987), this study shows that persistence is also possible in areas with intensive agriculture, such as orchards, as long as key basic resources are present. This is an opportunity for the recovery of this endangered species. It is noteworthy that similar key habitat features as identified here are apparently found in other savannah-like landscapes favoured by Wrynecks, such as light woods, orchards, parks, vineyards, aso (Glutz von Blotzheim & Bauer 1980). Conservation strategies developed for different contexts should therefore aim at offering these resources to Wrynecks.

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Table 1 Description and summary statistics of recorded habitat types for each of the 100 territories. The number of territories indicates in how many of the territories the corresponding habitat type was found.

Habitat type	Description	Total area (ha)	Mean size (ha)	Number of parcels	Number of territories
Anthropogenic	Road, building	35.93	0.06	605	100
Water	Canal, Rhone river, ponds	11.04	0.13	84	55
Vegetable	Vegetable cultures, garden	46.21	0.17	271	74
Fallow land	Fallow land, vegetated canalbanks	27.54	0.09	308	88
Woodland		12.52	0.19	66	35
Pasture		9.52	0.28	34	19
Meadow		26.13	0.18	147	62
Riverbank		6.46	0.31	21	13
Vineyards		18.75	0.16	115	25
Old apple orchard	Stem diameter > 15 cm	20.20	0.17	120	64
Medium aged apple orchard	Stem diameter 5 – 15 cm	46.17	0.22	210	78
Young apple orchard	Stem diameter < 5 cm	46.09	0.24	194	72
Old pear orchard	Stem diameter > 15 cm	23.12	0.17	137	61
Medium aged pear orchard	Stem diameter 5 – 15 cm	17.69	0.20	89	51
Young pear orchard	Stem diameter < 5 cm	5.02	0.17	29	23
Old apricot orchard	Stem diameter > 15 cm	12.62	0.19	68	30
Medium aged apricot orchard	Stem diameter 5 – 15 cm	6.19	0.15	40	21
Young apricot orchard	Stem diameter < 5 cm	9.26	0.20	47	29

Table 2 Description and summary statistics of additional territory variables (food resources, bare ground, tall trees, competition, conspecifics and heterogeneity) for each of the 100 territories with a total area of 390 ha. The number of territories indicates in how many of the territories the corresponding variable was found.

Territory variable	Description	Mean (range)	Number of territories
Ant with perches	Total number of ant nests in the habitat types orchards, riverbank, pasture and vineyards	6696.00 (182 – 12512)	98
Ant without perches	Total number of ant nests in the habitat types vegetable cultures, fallow land and meadow	1303.00 (4 – 4523)	90
Bare ground with perches	Total percentage of bare ground in the habitat types orchards, riverbank, pasture and vineyards	19.42 (0.47 – 50.62)	98
Bare ground without perches	Total percentage of bare ground in the habitat types vegetable cultures, fallow land, and meadow	7.47 (0.09 – 50.01)	92
Total bare ground	Total percentage of bare ground within territory	25.90 (5.94 – 57.66)	100
Number of tall trees	Number of trees higher than 4 m	20.71 (1 – 118)	49
Number of parcels	Number of parcels within territory	19.03 (6 – 37)	100
Hoopoe	Number of years a Hoopoe occupied same territory	3.07 (1 – 6)	58
Presence of conspecifics	Boolean, whether or not a conspecific was breeding within < 500 m	–	–

Table 3 Model selection summary of detection probability of ant nests as a function of season (time), ambient temperature, percentage of bare ground, and vegetation height evaluated by occupancy models. Given are the ΔAIC_c, AIC_c weights (w_i), number of parameters (K) and the residual deviance. The occupancy probability was constant for all models. Models are ranked according to ΔAIC_c.

Model	ΔAIC_c	w_i	K	Deviance
Time + temperature + vegetation height	0.000	0.527	6	358.017
Time + temperature + bare ground + vegetation height	1.160	0.295	7	356.844
Time + vegetation height	3.577	0.088	5	363.875
Time + bare ground + vegetation height	4.393	0.059	6	362.410
Time + temperature + bare ground	6.936	0.016	6	364.953
Time + bare ground	8.610	0.007	5	368.908
Time + temperature	10.153	0.003	5	370.451
Temperature + vegetation height	11.514	0.002	4	374.041
Time	11.682	0.002	4	374.209
Vegetation height	13.309	0.001	3	378.017
Temperature + bare ground + vegetation height	13.497	0.001	5	373.794
Bare ground + vegetation height	15.053	0.000	4	377.580
Temperature + bare ground	17.566	0.000	4	380.093
Temperature	17.911	0.000	3	382.618
Bare ground	18.139	0.000	3	382.847
Constant model	18.753	0.000	2	385.594

Table 4 Summary of the static occupancy model results for Wryneck territories, when the three explanatory variables selected in the first step (Appendix B) are used together. Given are the ΔAIC_c, AIC_c weights (w_i), number of parameters (K) and the residual deviance. The models are ranked according to their AIC_c weight.

Model	ΔAIC_c	w_i	K	Deviance
Old pear orchards + vegetable cultures	0.00	0.538	3	218.52
Old pear orchards + vegetable cultures + ant with perches	1.99	0.199	4	218.44
Old pear orchards	3.17	0.110	2	223.69
Old pear orchards + ant with perches	3.41	0.098	3	222.80
Ant with perches + vegetable cultures	6.66	0.019	3	226.64
Vegetable cultures	6.81	0.018	2	227.33
Ant with perches	6.91	0.017	2	230.27
Constant model	12.43	0.001	1	234.94

Table 5 Summary of desertion (ε) and colonisation (γ) probabilities for Wryneck territories. Shown are the 13 best models (from originally 36 fitted models). Given are the ΔAIC_c, AIC_c weights (w_i), number of parameters (K) and the residual deviance. A constant intercept is indicated with (.), and a time-dependent intercept with "year". The initial occupancy probability (Ψ) is constant for every model. See appendices 3 and 4 for the first modelling steps.

Model	ΔAIC_c	w_i	K	Deviance
ε (number of parcels) γ(year + old pear orchards)	0.000	0.439	9	595.385
ε (number of parcels) γ(year + presence of conspecifics)	2.923	0.102	9	598.308
ε (year + number of parcels) γ(year + old pear orchards)	2.958	0.100	13	590.027
ε (.) γ(year + old pear orchards)	3.703	0.069	8	601.149
ε (number of parcels) γ(presence of conspecifics)	3.839	0.064	5	607.428
ε (young apple orchards) γ(year + old pear orchards)	3.966	0.060	9	599.351
ε (number of parcels) γ(old pear orchards)	5.881	0.023	13	592.950
ε (year number of parcels) γ(year + presence of conspecifics)	6.626	0.016	8	604.072
ε (.) γ(year + presence of conspecifics)	6.685	0.016	9	602.070
ε (year + number of parcels) γ(presence of conspecifics)	6.889	0.014	9	602.274
ε (young apple orchards) γ(year + presence of conspecifics)	7.264	0.012	12	596.422
ε (year) γ(year + old pear orchards)	7.307	0.011	13	594.375
ε (year + young apple orchards) γ(year + old pear orchards)	2.923	0.102	9	598.308

Table 6 Model selection results for the number of fledglings from successful broods (n = 97), in relation to the amount of old pear orchards and the number of parcels within the territories (n = 50), evaluated with a generalized liner mixed model with a Poisson error distribution. Year is included as a fixed effect in all models, and territory as a random effect. Given are the ΔAIC, AIC weights (w_i), number of estimated parameters (K) and the deviance.

Model	ΔAIC	w_i	K	Deviance
Intercept	0.000	0.494	7	439.594
Old pear	1.467	0.237	8	439.062
Number of parcels	1.998	0.182	8	439.591
Old pear + number of parcels	3.463	0.087	9	439.057

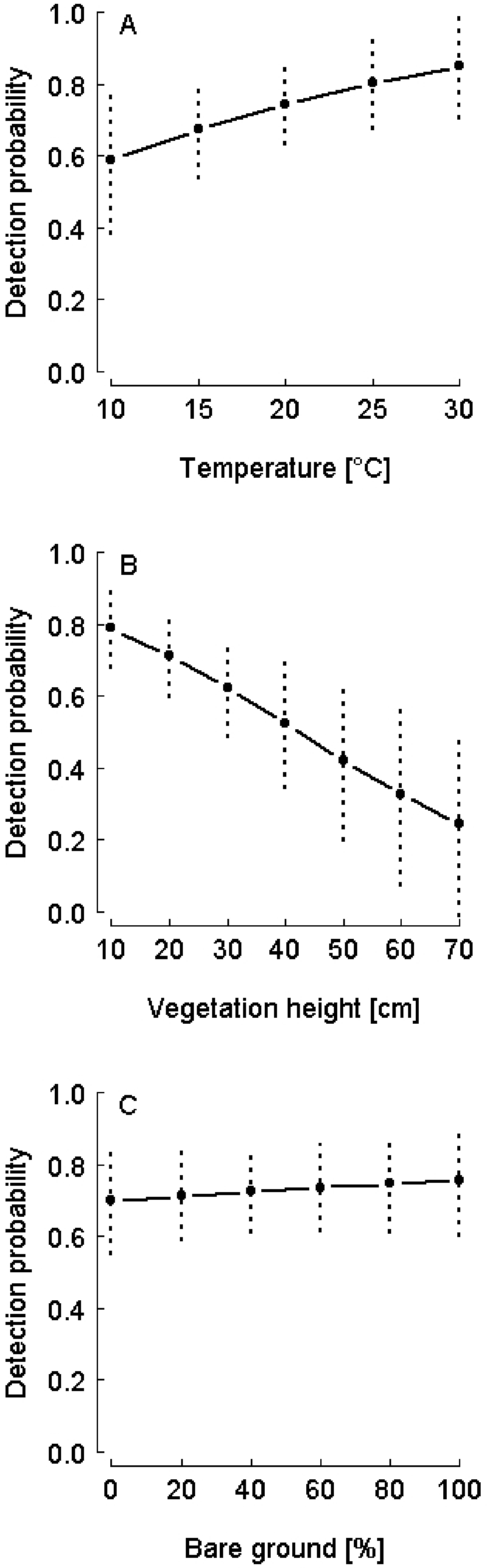


Figure 1 Relationship between detection probability of ant nests and temperature (a); vegetation height (b) and; amount of bare ground (c). Shown are model averaged predictions (based on results in Table 3) with 95% confidence intervals.

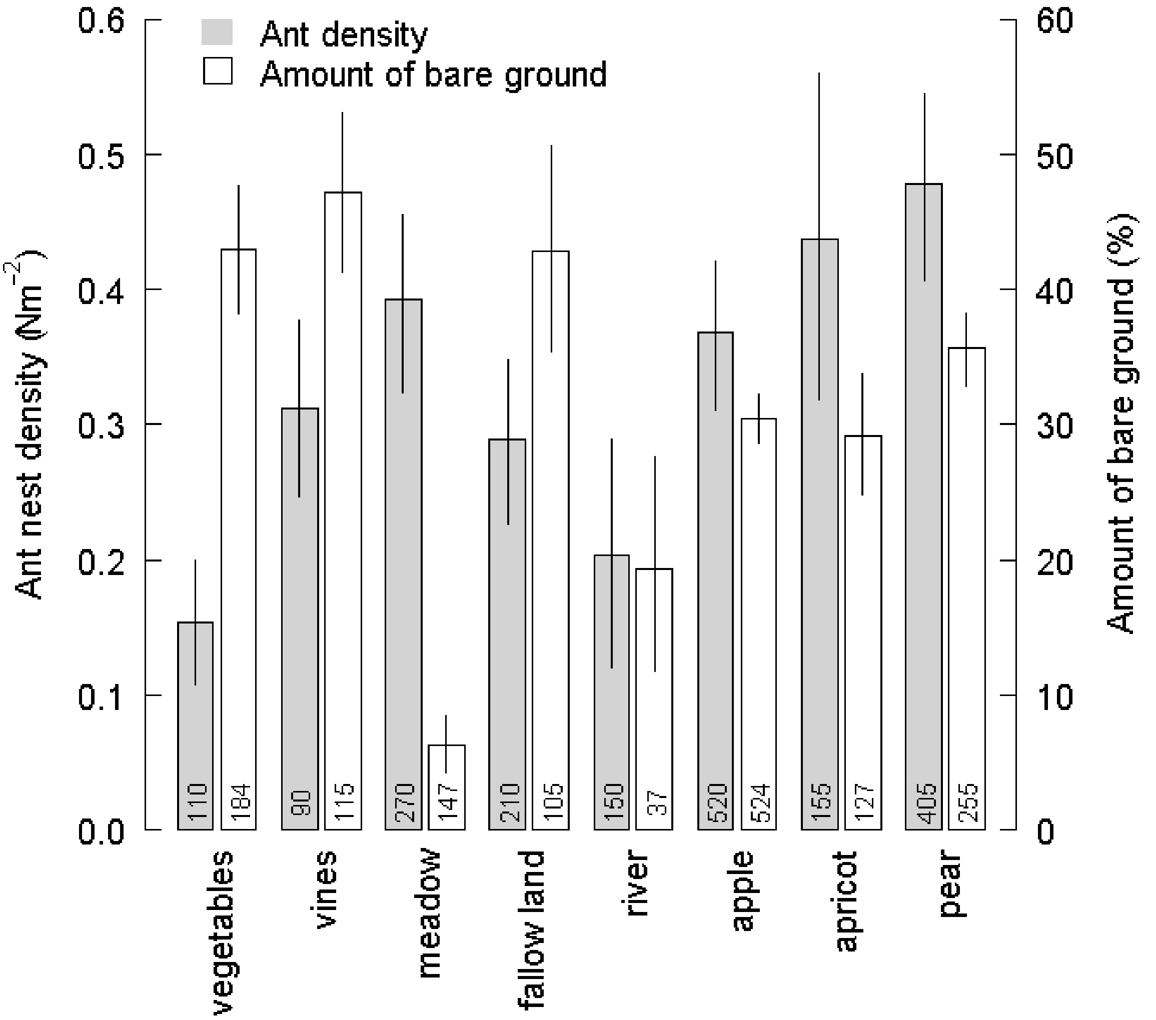


Figure 2 Estimated ant nest densities and amount of bare ground per habitat type, obtained by fitting linear mixed models. Shown are the estimates for each habitat type with 95% confidence intervals. Ant densities are corrected for imperfect detection probability. The number of samples for each habitat type is given at the bottom of each bar.

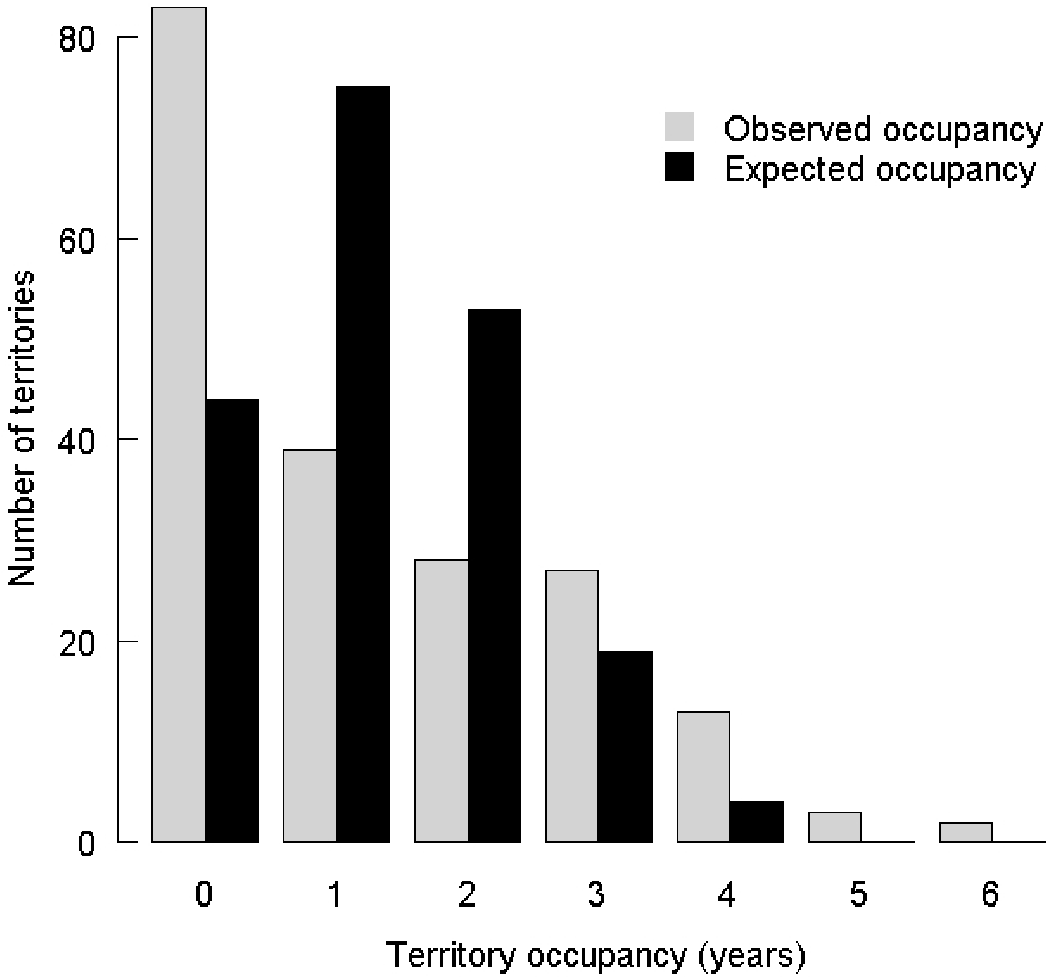


Figure 3 Expected and observed frequencies of Wryneck territory occupancy over the six study years. Expected frequencies are calculated using a binomial distribution. The observed frequency of territory occupancy significantly deviates from the expected frequency.

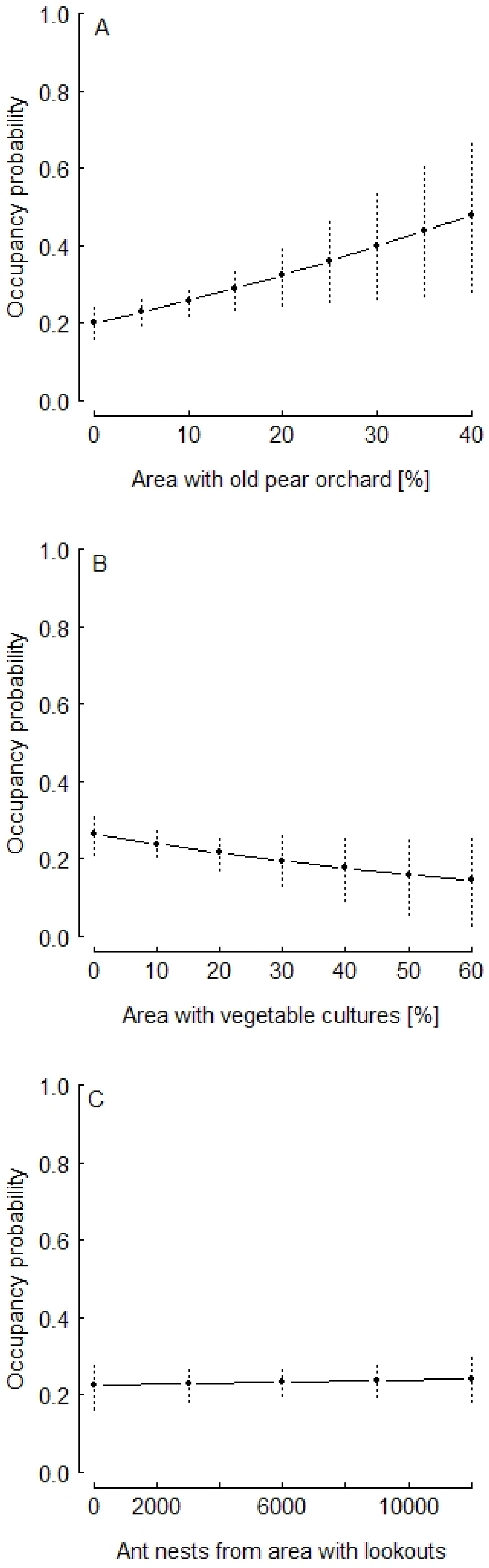


Figure 4 Predicted model averaged probability of Wryneck territory occupancy, calculated from the best models accounting for 0.95 of the AIC$_c$ weight (Table 4), in relation to the proportion of old pear orchards (a), vegetable cultures (b), and ant nests from area with perches (c), within territories. The figures show averaged estimates with 95% confidence intervals.

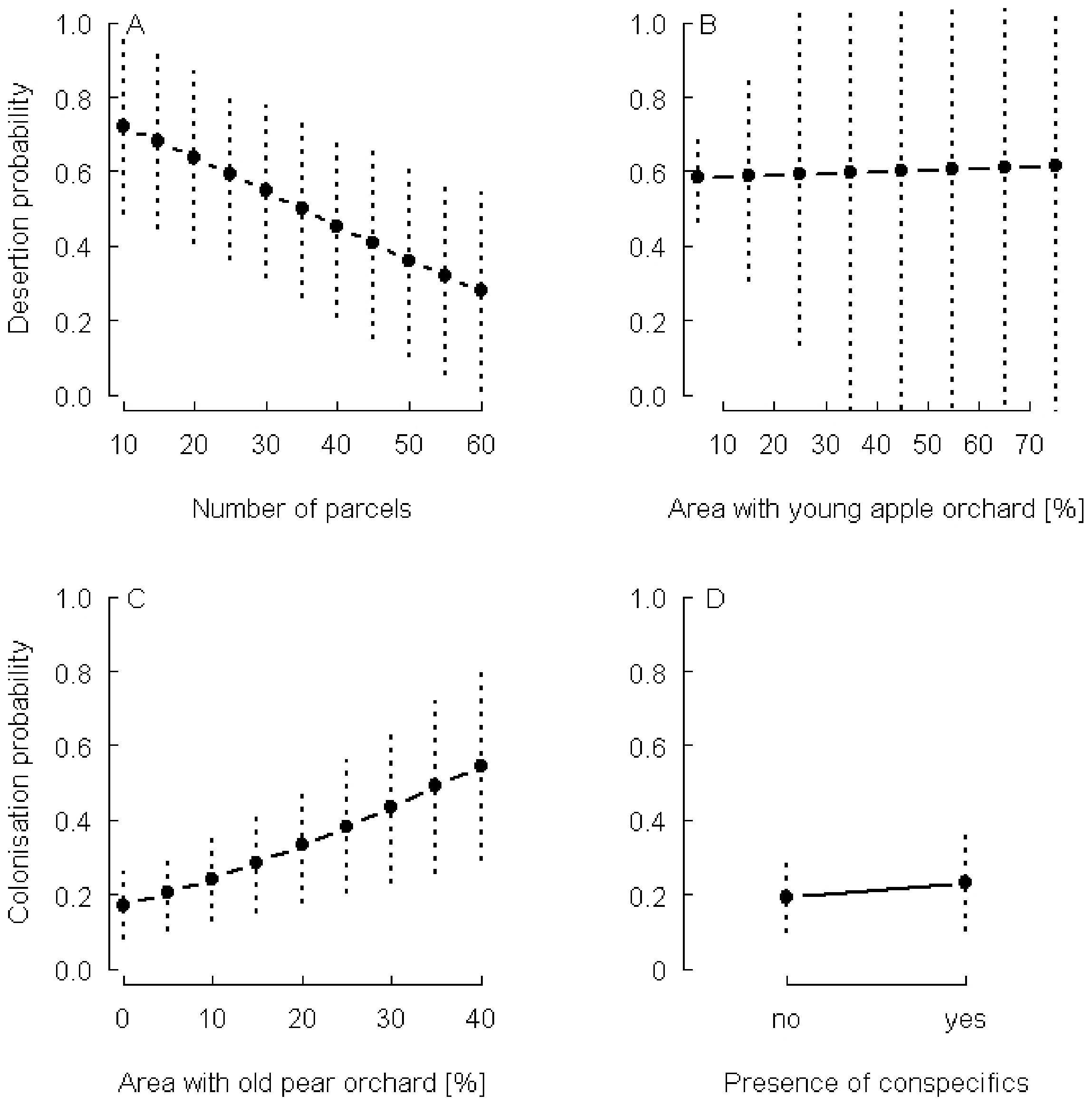
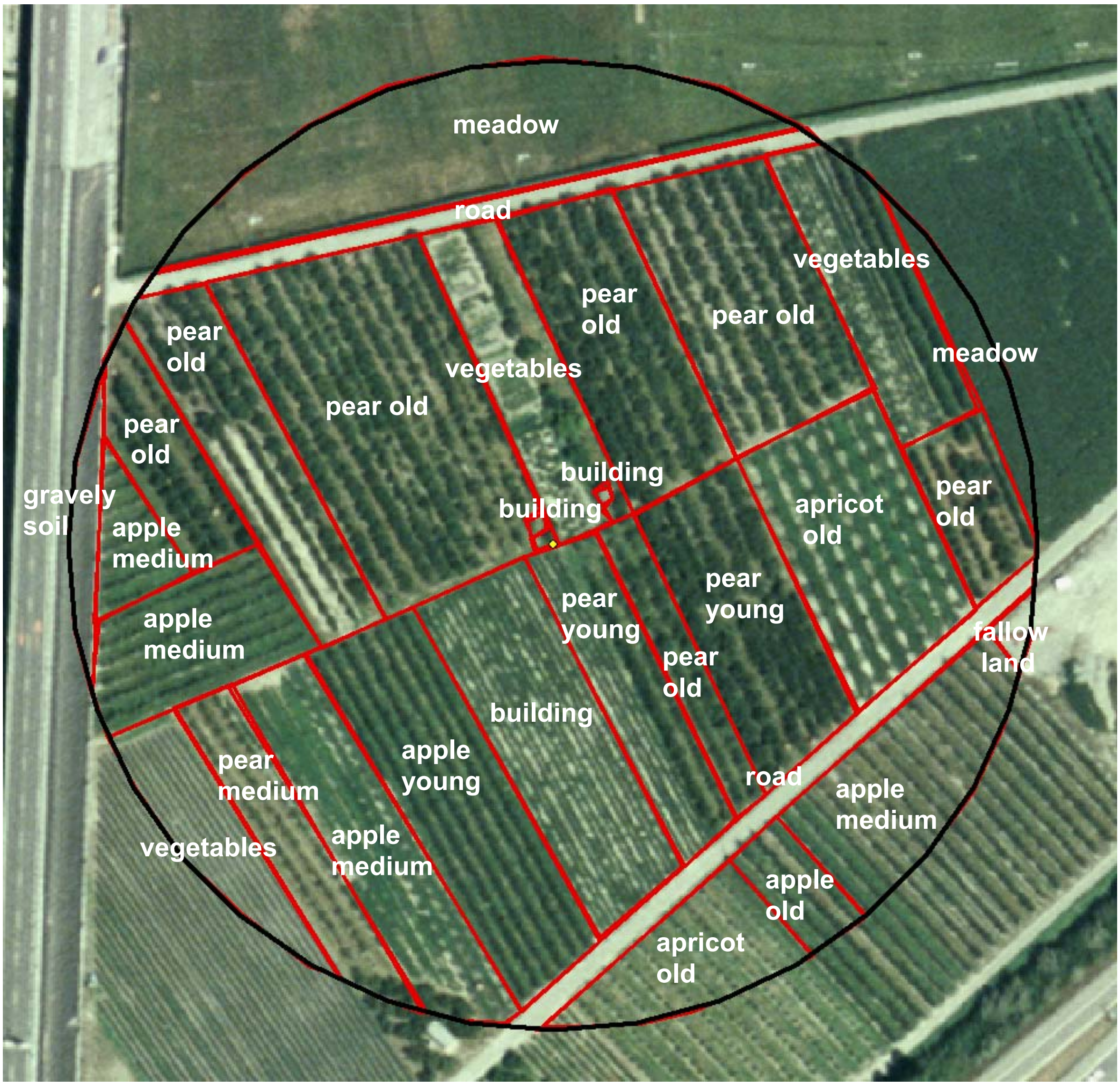


Figure 5 Predicted model averaged probabilities of Wryneck territory desertion and colonisation from the best models accounting for 0.95 of the AIC_c weight (Table 5). Shown are the number of parcels (a), and the proportion of young apple orchards within the territory (b) in relation to desertion probability; and the proportion of old pear orchards within a territory (c), and the presence of conspecifics within a radius of 500 m to the nest site (d) in relation to colonisation probability. For time-dependent models, the predictions shown are for the year 2004. The figures show averaged estimates with 95% confidence intervals.

Appendix A An example of a mapped, digitised territory. The borders of each parcel were drawn directly on the orthophoto in the field and were subsequently digitised using GIS. As the orthophotos were taken in 2004/2005, some cultures have changed since then and 2007 (e.g. on this map the parcel below the centre was recorded as building in 2007 instead of a vegetable culture as displayed). Reproduced with authorisation of the Bundesamt für Landestopographie.



Appendix B Summary results for static occupancy models of Wryneck territories, modelling all 26 explanatory variables singly (note that the squared variables also contained the main effect). Given are the ΔAIC_c, AIC_c weights (w_i), number of parameters (K) and the residual deviance. Models are ranked according to ΔAIC_c. The first three models (bold) are within $\Delta AIC < 4$ and were thus selected for the second step of the analysis (Table 4).

Model	ΔAIC_c	w_i	K	Deviance
Old pear orchard	**0.00**	**0.612**	**2**	**223.69**
Vegetable cultures	**3.64**	**0.099**	**2**	**227.33**
Ant with perches	**3.74**	**0.094**	**2**	**227.43**
Number of parcels	5.36	0.042	2	229.05
Bare ground with perches	6.86	0.020	2	230.55
Hoopoe	7.38	0.015	2	231.07
Medium apple orchard	7.52	0.014	2	231.21
Medium apricot orchard	7.59	0.014	2	231.28
Old apricot orchard	8.37	0.009	2	232.06
Total bare ground	9.00	0.007	2	232.69
Total bare ground^2	9.11	0.006	3	232.80
Constant model	9.26	0.006	1	234.94
Number of tall trees	9.28	0.006	2	232.97
Young pear orchard	9.36	0.006	2	233.05
Bare ground with perches^2	9.47	0.005	3	233.16
Young apricot orchard	9.72	0.005	2	233.41
Woodland	10.49	0.003	2	234.18
Vineyards	10.59	0.003	2	234.28
Bare ground without perches	10.64	0.003	2	234.33
Fallow land	10.79	0.003	2	234.48
Young apple orchard	11.13	0.002	2	234.82
Old apple orchard	11.23	0.002	2	234.92
Bare ground without perches^2	11.23	0.002	3	234.92
Medium pear orchard	11.25	0.002	2	234.94
Meadow	11.26	0.002	2	234.94

Appendix C Summary results for dynamic occupancy modelling of colonisation probability (γ), using all 27 explanatory variables singly (note that the squared variables also contained the main effect). Desertion probability (ε) was time-dependent in all models. Given are the ΔAIC_c, AIC_c weights (w_i), number of parameters (K) and the residual deviance. Models are ranked according to their ΔAIC_c. The first three models are within $\Delta \text{AIC} < 4$ and their variables are selected for the second step of the analysis (Table 5).

Model	ΔAIC_c	w_i	K	Deviance
ε (year) γ(year + old pear orchard)	**0.000**	**0.598**	**12**	**596.422**
ε (year) γ(year + presence of conspecifics)	**2.923**	**0.139**	**12**	**599.345**
ε (year) γ(presence of conspecifics)	**3.756**	**0.091**	**8**	**608.465**
ε (year) γ(old pear orchard)	5.621	0.036	8	610.331
ε (year) γ(year + ant with perches)	7.300	0.016	12	603.722
ε (year) γ(year + total bare ground)	7.481	0.014	12	603.903
ε (year) γ(year + vegetable cultures)	7.544	0.014	12	603.966
ε (year) γ(year + bare ground with perches)	8.714	0.008	12	605.136
ε (year) γ(year + total bare ground^2)	8.992	0.007	13	603.324
ε (year) γ(year + old apricot orchard)	9.181	0.006	12	605.603
ε (year) γ(year + bare ground with perches^2)	9.458	0.005	13	603.790
ε (year) γ(year)	9.459	0.005	11	607.963
ε (year) γ(year + medium apple orchard)	9.964	0.004	12	606.386
ε (year) γ(year + old apple orchard)	10.147	0.004	12	606.569
ε (year) γ(year + bare ground without perches^2)	10.386	0.003	13	604.718
ε (year) γ(year + young apple orchard)	10.602	0.003	12	607.024
ε (year) γ(year + young apricot orchard)	10.616	0.003	12	607.037
ε (year) γ(year + meadow)	10.896	0.003	12	607.318
ε (year) γ(year + medium pear orchard)	11.149	0.002	12	607.571
ε (year) γ(year + tall trees)	11.201	0.002	12	607.623
ε (year) γ(year + vineyard)	11.262	0.002	12	607.684
ε (year) γ(year + fallow land)	11.412	0.002	12	607.834
ε (year) γ(year + medium apricot orchard)	11.445	0.002	12	607.867
ε (year) γ(year + bare ground without perches)	11.475	0.002	12	607.897
ε (year) γ(year + Hoopoe)	11.485	0.002	12	607.907
ε (year) γ(year + young pear orchard)	11.515	0.002	12	607.937
ε (year) γ(year + woodland)	11.523	0.002	12	607.945
ε (year) γ(year + number of parcels)	11.541	0.002	12	607.963
ε (year) γ(total bare ground)	11.869	0.002	8	616.579
ε (year) γ(ant with perches)	12.267	0.001	8	616.973
ε (year) γ(vegetable cultures)	12.627	0.001	8	617.337
ε (year) γ(total bare ground^2)	13.228	0.001	9	615.876

ε (year) γ(bare ground with perches)	13.471	0.001	8	618.180
ε (year) γ(old apricot orchard)	13.749	0.001	8	618.459
ε (year) γ(.)	14.064	0.001	7	620.828
ε (year) γ(bare ground with perches^2)	14.328	0.000	9	616.976
ε (year) γ(old apple orchard)	14.702	0.000	8	619.412
ε (year) γ(medium apple orchard)	14.887	0.000	8	619.597
ε (year) γ(young apple orchard)	14.917	0.000	8	619.627
ε (year) γ(young apricot orchard)	14.981	0.000	8	619.691
ε (year) γ(bare ground without perches^2)	15.028	0.000	9	617.676
ε (year) γ(meadow)	15.517	0.000	8	620.227
ε (year) γ(vineyard)	15.694	0.000	8	620.404
ε (year) γ(Hoopoe)	15.708	0.000	8	620.418
ε (year) γ(medium pear orchard)	15.786	0.000	8	620.496
ε (year) γ(tall trees)	15.793	0.000	8	620.503
ε (year) γ(bare ground without perches)	15.990	0.000	8	620.700
ε (year) γ(fallow land)	15.996	0.000	8	620.706
ε (year) γ(young pear orchard)	16.013	0.000	8	620.722
ε (year) γ(woodland)	16.054	0.000	8	620.764
ε (year) γ(medium apricot orchard)	16.077	0.000	8	620.787
ε (year) γ(number of parcels)	16.111	0.000	8	620.821

Appendix D Summary results for dynamic occupancy modelling of desertion probability (ε), using all 27 explanatory singly (note that the squared variables also contained the main effect). Colonisation probability (γ) was time-dependent in all models. Given are the ΔAIC_c, AIC_c weights (w_i), number of parameters (K) and the residual deviance. Models are ranked according to their ΔAIC_c. The first four models are within $\Delta AIC < 4$ and their variables are selected for the second step of the analysis (Table 5).

Model	ΔAIC_c	w_i	K	Deviance
ε (number of parcels) γ(year)	**0.000**	**0.299**	**8**	**606.926**
ε (year + number of parcels) γ(year)	**2.930**	**0.069**	**12**	**601.568**
ε (.) γ(year)	**3.710**	**0.047**	**7**	**612.690**
ε (young apple orchard) γ(year)	**3.966**	**0.041**	**8**	**610.892**
ε (Hoopoe) γ(year)	4.575	0.030	8	611.501
ε (medium apricot orchard) γ(year)	4.906	0.026	8	611.832
ε (young pear orchard) γ(year)	5113	0.023	8	612.039
ε (old apple orchard) γ(year)	5.176	0.022	8	612.102
ε (tall trees) γ(year)	5.207	0.022	8	612.133
ε (young apricot orchard) γ(year)	5.259	0.022	8	612.185
ε (presence of conspecifics) γ(year)	5.298	0.021	8	612.223
ε (woodland) γ(year)	5.386	0.020	8	612.311
ε (old apricot orchard) γ(year)	5.512	0.019	8	612.437
ε (ant with perches) γ(year)	5.585	0.018	8	612.510
ε (old pear orchard) γ(year)	5.669	0.018	8	612.594
ε (bare ground with perches) γ(year)	5.678	0.018	8	612.604
ε (vineyard) γ(year)	5.682	0.017	8	612.608
ε (bare ground without perches) γ(year)	5.696	0.017	8	612.622
ε (fallow land) γ(year)	5.726	0.017	8	612.652
ε (meadow) γ(year)	5.736	0.017	8	612.661
ε (vegetable cultures) γ(year)	5.742	0.017	8	612.668
ε (medium apple orchard) γ(year)	5.757	0.017	8	612.683
ε (medium pear orchard) γ(year)	5.758	0.017	8	612.684
ε (total bare ground) γ(year)	5.761	0.017	8	612.687
ε (year) γ(year)	7.243	0.008	11	607.963
ε (year + young apple orchard) γ(year)	7.279	0.008	12	605.916
ε (bare ground with perches^2) γ(year)	7.548	0.007	9	612.412
ε (bare ground without perches^2) γ(year)	7.711	0.006	9	612.576
ε (total bare ground^2) γ(year)	7.819	0.006	9	612.683
ε (year + presence of conspecifics) γ(year)	8.373	0.005	12	607.011
ε (year + tall trees) γ(year)	8.574	0.004	12	607.212
ε (year + Hoopoe) γ(year)	8.641	0.004	12	607.279

ε (year + young apricot orchard) γ(year)	8.712	0.004	12	607.350
ε (year + old apple orchard) γ(year)	8.746	0.004	12	607.384
ε (year + medium apricot orchard) γ(year)	8.919	0.003	12	607.557
ε (year + young pear orchard) γ(year)	8.982	0.003	12	607.620
ε (year + bare ground without perches) γ(year)	9.020	0.003	12	607.658
ε (year + old apricot orchard) γ(year)	9.087	0.003	12	607.724
ε (year + vegetable cultures) γ(year)	9.095	0.003	12	607.733
ε (year + bare ground with perches) γ(year)	9.100	0.003	12	607.738
ε (year + woodland) γ(year)	9.156	0.003	12	607.793
ε (year + old pear orchard) γ(year)	9.226	0.003	12	607.864
ε (year + ant with perches) γ(year)	9.229	0.003	12	607.866
ε (year + meadow) γ(year)	9.289	0.003	12	607.926
ε (year + medium apple orchard) γ(year)	9.302	0.003	12	607.940
ε (year + fallow land) γ(year)	9.310	0.003	12	607.948
ε (year + vineyard) γ(year)	9.324	0.003	12	607.961
ε (year + total bare ground) γ(year)	9.325	0.003	12	607.962
ε (year + medium pear orchard) γ(year)	9.325	0.003	12	607.962
ε (year + bare ground without perches^2) γ(year)	11.093	0.001	13	607.642
ε (year + bare ground with perches^2) γ(year)	11.110	0.001	13	607.659
ε (year + total bare ground^2) γ(year)	11.399	0.001	13	607.947

6

Eurasian Hoopoe *Upupa epops* breeding pair raises Eurasian Wryneck *Jynx torquilla* nestlings until they fledge

Eurasian Hoopoe *Upupa epops* breeding pair raises Eurasian Wryneck *Jynx torquilla* nestlings until they fledge

(Wiedehopfpaar zieht Wendehalsnestlinge bis zum Ausfliegen auf)

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6.1 Abstract

Between 29th April and 21st June 207 we observed in Valais, Switzerland, a breeding pair of Eurasian Hoopoes that adopted a brood of Eurasian Wrynecks after its own brood had failed. Both Wryneck and Hoopoe parents fed the Wryneck nestlings with ants and molecrickets, respectively. The growth rate of the nestlings was lower than on average, but three out of eight nestlings still managed to fledge.

6.2 Einleitung

Vogeleltern investieren viel Energie, um ihre eigenen Jungen aufzuziehen. Die Belohnung dieses Aufwandes besteht in der Weitergabe der eigenen Gene. Vogeleltern, die artfremde Junge (z.B. Brutparasitismus durch Kuckuck *Cuculus canorus*) aufziehen, investieren viel Energie, haben davon aber keinen Nutzen, da ihre Gene nicht vererbt werden. Deshalb macht es evolutionär keinen Sinn, freiwillig artfremde Junge aufziehen. Obwohl diese Ereignisse selten sein müssten, gibt es einige dokumentierte Beobachtungen zur freiwilligen Aufzucht artfremder Jungvögel (z.B. Shy 1982, von Hirschheydt 1998, Nicolai 2003). Hier beschreiben wir eine solche aussergewöhnliche Beobachtung. Ein Wiedehopfpaar übernahm die 8 Jungen einer Wendehalsbrut und zog diese auf.

Wendehals *Jynx torquilla* und Wiedehopf *Upupa epops* unterscheiden sich in ihrer evolutionären Herkunft, ihrem Verhalten und ihrer Nahrung beachtlich. So ernähren sich Wiedehopfe von im Boden lebenden Grossinsekten (im Wallis bevorzugt Maulwurfsgrillen *Gryllotalpa gryllotalpa*, Fournier & Arlettaz 2001), während Wendehälse fast ausschliesslich von Wiesenameisen *Lasius sp.* leben (Hölzinger 1992, Bitz & Rohe 1993, Freitag 1996). Gemeinsam ist den beiden Arten, dass sie in Höhlen brüten und zur Nahrungssuche Stellen mit lückiger Vegetation bevorzugen (Weisshaupt 2007, Ioset 2007), weshalb sie im selben Gebiet vorkommen können.

6.3 Beobachtungen

Unsere Beobachtungen erfolgten zwischen dem 29. April und dem 21. Juni 207 an zwei Wiedehopfnistkästen (A und B), welche im Rahmen eines Artenschutz- und Forschungsprogramms der Universität Bern und der Schweizerischen Vogelwarte Sempach in einem Geräteschuppen östlich von Riddes (Kanton Wallis) installiert worden sind. Die beiden Nistkästen hängen an derselben Wand in 2 m Entfernung zueinander. Bei der Nistkastenkontrolle am 29. April entdeckten wir mit Hilfe eines Spiegels und einer Lampe, welche durch die Nistkastenöffnung gehalten werden, einen Wiedehopf im Nistkasten A. Es handelte sich vermutlich um das Weibchen, da beim Wiedehopf die Eier von den Weibchen bebrütet werden. Am 14. Mai bebrütete das Weibchen mindestens vier Eier und der Schlupftermin wurde zwischen Mitte und Ende Mai erwartet. Am 28. Mai wurde das Weibchen jedoch immer noch brütend im Kasten A angetroffen. Am 11. Juni war die Brut verlassen (Tab. 1); aus keinem der 7 Eier schlüpfte ein Junges. Neben dem unterschiedlichen Brutverhalten konnte das Geschlecht der Wiedehopfe zeitweise durch den direkten Vergleich beider Individuen bestimmt werden. Männchen weisen den deutlicheren Farbkontrast und die intensivere Färbung als die Weibchen auf.

Im Nistkasten B entdeckten wir am 14. Mai 6 Wendehalseier. Drei Tage später war das Gelege mit 9 Eiern vollständig und wurde ordnungsgemäss 13 Tage lang bebrütet. Am 30. Mai schlüpften die ersten Jungen, einen Tag später wurden 9 geschlüpfte Junge gezählt. Die Wendehalseltern wurden am 31. Mai und am 4. Juni gefangen. Das Männchen (Ringnummer Y28621) war 2006 in einem 1.3 km entfernten Nistkasten aufgezogen worden. Das Weibchen (Ringnummer Y25933) war ein mindestens 3-jähriger Altvogel, der 2005 in einer Distanz von 3.3 km erfolglos gebrütet hatte. Die Geschlechter der beiden Tiere wurden genetisch anhand von Blutproben bestimmt. Im Feld sind die Geschlechter nicht zu unterscheiden, weshalb im Folgenden auch nicht klar ist, ob sich beide Eltern an den Fütterungen beteiligt haben und welcher Elternteil jeweils beobachtet wurde.

Am 6. Juni wurde wiederum anhand Spiegel und Lampe erstmals ein Wiedehopf bei den Wendehalsjungen im Nistkasten B beobachtet, ein weiteres Mal am 11. Juni (Tab. 1). Ein Wendehalsnestling hatte eine Maulwurfsgrille im Schnabel und konnte diese während den 5 Beobachtungsminuten nicht schlucken. Auf Grund dieser Feststellungen wurden an den Folgetagen intensive Beobachtungen durchgeführt.

Am 14. Juni wurde das Geschehen von 7:55 h bis 9:50 h aus dem Auto aus etwa 20 m Entfernung intensiv beobachtet. Zu dieser Zeit befanden sich noch 8 Wendehalsnestlinge im Nistkasten, einer war schon gestorben. Während der Beobachtungszeit erfolgten 9 Nestanflüge, 7 durch Wiedehopfe und 2 durch Wendehälse. Um 8:07 h ging ein Wiedehopf, um 8:16 h ein Wendehals kurz in den Kasten. Um 8:42 h tauchte erneut ein Wendehals auf und ging kurz in den Kasten. Ob bei diesen 3 Nestanflügen gefüttert wurde, war nicht sicher. Um 8:46 h erschien das Wiedehopfmännchen mit einer Maulwurfsgrille und fütterte die Nestlinge. Zwei Minuten später erschien erneut ein Wiedehopf mit einer Maulwurfsgrille, entfernte sich jedoch wieder, ohne die Beute den Jungen zu bringen. Fünf Minuten später kam wieder ein Wiedehopf mit einer Maulwurfsgrille und wartete am Boden vor dem Nistkasten, bis kurz darauf auch der zweite Wiedehopf mit Futter auftauchte. Gleichzeitig erschien auch ein Wendehals mit Futter, welcher die beiden Wiedehopfe vom Boden aus beobachtete. Ein Wiedehopf flog die Nistkastenöffnung an, entfernte sich aber wieder, ohne die Nestlinge zu füttern. Dann näherte sich der Wendehals dem noch am Boden wartenden Wiedehopf, welcher sich darauf wenige Meter von der Hütte entfernte. Der Wendehals fütterte nun kurz seine Jungen. Kaum war er wieder verschwunden, besuchte erneut ein Wiedehopf den Nistkasten. Ob dieser Futter brachte, konnte nicht erkannt werden.

Am 15. Juni wurde zwischen 7:36 h und 9:20 h wiederum intensiv aus dem Auto beobachtet. Um 7:48 h erschien das Wiedehopfmännchen mit einer Maulwurfsgrille und flog an die Nistkastenöffnung. Er entfernte sich jedoch wieder ohne zu füttern. Um 8:16 h schlüpfte ein Wiedehopf, vermutlich das Weibchen, in den Nistkasten und blieb darin. Um 8:22 h erschien das Wiedehopfmännchen und übergab dem im Nistkasten sitzenden

Weibchen eine kleine Beute an der Nistkastenöffnung. Gleich darauf verliess das Weibchen den Kasten. Eine Minute später erschien wiederum das Wiedehopfmännchen mit einer relativ kleinen Beute (keine Maulwurfsgrille), verschwand kurz im Kasten und verliess ihn ohne Beute wieder. Um 8:31 h und 8:37 h wiederholte sich dasselbe. Drei Minuten später flog ein Wendehals mit vollem Schnabel zuerst auf das Dach des Geräteschuppens, um dann - sich stetig umschauend - auf dem Boden zu landen. Danach schlüpfte er in den Kasten und blickte Sekunden später wieder aus der Öffnung. Er hatte das Futter noch immer im Schnabel und den Schluckbewegungen nach schien er einen Teil des Futters selber zu fressen. Ohne die Jungen zu füttern, entfernte er sich wieder. Um 8:47 h befanden sich sowohl ein Wendehals als auch das Wiedehopfmännchen in unmittelbarer Nähe des Nistkastens. Der Wendehals verschwand, oft um sich blickend, im Kasten und schaute auch gleich wieder aus dem Loch, dieses Mal ohne Futter. Sobald er sich entfernt hatte, erschien das Wiedehopfweibchen mit einer Raupe und fütterte die Wendehalsjungen. Um 8:54 h landete der Wendehals auf dem Dach der Hütte, flog auf den Boden und näherte sich dem am Boden wartenden Wiedehopfmännchen, welches etwas zurückwich. Inzwischen fütterte das Wiedehopfweibchen die Jungen erneut, übernahm auch das Futter des Wiedehopfmännchens und verfütterte es ebenfalls an die Jungen. Beide Wiedehopfe flogen darauf davon. Nun besuchte der Wendehals den Kasten, schaute jedoch gleich wieder aus der Öffnung und schien das Futter wiederum selbst zu fressen. Zwischen 8:58 h und 9:04 h wurden die Jungen viermal vom Wiedehopfmännchen und einmal vom Wiedehopfweibchen gefüttert. Um 9:05 h fütterte ein Wendehals die Jungen und verschwand gleich wieder. Drei Minuten später landete ein Wendehals auf dem Dach und das Wiedehopfmännchen auf dem Boden, während das Wiedehopfweibchen zielstrebig den Kasten anflog und die Jungen fütterte. Es verliess den Kasten und das Wiedehopfmännchen fütterte seinerseits die Jungen. Drei Minuten später schlüpfte der Wendehals, welcher die Fütterungen der Wiedehopfe vom Boden aus aus etwa 2-3 m Entfernung beobachtet hatte, in den Nistkasten. Wiederum verspeiste er das Futter beim Herausschauen aus der Nistkastenöffnung selbst. Um 9:20 h besuchte das Wiedehopfweibchen wieder den Nistkasten und wurde von uns herausgegriffen. Es handelte sich um ein vorjähriges Individuum (Ringnummer H96328), welches in einem 2.7 km entfernten Nistkasten aufgezogen worden war. Das Wiedehopfmännchen war ebenfalls schon beringt, konnte jedoch nicht kontrolliert werden.

Am 15. Juni wurden die 8 Wendehalsnestlinge, die 17 Tage alt waren, beringt. Sie wogen zwischen 18.5 g und 27.0 g, waren also relativ leicht für ihr Alter (Tab. 2). Auch die übrige Körperentwicklung, besonders die Länge der 8. Handschwinge (deszendent gezählt; s. auch Abb. 1) war unterdurchschnittlich, wie ein Vergleich mit der Normalentwicklung zeigt (Tab. 2).

Am 18. Juni beobachteten wir die Brut von 14:06 h bis 14:32 h. Beide Wiedehopfe warteten mit Beute vor dem Nistkasten. Mehrmals flogen sie die Öffnung des Nistkastens an und versuchten erfolglos, die Nahrung an die Wendehalsjungen abzugeben, welche nun bereits in der Öffnung sassen. Die Wiedehopfe schlüpften nicht mehr in den Kasten hinein. In dieser Zeit wurde kein Anflug eines Wendehalses festgestellt.

Am 19. Juni wurde von 12:23 h bis 12:43 h beobachtet. Das Wiedehopfmännchen wartete mit einer Maulwurfsgrille am Boden. Als das Wiedehopfweibchen um 12:30 h erschien, übernahm es die Beute des Männchens und flog damit an die Nistkastenöffnung, wo ein junger Wendehals lauthals bettelte. Die Übergabe der Beute an das Junge verlief aber nicht reibungslos: Das Weibchen musste die Öffnung während einer Viertelstunde über zehnmal anfliegen, bis das Junge die Maulwurfsgrille endlich mit dem Schnabel ergreifen konnte. Im Nistkasten befanden sich bei der anschliessenden Kontrolle nur noch 6 Wendehalsjunge, eines war vermutlich schon ausgeflogen, ein weiteres der zuletzt 8 Jungen war tot. Die 6 verbliebenen Jungen hatten an Gewicht verloren und wogen nur noch zwischen 15.0 g und 21.5 g (Tab. 2). Als Notmassnahme wurden alle Jungen an diesem Tag von uns zweimal mit Ameisenpuppen und Ameisenlarven gefüttert (ca. 20 – 30 grosse Puppen und Larven pro Junges und Fütterung). Es wurde auch eine Videokamera installiert, welche am Nachmittag während 5 Stunden das Geschehen im Nistkasten filmte. Auf diesem Video war unter anderem sichtbar, wie ein Wendehalsjunges, welches bis zur Nistkastenöffnung hochfliegen konnte, nach langem Betteln mit einer Maulwurfsgrille im Schnabel in den Kasten zurückfiel und die grosse Beute verschlang. Auch an diesem Tag konnten keine Anflüge der Wendehälse mehr beobachtet werden.

Am 20. Juni beobachteten wir von 8:00 h bis 8:19 h. Ein Wiedehopf erschien ohne Futter, schritt am Boden vor dem Nistkasten umher und verschwand nach 5 Minuten wieder. Es befanden sich jetzt noch 5 Junge im Nistkasten. Ein weiteres Junges wurde an diesem Abend laut bettelnd auf dem Dach der Hütte gesehen. Die verbliebenen Jungen verloren weiter an Gewicht und wogen nur noch zwischen 14.5 g und 21.5 g (Tab. 2). Unsere Ameisenfütterungen schienen sich nicht zu lohnen und wurden nicht mehr wiederholt. Verglichen mit einem normal entwickelten Nestling, wiesen unsere Nestlinge kärglich ausgebildete Federn auf (Abb. 1, 2) und einige konnten ihre Beine nicht gut bewegen, so dass sie sich nicht in normaler Sitzposition halten konnten.

Am 21. Juni wurden zwei Junge laut bettelnd ausserhalb des Nistkastens gesehen. 4 Junge befanden sich tot im Nistkasten. Daher is offenbar auch ein dritter Jungvogel ausgeflogen. Normalerweise werden Wendehalsflügglinge von ihren Eltern einige Tage geführt, bis sie selbstständig sind und sich die Familie nach 10 bis 14 Tagen auflöst (Menzel 1968). Ob die drei flüggen Wendehälse durch die Wiedehopfe oder die Wendehälse noch geführt wurden, blieb unbekannt. Von den neun geschlüpften Wendehälsen starb somit ein

Junges kurz nach dem Schlupf, fünf Junge starben kurz vor dem Flüggewerden und drei Junge flogen aus.

6.4 Diskussion

Bis zum Alter von 8 Tagen wurden die Wendehalsnestlinge vermutlich nur von ihren eigenen Eltern und mit dem für Wendehälse typischen Futter (Ameisenlarven und -puppen) aufgezogen. Danach wurde erstmals ein Wiedehopf am Kasten beobachtet. Im Alter von 13 Tagen wurden die jungen Wendehälse auch mit Maulwurfsgrillen gefüttert, vermutlich aber schon früher. Mit 16 und 17 Tagen wurden sie sowohl vom Wendehals mit Ameisen als auch vom Wiedehopf mit Maulwurfsgrillen und Raupen gefüttert. Ab dem 20. Lebenstag wurde nur noch das Wiedehopfpaar mit abnehmender Fütterungsintensität beobachtet. Im Nistkasten fanden wir mehrmals tote Maulwurfsgrillen und etwa 3 cm grosse Raupen, welche eventuell aufgrund ihrer Grösse oder ungeschickter Nahrungsübergabe nicht verschlungen werden konnten. Die körperliche Entwicklung dieser Wendehalsnestlinge war wesentlich schlechter als die Entwicklung von Wendehalsnestlingen, die nur von ihren eigenen Eltern aufgezogen werden. Dies wurde insbesondere bei der Länge der 8. Handschwinge deutlich, welche im Alter von 8 bis 20 Tagen stark wachsen (Geiser et al. 2008). Weniger ausgeprägt war die defizitäre Entwicklung bei den Tarsi, deren Wachstum im Alter von etwa 12 Tagen abgeschlossen ist (Geiser et al. 2008). Dies deutet darauf hin, dass die Entwicklung der Brut zu Beginn normal verlief und die Nestlinge nur durch die Wendehälse aufgezogen wurden. Das Gewicht aller Nestlinge nahm ab dem 17. Alterstag ab – diejenigen drei Nestlinge, die dann am schwersten waren, flogen schliesslich aus. Die mangelhalfte Entwicklung kann zwei Gründe haben: Erstens ist es möglich, dass die Wendehalsnestlinge spezifisch auf die proteinreiche Ameisenbrut angewiesen sind. Wendehälse können von Hand nur mit einem grossen Anteil an Ameisenbrut erfolgreich aufgezogen werden (Heinroth & Heinroth 1926). Zweitens könnten die Jungen verhungert sein, weil sie schlicht zu wenig gefüttert wurden. Die beiden Elternpaare schienen sich gegenseitig zu stören, denn die Wendehälse flogen wiederholt mit dem Futter im Schnabel weg oder frassen es selbst. Zudem waren einige Beutestücke der Wiedehopfe zu gross für die Wendehalsnestlinge.

Erstaunlicherweise zeigten die adulten Wendehälse gegenüber den Wiedehopfen kaum Aggressivität. Wir konnten lediglich beobachten, wie sich die Wendehälse den Wiedehopfen näherten, worauf sie zurückwichen. Auch warnten die Wendehälse nie, wenn sich die Wiedehopfe in der Nähe befanden oder gar in den Nistkasten schlüpften, wie sie es sonst bei möglicher Gefahr tun. Möglicherweise zeigten die Wendehälse zu Beginn der Brutübernahme aggressiveres Verhalten und hatten zum Zeitpunkt unserer Beobachtungen aufgegeben.

Dass Wiedehopf und Wendehals so nahe beieinander brüten, ist nichts Aussergwöhnliches, denn im Studiengebiet brüteten die beiden Arten zwischen 2002 und 2007 23-Mal so nahe zusammen wie im beschriebenen Fall (2 m Distanz). Bisher wurde nie eine Brutübernahme festgestellt. In elf von diesen 23 Fällen wurde die Wendehalsbrut vor oder nach dem Schlupf aufgegeben (= 47.8%), Wiedehopfbruten wurden in fünf Fällen aufgegeben. Diese Abbruchrate der Wendehalsbruten unterscheidet sich nicht signifikant vom langjährig beobachteten Mittel von Bruten ohne Wiedehopfe im benachbarten Nistkasten (42.5%, $n = 346$; $\chi^2 = 0.08$, $p = 0.78$).

Evolutionär macht die Übernahme der artfremden Nestlinge keinen Sinn; auch kann bei zwei verschiedenen Arten die Funktion als Bruthelfer ausgeschlossen werden (z.B. Nicolai 2001). Shy (1982) beschreibt als eine der häufigsten Ursachen für zwischenartliche Fütterungen die Nähe zweier Bruten zueinander. Dies lässt vermuten, dass es sich beim beobachteten Wiedehopfpaar tatsächlich um das Brutpaar aus Kasten A handelt. Unter anderem nennt Shy (1982) auch (Bettel-)Rufe von Jungvögeln und den Verlust der eigenen Brut als mögliche Ursachen. In dem von uns beobachteten Fall waren also gleich mehrere potenzielle Auslöser vorhanden, welche die Chance erhöhten, dass das Wiedehopfpaar die artfremden Wendehalsnestlinge zu füttern begann. Zum Zeitpunkt, als aus dem Wiedehopf-Gelege die eigenen Jungen hätten schlüpfen sollen, waren aus dem Nistkasten nebenan die allerdings völlig unähnlichen Bettelrufe der Wendehälse zu hören und die Wiedehopfe begannen diese zu füttern. Die Unerfahrenheit des einjährigen Wendehalsweibchens in der Brutaufzucht könnte dieses Verhalten begünstigt haben. Auch Nicolai (2003) berichtet, dass das Füttern fremder Jungen meistens durch den „Verlust eigener Jungvögel bei noch vorhandenem starken Fütterungstrieb und dem Vorhandensein bettelnder Jungvögel in der Nähe“ ausgelöst wird.

Letztlich war die Brutübernahme für beide Arten nachteilig, obwohl drei Jungvögel flügge wurden. Die Wiedehopfe verpassten die Chance, eine Ersatzbrut zu beginnen, und die Wendehälse hatten höchstwahrscheinlich keinen Bruterfolg, denn die drei unterernährten Nestlinge hatten nach dem Ausfliegen kaum Überlebenschancen.

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Tabelle 1 Zusammenfassende Übersicht der beiden Wendehals- und Wiedehopfbruten 2007. – *Overview of the Eurasian Wryneck and the Eurasian Hoopoe broods and adoption of the Wryneck nestlings by the Hoopoe parents in 2007*.

Datum	Alter Wendehalsnestlinge	Wiedehopfbrut (Kasten A)	Wendehalsbrut (Kasten B)
29. April		Legebeginn	
9. Mai			Legebeginn
17. Mai		Schlupf der 7 Eier ab hier bis Ende Mai erwartet	Gelege vollständig mit 9 Eiern, Brutbeginn
30. Mai	1 Tag		Schlupf von mindestens 2 Nestlingen
31. Mai	2 Tage		9 Nestlinge geschlüpft, 1 Nestling stirbt kurze Zeit später
6. Juni	8 Tage	7 Eier, unbebrütet	Erstmals Wiedehopf bei den 8 Nestlingen beobachtet
11. Juni	13 Tage	7 Eier, Brut verlassen	Wiedehopf bei den 8 Nestlingen
14. Juni	16 Tage	7 Eier, Brut verlassen	8 Nestlinge, Wendehals und Wiedehopf füttern
15. Juni	17 Tage		8 Nestlinge, Wendehals und Wiedehopf füttern
18. Juni	21 Tage		8 Nestlinge, Wiedehopf füttert, kein Wendehals beobachtet
19. Juni	22 Tage		Wiedehopf füttert 6 Nestlinge, 1 Nestling ist tot, 1 Nestling ist wohl bereits ausgeflogen
20. Juni	23 Tage		5 Nestlinge, 1 weiteres Junges fliegt aus, Wiedehopf ohne Futter vor Nistkasten
21. Juni	24 Tage		4 Nestlinge tot, 1 weiteres Junges fliegt aus; 2 Junge sind laut bettelnd in der Nähe des Nistkastens

Tabelle 2 Körpermasse, Gewicht und Schicksal der 8 Wendehalsjungen im Alter von 17 Tagen (15. Juni), 21 Tagen (19. Juni) und 22 Tagen (20. Juni) sowie Vergleichswerte von normal entwickelten, 16 Tage alten Nestlingen (Geiser et al. 2008). Der 9. Nestling starb einige Tage nach dem Schlupf und konnte nicht vermessen werden – *Body measures, weight and destiny of the 8 Eurasian Wryneck nestlings at the age of 17 days (15th June), 21 days (19th June), and 22 days (20th June), respectively, and reference values of normally developed nestlings at the age of 16 days (Geiser et al. 2008). The ninth nestling died few days after hatching and no measurements could be taken*.

Ring nummer	17 Tage			21 Tage	22 Tage	Schicksal
	Tarsus (mm)	8. Handschwinge (mm)	Gewicht (g)	Gewicht (g)	Gewicht (g)	
Y31459	20.0	17.0	18.5	-	-	Tot am 19. Juni
Y31460	20.5	28.0	22.5	18.0	16.0	Tot am 21. Juni
Y31461	21.9	32.0	24.0	19.0	21.5	Ausgeflogen am 21. Juni
Y31462	20.8	26.0	25.0	17.0	15.0	Tot am 21. Juni
Y31463	21.1	25.0	23.0	17.0	15.0	Tot am 21. Juni
Y31464	21.7	30.0	27.0	-	-	Ausgeflogen am 19. Juni
Y31465	22.1	32.0	23.5	21.5	-	Ausgeflogen am 20. Juni
Y31466	21.0	18.0	20.0	15.0	14.5	Tot am 21. Juni
Mittelwert	21.1	26.0	22.9	17.9	16.4	-
Mittelwert (SE) normal entwickelter Nestlingen	23.1 (0.7)	39.3 (3.9)	27.9 (2.2)	-	-	-

Abbildung 1 Das kleinste Junge der Brut (Y31459) im Alter von 17 Tagen (15. Juni 2007). Die Federn sind kärglich ausgebildet. – *The smallest Eurasian Wryneck nestling of the brood (Y31459) at the age of 17 days (15th June 2007). The feathers are not well developed.*

Abbildung 2 Zum Vergleich ein normalentwickelter, 13 Tage alter Nestling. welcher von den eigenen Eltern mit Ameisen aufgezogen wurde. – *For comparison, a normally, 13 day old nestling, raised by its own parents with ants.*

7

Brood size variation in European Wrynecks *Jynx torquilla* between a German and a Swiss breeding population

Brood size variation in European Wrynecks *Jynx torquilla* between a German and a Swiss breeding population

(Variation der Gelegegröße des Wendehalses *Jynx torquilla* in Untersuchungsgebieten Deutschlands und der Schweiz)

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7.1 Zusammenfassung

Wir untersuchten die Gelegegrössen und der Anteil Zweitbruten von Wendehälsen in zwei Untersuchungsgebieten in Deutschland und der Schweiz. An beinahe 600 Bruten (306 im Halberstädter Raum und 265 im Wallis) konnten Daten zur Gelegegröße gewonnen werden, wobei nur Vollgelege in die Auswertung eingingen. Es handelt sich um 426 Erst-, 32 Ersatz- und 113 Zweitbruten. Die durchschnittliche Größe aller Gelege betrug im Halberstädter Raum 9.3 Eier (*n* = 306), im Wallis 9.0 (*n* = 265). Die durchschnittlichen Größen der Erstgelege von 9.87 Eiern (Halberstadt, *n* = 212) bzw. 9.23 (Wallis, *n* = 214) sind untereinander signifikant verschieden, was ebenso innerhalb der Gebiete für den Vergleich zwischen Erst- und Zweitbruten gilt. In beiden Gebieten zeigt sich bei den Erstgelegen ein ausgeprägter Kalendereffekt. Die Größe der Zweitbruten weist hingegen zwischen beiden Gebieten keine Unterschiede auf. Bei einem jährlichen Vergleich der Größe der Erstgelege zeichnen sich lediglich geringe Schwankungen ab, die allein im Wallis Signifikanzniveau erreichen. In beiden Untersuchungsgebieten treten in jedem Jahr Zweitbruten auf. Ihr Anteil – gemessen an den Brutpaaren – schwankt zwischen den Jahren erheblich und erreicht durchschnittlich 32.1% in Halberstadt und 11.1% im Wallis. In einzelnen Jahren schreiten im Halberstädter Raum mehr als 50% der Brutpaare zu Zweitbruten.

Im Vergleich mit anderen Untersuchungen in Mitteleuropa erscheinen die Erstgelege in beiden Gebieten ungewöhnlich groß. Die Ursache hierfür könnte allerdings methodischer Natur sein, weil in den meisten Untersuchungen bei der Gelegegröße nicht zwischen Erst- und Zweitbruten differenziert wurde. Der gefundene Anteil an Zweitbruten und ihr alljährliches Auftreten stehen zumindest für den Halberstädter Raum mit seiner nördlichen Lage im Widerspruch zu den bisher in der Literatur zu findenden Angaben.

7.2 Einleitung

Zur Brutbiologie des Wendehalses *Jynx torquilla* existieren einige grundlegende Arbeiten (Bussmann 1941, Steinfatt 1941, Creutz 1964, Klaver 1964, Ruge 1971). Doch abgesehen von zwei skandinavischen Studien (Linkola 1978 und Ryttman 2003) berücksichtigten sie jeweils nur eine geringe Anzahl von Bruten, so dass wesentliche Parameter wie saisonale und jährliche Veränderungen der Gelegegrößen, ihre geografischen Verschiebungen sowie Anteil und Größe von Zweitbruten bislang nur unzureichend bekannt sind.

Der Wendehals nimmt seit Jahrzehnten in ganz West- und Mitteleuropa ab (Bauer et al. 2005, Burfield & Van Bommel 2004), im Zeitraum 1980 bis 2005 gehörte er gar zu den zehn Arten mit dem größten Bestandsrückgang in Europa (PECBMS 2007). Schutzbemühungen erscheinen daher unumgänglich, setzen aber vertiefte Kenntnisse über die Populationsbiologie voraus. Die Gelegegröße ist eine wichtige demographische Komponente über die man wenig weiß und die möglicherweise mit dem Bestandsrückgang zusammenhängen könnte (Bauer et al. 2005).

Mit der vorliegenden Arbeit sollen Ergebnisse paralleler Untersuchungen in Deutschland und der Schweiz vorgestellt werden. In beiden Gebieten wurde die Gelegegröße mehrerer hundert Bruten erfasst. Damit können erstmals anhand größerer Datenreihen die skizzierten Fragen untersucht werden. Der Vergleich beider Gebiete belegt dabei erhebliche Unterschiede innerhalb des mitteleuropäischen Raumes.

7.3 Untersuchungsgebiete

Die beiden Untersuchungsgebiete in Deutschland und der Schweiz haben eine Distanz von annähernd 700 km zueinander und unterscheiden sich erheblich in ihrer naturräumlichen Ausstattung.

a) Das Untersuchungsgebiet in Deutschland mit einer Gesamtgröße von 450 ha liegt im Harzkreis bei Halberstadt (Sachsen-Anhalt; 51.54 °N, 11.03 °E). Es besteht aus drei Teilgebieten: Flächen im NSG Harslebener Berge und Steinholz (100 ha, Abb. 1), in den Klusbergen (100 ha, Abb. 2) sowie im Bereich des Osthuys (250 ha). Der Abstand zwischen den beiden erstgenannten Teilgebieten beträgt 2 km, der Osthuy ist von ihnen 10 bis 12 km entfernt.

Klimatisch wird der Halberstädter Raum durch den Regenschatten des Harzes geprägt. Die Jahresniederschläge liegen unter 600 mm, die mittlere Jahrestemperatur beträgt auf den Höhenzügen um Halberstadt 8.0 °C, die mittlere Julitemperatur 18.0 °C.

Die weitgehend offenen Bereiche des Untersuchungsgebietes werden von verschiedenen Trocken- und Magerrasengesellschaften geprägt (Landesamt für

Umweltschutz Sachsen-Anhalt 1997, 2000). Größtenteils handelt es sich um bis zu Beginn der 1990er Jahre genutztes militärisches Übungsgelände, das nunmehr einer – in größeren Bereichen intensiven – Beweidung mit Schafen und Ziegen unterliegt, gelegentlich auch mechanisch entbuscht wird. Das Teilgebiet Osthuy zeigt insgesamt eine größere Vielfalt an Landschaftselementen mit nicht mehr genutzten Streuobstwiesen von bis zu 5 ha Größe, Flächen mit Niederwaldcharakter sowie stark eingeschnittenen Trockentälern. Die Flächen liegen auf Höhen zwischen 125 und 230 m ü.NN (Abb. 3 und 4).

Nistkästen werden seit 1999 in den offensten Bereichen mit wenigen einzelnen Bäumen, kleinen Baumgruppen oder Hecken angeboten. Naturhöhlen fehlen fast vollständig. An einigen Stellen grenzen die Teilflächen an geschlossene Waldbestände, in denen auch mit Naturhöhlen zu rechnen ist. Es handelt sich bei den Nistkästen um selbst gebaute Holznistkästen mit den Maßen 120x120x250 mm und Holzbetonhöhlen. Das Flugloch ist bei allen Typen 36 mm weit. Nach einem Anstieg der Nistkastenzahlen in den ersten Jahren schwankt deren Zahl seit 2004 um den Wert von 90. Sie werden auf den Flächen – soweit die Strukturen dies zulassen – möglichst regelmäßig in Abständen zwischen 50 und 200 m verteilt. In für den Wendehals besonders günstigen Bereichen ist die Dichte allerdings deutlich höher; hier kommt ein Nistkasten auf einen Hektar Fläche (Näheres bei Becker & Tolkmitt 2007).

b) Das Untersuchungsgebiet in der Schweiz mit einer Gesamtgröße von 62 km^2 liegt in der Rhôneebene zwischen Martigny und Sierre (Kanton Wallis; 46.2 °N, 7.4 °E; 482 m ü.M). Das Wallis ist ein inneralpines Trockental mit einer mittleren Julitemperatur von 19.1°C und einer Jahresniederschlagsmenge von 598 mm. Die Ebene wird intensiv landwirtschaftlich genutzt, wobei Niederstamm-Obstanlagen (Apfel, Birne, Aprikosen) der dominante Landschaftstyp sind (Abb. 5). Daneben kommen noch Reben vor, Wiesen und Weiden nehmen nur kleine Flächen ein. In diesem Gebiet sind etwa 700 Nistkästen meist in landwirtschaftlich genutzten, kleinen Hütten installiert worden. Diese Nistkästen sind zur Förderung des Wiedehopfs *Upupa epops* angebracht worden. Sie sind eigentlich zu gross für den Wendehals (250x250x300 mm, Fluglochdurchmesser 50 bis 60 mm), werden aber aus Mangel an Alternativen trotzdem von diesem genutzt.

7.4 Methode

In beiden Gebieten wurden die Daten ausschließlich an Bruten in Kunsthöhlen gewonnen. Natürliche Bruthöhlen stellen wegen der Offenheit der Landschaften (Harz) und wegen der intensiven landwirtschaftlichen Nutzung (Wallis) einen limitierenden Faktor für das Vorkommen des Wendehalses dar. Die Ausbringung von Nistkästen hat deshalb zu einer erheblichen Steigerung der Abundanz der Art geführt, in Teilflächen überhaupt zu einer erstmaligen Besiedlung.

Das Untersuchungsgebiet im Harzvorland wurde ab 1999 jährlich bearbeitet, dasjenige im Wallis ab dem Jahr 2002. In beiden Gebieten wurden alle Brutversuche in den Nistkästen erfasst. Der Kontrollrhythmus lag über die gesamte Brutzeit bis Anfang August bei wöchentlichen oder zumindest vierzehntägigen Besuchen. Die Altvögel wurden dabei ab Mitte Mai in den Nistkästen gefangen, kontrolliert und beringt. Soweit möglich wurde zwischen Erst-, Ersatz- und Zweitbruten unterschieden. Ersatzbruten, also Brutversuche von Vögeln, die in derselben Saison bereits an einem erfolglosen Brutversuch beteiligt waren, ließen sich einmal durch die Kontrolle beringter Vögel nachweisen. Daneben wurde von einer Ersatzbrut aber auch dann ausgegangen, wenn innerhalb einer Woche nach Verlust der Brut im selben Nistkasten ein neues Gelege begonnen wurde.

Zweitbruten, also Brutversuche an denen mindestens ein Altvogel beteiligt ist, der zuvor in derselben Saison bereits sozialer Elternteil einer erfolgreichen Brut war, konnten methodisch ebenfalls anhand zweier alternativer Merkmale bestimmt werden. Die Kontrolle der beringten Altvögel vermag das Vorliegen einer Zweitbrut zweifelsfrei zu bestätigen. Daneben galten aber auch alle nach dem 15. Juni begonnenen Gelege als Zweitbruten, es sei denn, die Kontrolle der beringten Altvögel belegte eine Ersatzbrut (näher hierzu Tolkmitt & Becker 2006, Becker & Tolkmitt 2007).

Bei der Auswertung fanden nur Vollgelege Berücksichtigung. Im Harz galt als Vollgelege dabei ein von den Altvögeln kontinuierlich bebrütetes Gelege. Zwar beginnt die Bebrütung gelegentlich schon mehrere Tage vor Ablage des letzten Eies (Creutz 1964, Ruge 1971). Solche Fälle traten aber nach unseren Beobachtungen sehr selten auf, so dass bebrütete Gelege grundsätzlich mit Vollgelegen gleichgesetzt werden können. Wegen der Größe der Stichproben dürfte der hieraus resultierende Fehler jedenfalls zu vernachlässigen sein. Im Wallis wurden nur Gelege eingeschlossen, aus denen mindestens ein Jungvogel schlüpfte. Somit kann hier mit Sicherheit von Vollgelegen ausgegangen werden.

Die Auswertung der Daten erfolgte mittels des frei erhältlichen Statistikprogramms R (www.r-project.org).

7.5 Ergebnisse

Insgesamt stehen zur Auswertung Daten von 571 Vollgelegen zur Verfügung (306 aus dem Harzvorland; 265 aus dem Wallis). Dabei handelt es sich um 426 Erst-, 32 Ersatz- sowie 113 Zweitbruten.

Die Größen der Erstgelege wiesen eine beachtliche Spanne auf (2 bis 15 Eier, Abb. 6). Im Mittel waren die Gelege im Harzvorland signifikant größer als im Wallis ($t = 4.42$;

df = 423.99; p < 0.001; Tabelle 1). Zweitgelege waren in beiden Gebieten jeweils signifikant kleiner als die Erstgelege (Harzvorland: t = 9.13; df = 101.27; p < 0.001; Wallis: t = 5.68; df = 63.73; p < 0.001; Abb. 7), sie unterschieden sich aber zwischen den Gebieten nicht signifikant (t = -0.28; df = 103.76; p = 0.78). Die Größe der Ersatzgelege war in beiden Gebieten ebenfalls nicht unterschiedlich (t = -0.94; df = 8.52; p = 0.37). Ersatzgelege waren nicht signifikant größer als Zweitgelege (Harzvorland: t = -1.71, df = 42.20, p = 0.095; Wallis: t = -2.01, df = 7.04, p = 0.084), im Harzvorland aber signifikant kleiner als Erstgelege (t = 3.68, df = 29.04, p < 0.001), jedoch nicht im Wallis (t = -0.06, df = 5.25, p = 0.951).

Die durchschnittliche Größe aller Erstgelege einer Saison wies zwischen den Jahren eher geringe Schwankungen auf (Abb. 8), die im Wallis allerdings Signifikanzniveau erreichten (F = 2.90; df = 5, 208; p = 0.014), im Harzvorland hingegen nicht signifikant waren (F = 1.69; df = 8, 203; p = 0.10). Einen zeitlichen Gleichlauf der Schwankungen in den Gebieten gab es offensichtlich nicht.

Ein Kalendereffekt der Gelegegröße war in beiden Untersuchungsgebieten deutlich sichtbar; die Grösse der Erstgelege nahm im Laufe der Saison um durchschnittlich 0.44 (StdAbw.: 0.08) Eier pro 10 Tage ab (Abb. 9). Die saisonale Abnahme der Gelegegrösse war in beiden Untersuchungsgebieten gleich (F = 0.09, df = 1, 421, p = 0.77).

Der mittlere Anteil an Zweitbruten war im Harzvorland signifikant größer (32.1%, Std.Abw: 3.2%) als im Wallis (11.1%, StdAbw: 2.1%; $\chi^2 = 17.99$, $p < 0.001$). Zweitbruten traten in jedem Jahr auf, wenn auch mit erheblich schwankendem Anteil (Abb. 10). Die jährlichen Schwankungen des Anteils der Zweitbruten verliefen in den beiden Gebieten unterschiedlich.

7.6 Diskussion

7.6.1 Gelegegrößen

Vergleiche der Gelegegrößen des Wendehalses anhand des bislang publizierten Datenmaterials müssen erheblichen Vorbehalten begegnen. Denn bis auf eine Ausnahme (Ballestrazzi et al. 1998) wird nicht zwischen Erst- und Zweitbruten differenziert. Die durchschnittliche Größe aller Vollgelege gibt aber nur ein unzureichendes Bild der Brutbiologie wieder, wie die vorliegenden Ergebnisse recht eindrucksvoll zeigen. So reiht sich zwar die durchschnittliche Größe aller Gelege von 9.3 Eiern im Halberstädter Raum bzw. 9.0 im Wallis recht gut zwischen den Werten von 7.0 für die Toskana (Ballestrazzi et al. 1998), 8.6 bzw. 8.7 für die Oberlausitz (Creutz 1964, 1976; Menzel 1962), 8.9 für Niedersachsen und die Schweiz (Winkel 1992, Sutter 1962) und 10.2 für Finnland (Linkola 1978) ein. Eine getrennte Auswertung nach Erst- und Zweitgelegen zeigt allerdings ein etwas anderes Bild. Die durchschnittliche Größe der Erstgelege von 9.87 Eiern im Halberstädter Raum bzw. 9.23 Eiern im Wallis liegt deutlich oberhalb der für diese geografischen Räume bislang bekannten Werte.

Verschiedene Ansätze sind möglich, um diese Unterschiede zu erklären. Zunächst einmal liegt es nahe, dass sich in den publizierten Ergebnissen ein erheblicher, nicht entdeckter Zweitbrutanteil versteckt, der den errechneten Durchschnittswert verringert. Wir vermuten, dass dies der Hauptgrund für die beobachteten Unterschiede ist. Zudem könnten auch geographische Unterschiede der Anteile von Ersatzbruten eine Rolle spielen. Im Halberstädter Gebiet liegen die Gelegegrößen von Erst- und Ersatzbruten über alle Jahre immerhin um 0.8 Eier auseinander. Ausserdem lassen sich methodische Unterschiede bei der Ermittlung der Gelegegröße nicht ganz ausschließen. Leider fehlen in den publizierten Arbeiten hierzu meist konkrete Angaben. Werden auch (noch) nicht bebrütete Gelege als Vollgelege gewertet, könnten in der Legephase verlassene in die Auswertung eingeflossen sein, was zu einer Unterschätzung der durchschnittlichen Gelegegröße führt.

Der signifikante Unterschied in der Größe der Erstgelege zwischen beiden Untersuchungsgebieten deutet auf eine Zunahme der Gelegegröße mit der nördlichen Breite hin, wie sie für den Wendehals vermutet wird (Scherner 1994), für eine Reihe weiterer Vogelarten belegt ist (Michalek & Miettinen 2003, Schön 1994, Dwenger 1991, Löhrl 1991, Übersicht bei Klomp 1970). Die Gelegegröße im Halberstädter Raume kommt dabei dem Wert der finnischen Untersuchung (Linkola 1978) schon recht nahe, wo es Zweitbruten aufgrund der Kürze der Brutperiode nicht geben kann. Dass sich in Skandinavien kein weiterer – gemessen am Vergleich der beiden Untersuchungsgebiete – annähernd linearer Anstieg der Gelegegröße zeigt, mag seine Ursache in sonstigen Begrenzungen der Gelegegröße haben.

Beide Untersuchungsgebiete weisen besonders hohe Siedlungsdichten des Wendehalses auf (Übersichten bei Scherner 1994 und Poeplau 2005), denn es handelt sich offenbar um optimale Lebensräume, in denen Nahrungsdichte und -erreichbarkeit kaum limitierend wirken. Hieraus mag auch der Umstand resultieren, dass sich die durchschnittliche Größe der Erstgelege zwischen den Jahren kaum unterscheidet, allein im Walliser Gebiet erreichen die Schwankungen Signifikanzniveau. Die Bedingungen im Brutgebiet scheinen mithin relativ konstant zu sein. Da die Vögel nach ihrer Ankunft im Frühjahr noch etwa vier Wochen bis zum Legebeginn zuwarten, sind sie zudem wahrscheinlich in der Lage, zug- und überwinterungsortsbedingte Konditionsdefizite vor Legebeginn weitgehend auszugleichen. Die Gelegegröße mag deshalb maßgeblich durch die Bedingungen am Brutplatz gesteuert sein, die eben sehr gut und konstant sind. In der Legephase dürfte auch die aktuelle Witterung – im Unterschied zur Nestlingszeit (Geiser et al. 2008) – eine eher unbedeutende Rolle spielen, so dass im Wesentlichen die Erreichbarkeit der Ameisen die Gelegegröße beeinflusst (Freitag 1996, 1998).

Den hoch signifikanten Unterschied in der durchschnittlichen Größe zwischen Erst- und Zweitgelegen, der sich im Halberstädter Raum wie auch im Wallis zeigt, wird man im Wesentlichen als endogen gesteuerten Kalendereffekt betrachten müssen, wie er auch schon innerhalb der Erstbruten zu beobachten ist. Auf die Brutvögel wirken erhebliche zeitliche Zwänge, weil Zweitbruten nicht selten erst Ende Juli oder Anfang August ausfliegen. Ein kleineres Gelege schafft dann zumindest gewisse zeitliche Einsparungen in der Legephase. Ganz ähnliche Ergebnisse hinsichtlich des Größenverhältnisses zwischen Erst- und Zweitgelegen zeigen sich im Übrigen in der Toskana, wo die Erstgelege im Durchschnitt aus 7.38 Eier bestehen und Neunergelege dominieren, die Zweitgelege hingegen nur aus 5.85 Eier, wobei Sechsergelege am häufigsten sind (Ballestrazzi 1998).

7.6.2 Anteil Zweitbrüter

In beiden Untersuchungsgebieten machte ein recht großer Anteil der Wendehälse eine Zweitbrut. Zweitbruten traten in allen Jahren auf, wenn auch mit stark schwankender Frequenz. Zur Häufigkeit von Zweitbruten im mitteleuropäischen Raum lagen bisher keine verlässliche Daten vor. Menzel (1968) erwähnt in seiner Monografie einzelne Fälle, was den Eindruck großer Seltenheit erwecken musste. Zweifel hieran äußerten allerdings schon Bussmann (1941) und Ruge (1971). Erst Creutz (1976) befasste sich eingehend mit dem Auftreten von Zweitbruten. Anhand einer kleinen Stichprobe (*n* = 39 Bruten) schätzte er ihren Anteil auf 20 %, schloss aber ein jährliches Auftreten aus. Diese einzig verfügbare quantitative Angabe fand schließlich im Handbuch Aufnahme (Scherner 1994), das als Voraussetzung für das Auftreten von Zweitbruten ein zeitiges Einsetzen der Erstbruten und günstige Witterung postuliert.

Etwas klarer erscheinen die Verhältnisse außerhalb Mitteleuropas. Mit den Ergebnissen Linkolas (1978) etwa kann kein Zweifel daran bestehen, dass in Finnland Zweitbruten nicht auftreten. Die Schlüpfzeitpunkte der Jungvögel liegen über alle Jahre zwischen den Extremwerten 7. Juni und 8. Juli, also eine Spanne von gerade einmal einem Monat, die für aufeinander folgende Bruten zu kurz ist. Für Schweden schließt Ryttman (2003) in seiner Untersuchung Zweitbruten ebenfalls aus, was im Übrigen für ganz Skandinavien gelten dürfte. Anders stellen sich die Verhältnisse hingegen im südlichen Europa dar. In einem Untersuchungsgebiet der Toskana ließen sich neben 40 Erst- immerhin 15 Zweitbruten beobachten, was einer Quote von 37.5% entspricht (Ballestrazzi et al. 1998). Auch in Spanien scheinen Zweitbruten nicht allzu selten zu sein. Jedenfalls werten González et al. (2002) in ihrer Arbeit neben acht Erst- auch vier Zweitbruten aus, ohne auf das Phänomen der Zweitbruten näher einzugehen.

Diese Ergebnisse deuten zunächst auf ein bekanntes Muster hin: Es scheint sich ein von Süden nach Norden verlaufender Gradient der Zweitbrutanteile abzuzeichnen. Ein vergleichbares Bild bietet sich bei einer Reihe von Vogelarten, insbesondere bei Wärme liebenden (für Wiedehopf Glutz von Blotzheim 1994) und solchen, die auf die Insektenjagd in der Luft angewiesen sind (für Rauchschwalbe Turner 2006).

Die hier vorgestellten Daten passen allerdings nicht ohne weiteres in diesen Kontext. So liegt der Zweitbrutanteil im Wallis signifikant niedriger als im Halberstädter Raum, und Literaturangaben machen ein wesentlich komplexeres Bild des Auftretens von Zweitbruten wahrscheinlich. So gibt es in Russland anscheinend so gut wie gar keine Zweitbruten, jedenfalls wird im Werk von Il'Icev & Flint (2005) nur ein einziger Fall aus dem Jahr 1976 erwähnt. Behält man die enorme Ausdehnung des russischen Verbreitungsgebietes der Art zwischen 45. und 69. Grad nördlicher Breite im Auge, ist das Fehlen von Zweitbruten kaum mit geografischen Gegebenheiten zu erklären. Bei einer Gesamtschau der publizierten Untersuchungen wird man deshalb weniger einen Gradienten vermuten dürfen, als vielmehr einen Gürtel mit höchsten Zweitbrutanteilen, der sich durch die gemäßigten Zonen der Westpaläarktis zieht. Für diesen Befund könnte vor allem das Nahrungsangebot verantwortlich sein, das in bestimmten Gebieten im Laufe der Brutsaison unter einen kritischen Mindestwert sinkt. Ein ganz ähnliches Muster des Auftretens von Zweitbruten beim Wiedehopf wird ebenfalls mit dem Nahrungsangebot in Zusammenhang gebracht (Grüll et al. 2008). Die Phänologie von Wiesenameisen, der Hauptbeute des Wendehalses in Mitteleuropa (Scherner 1994) ist allerdings zu wenig bekannt, um derzeit abschließende Aussagen zu treffen.

Die Annahmen zum jährlichen Auftreten der Zweitbruten bedürfen mit den vorliegenden Ergebnissen ebenfalls einer Revision. Wurde bislang von einem unregelmäßigen Auftreten in einzelnen Jahren ausgegangen (Creutz 1976), scheint nunmehr doch Einiges für ein im mitteleuropäischen Maßstab allgemein gültiges Auftreten jährlicher Zweitbruten zu sprechen. Die starken jährlichen Schwankungen des Anteils an Zweitbruten lassen vermuten, dass er stark von wechselnden Umweltbedingungen (Nahrungsangebote, Wetter) abhängt. Da wir aber in jedem der Untersuchungsjahre Zweitbruten gefunden haben, müssen die Umweltbedingungen wohl extrem schlecht sein, bis in einem Jahr gar keine Zweitbruten mehr gemacht werden.

Bislang unbekannt war der hohe Anteil an Brutpaaren mit Zweitbruten, wie er sich im Halberstädter Gebiet zeigt. Er erreicht in etwa den Bereich kleinerer, Höhlen brütender Passeres wie Grauschnäpper oder Kohlmeise (Glutz von Blotzheim 1993, Schmidt & Zub 1993). In einzelnen Jahren schreiten mehr als 50% der Brutpaare zu Zweitbruten. Die

Zweitbrut kann damit für das nördliche Mitteleuropa nicht mehr als Ausnahmeerscheinung angesehen werden. Im Wallis treten zwar Zweitbruten ebenfalls in jedem Jahr auf, allerdings mit einem deutlich geringeren Anteil. Hier ist die Ameisenfauna extrem monoton mit einer Dominanz der Schwarzen Wegameise (*Lasius niger*) (Mermod et al. in prep.). Dies kann möglicherweise dazu führen, dass das Nahrungsangebot später in der Saison ungenügend wird.

Die Bestandsveränderungen von Wendehalspopulationen von einem Jahr zum nächsten sind wahrscheinlich zu einem nicht unbedeutenden Teil vom Bruterfolg im Vorjahr verursacht. Die entscheidende Grösse ist die Zahl der pro Weibchen in einem Jahr produzierter Jungvögel. Diese wiederum hängt stark vom Anteil der Zweitbruten ab. Dies hat zwei Konsequenzen. Erstens könnte die Populationsdynamik stark vom Anteil der Zweitbruten beeinflusst sein, und zweitens muss der Anteil der Zweitbruten bekannt sein, um die Populationsdynamik des Wendehalses zu verstehen. Nur durch intensive Studien, in denen ein hoher Anteil der Altvögel gefangen wird, kann mit Sicherheit bestimmt werden, wie groß der Anteil der Zweitbruten ist. Wir haben als zusätzliches Kriterium einen Stichtag verwendet (15. Juni), um zu entscheiden, ob eine Brut eine Erst- oder eine Zweitbrut ist. Dieser Ansatz ist sicher offen für Diskussionen, hat sich aber in unserer Erfahrung als nützlich erwiesen.

Beeindrucken muss schließlich das Investment jener Weibchen, die innerhalb einer Saison zwei Gelege zeitigen. Addiert man die durchschnittliche Größe der Erst- und Zweitgelege, ergeben sich 17 bis 18 Eier, einzelne Weibchen legen mehr als 20 Eier. Für Standvögel mag dies kein ungewöhnlicher Wert sein. Der Wendehals als Transsahara-Zieher übertrifft damit aber die Arten einer vergleichbaren Zugstrategie erheblich. Am ehesten reicht noch der Wiedehopf an diese Leistung heran, der bei Gelegegrößen von bis zu zehn Eiern ebenfalls in größeren Anteilen Zweitbruten versucht (Glutz von Blotzheim 1994). Welche Auswirkungen das Zeitigen zweier Gelege auf die Fitness der Weibchen hat, insbesondere deren Überlebenswahrscheinlichkeit verringert, bleibt derzeit offen. Da wegen der geringen Lebenserwartung des Wendehalses die Masse der Vögel aber ohnehin höchstens eine Brutsaison erlebt, dürfte die Strategie der Zweitbruten selbst bei einer hieraus resultierenden erhöhten Sterblichkeit der Altvögel erfolgreich sein. Interessant erscheint aber doch der Umstand, dass im Halberstädter Gebiet neben dem sehr hohen Zweitbrutanteil auch die Größe der Erstgelege fast den europäischen Spitzenwert erreicht. Weshalb die Brutvögel gerade hier einen derart hohen Aufwand betreiben und welche demografischen Auswirkungen er hat, bedarf ebenfalls weiterer Untersuchungen.

7.7 Literatur

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Tabelle 1 Beschreibende Statistik der Gelegegrössen von Wendehälsen im Harzvorland und im Wallis.

	Harz			Wallis		
	Mittelwert	Std.Abw	*n*	Mittelwert	Std.Abw	*n*
Erstgelege	9.87	1.50	212	9.23	1.51	214
Zweitgelege	7.74	1.73	68	7.82	1.51	45
Ersatzgelege	8.46	1.88	26	9.17	1.60	6
Total	9.28	1.83	306	8.99	1.59	265

Abbildung 1 Ausschnitt des NSG Harslebener Berge und Steinholz im Untersuchungsgebiet Halberstadt. (Foto D. Tolkmitt)

Abbildung 2 Blick auf Teile der Untersuchungsfläche Klusberge im Untersuchungsgebiet Halberstadt. (Foto D. Tolkmitt)

Abbildung 3 Blick auf offene Bereiche des Teilgebietes Osthuy im Untersuchungsgebiet Halberstadt. (Foto D. Tolkmitt)

Abbildung 4 Typische Streuobstwiese am Osthuy im Untersuchungsgebiet Halberstadt. (Foto D. Tolkmitt)

Abbildung 5 Niederstamm-Obstanlagen prägen die Landschaft im Walliser Untersuchungsgebiet. (Foto S. Ehrenbold)

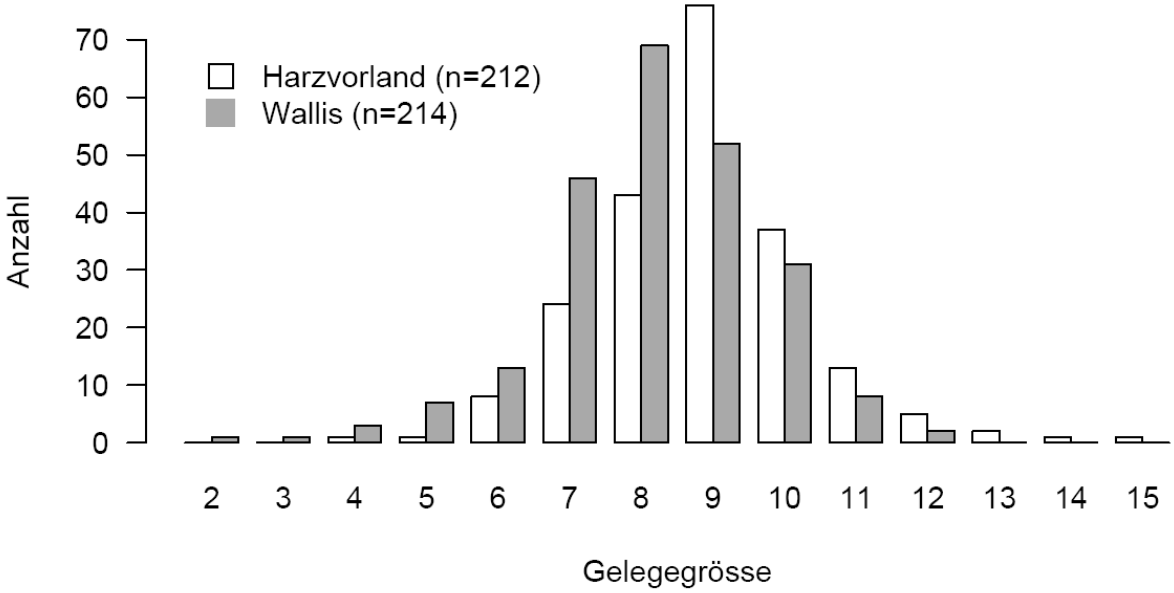

Abbildung 6 Häufigkeitsverteilung der Erstgelege von Wendehälsen aus dem Harzvorland und dem Wallis.

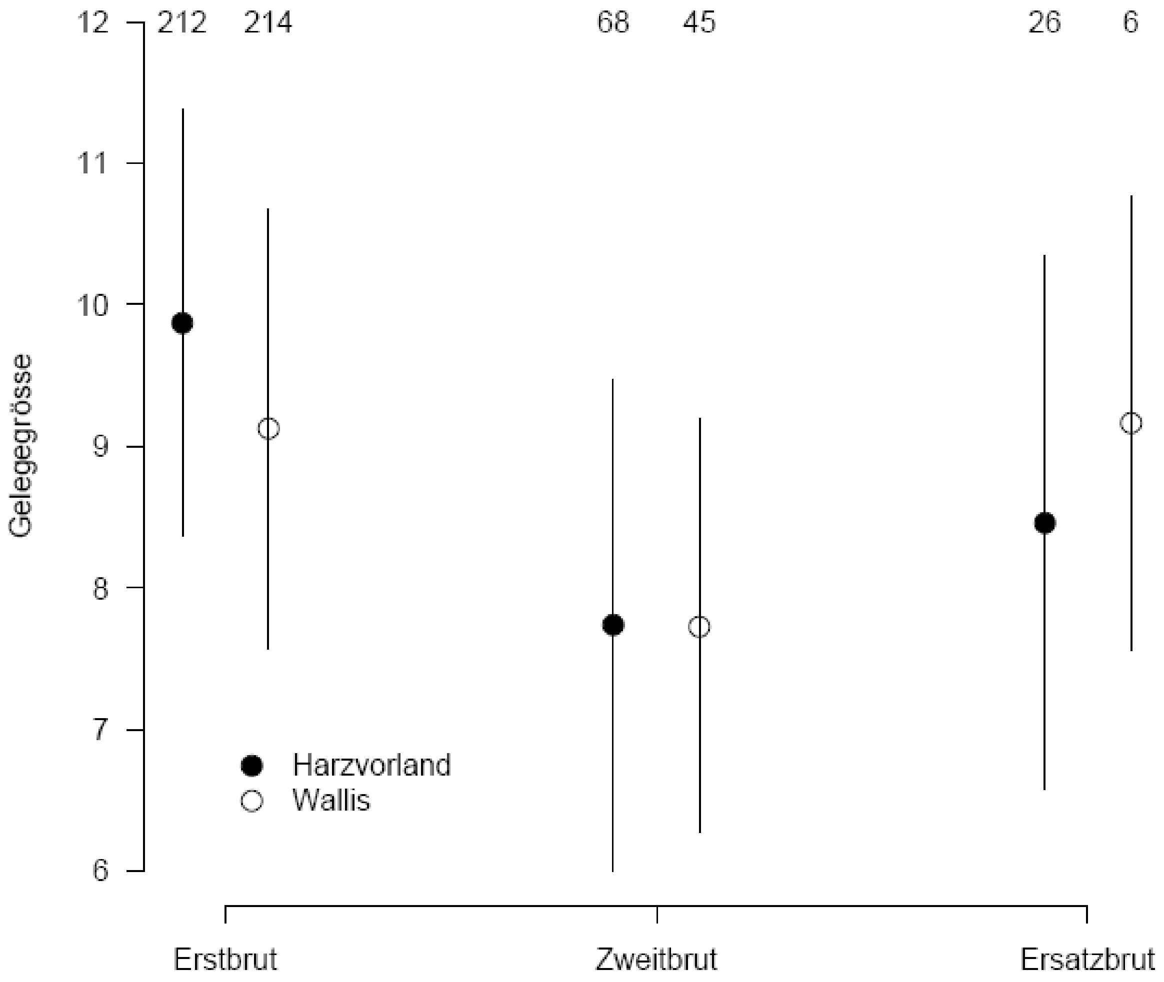

Abbildung 7 Mittlere Grösse mit 95% Vertrauensintervall für Erst-, Zweit- und Ersatzgelege von Wendehälsen im Harzvorland und im Wallis. Die obere Zahlenreihe gibt die jeweilige Stichprobengrösse an.

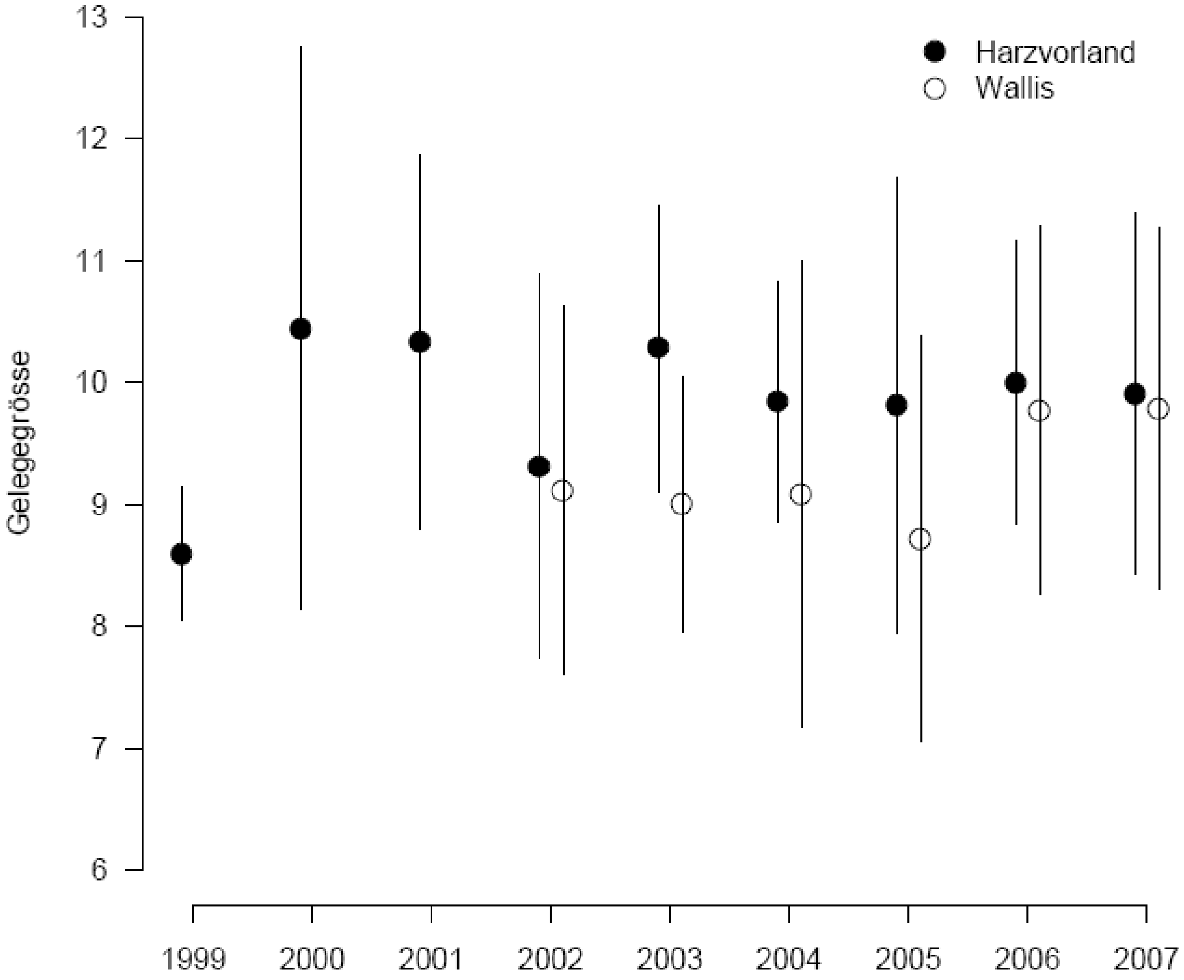

Abbildung 8 Durchschnittliche Größe aller Erstgelege mit 95% Vertrauensintervall für die Jahre 1999 bis 2007 in beiden Untersuchungsgebieten.

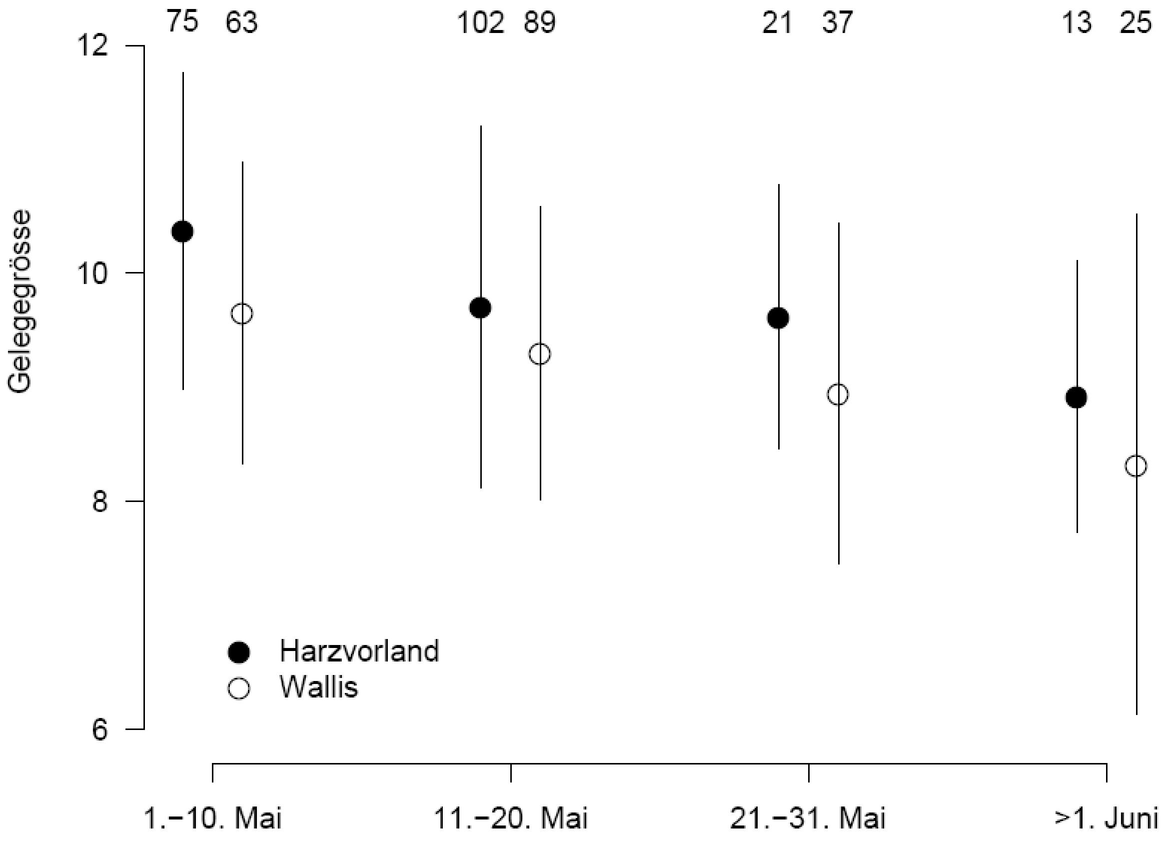

Abbildung 9 Entwicklung der Größe der Erstgelege innerhalb der Saison. Die obere Zahlenreihe gibt die jeweilige Stichprobengrösse an.

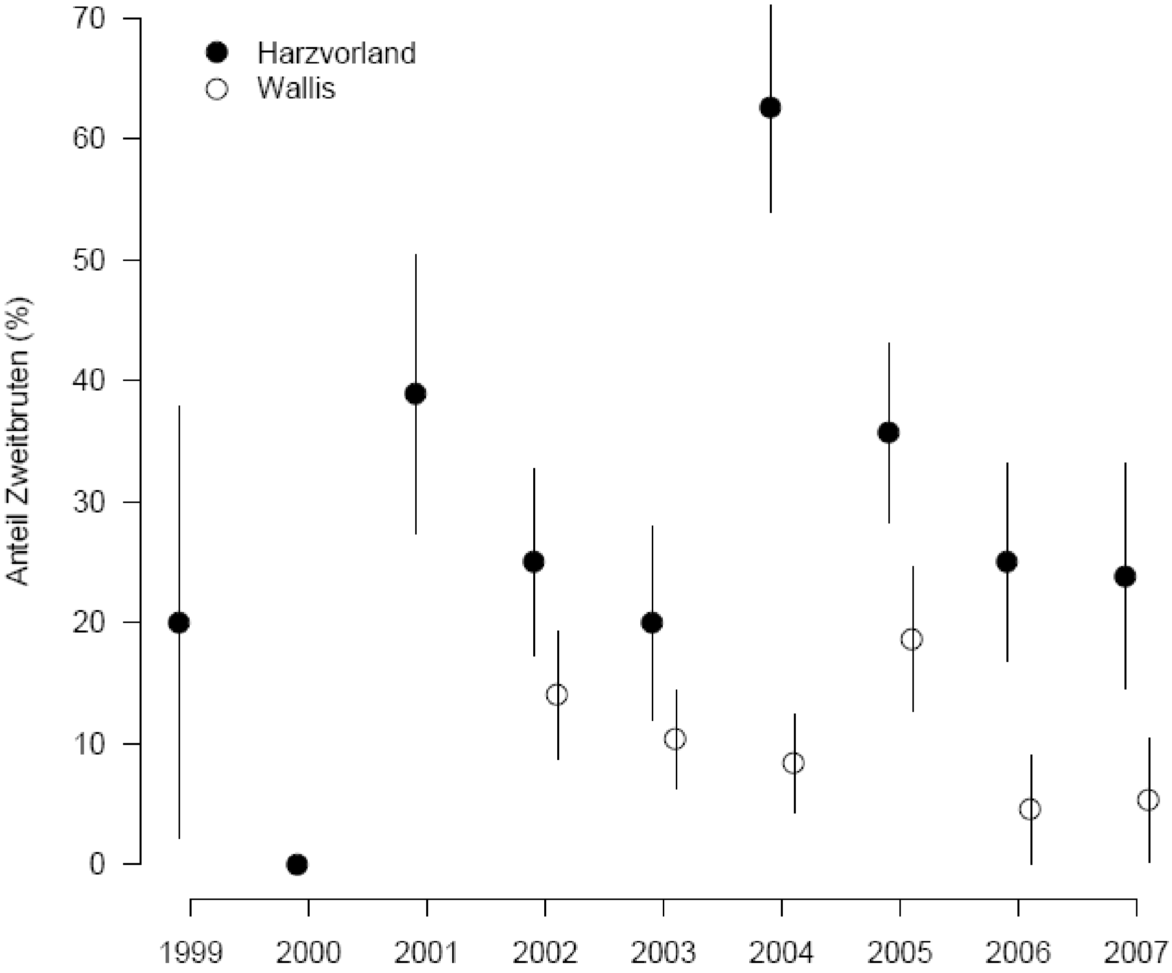

Abbildung 10 Jährlicher Anteil von Zweitbruten mit 95% Vertrauensintervall für die Jahre 1999 bis 2007 in beiden Untersuchungsgebieten.

8

Impact of weather variation and density-dependence on the trophic and reproductive ecology of a small, marginal Hoopoe population

Impact of weather variation and density-dependence on the trophic and reproductive ecology of a small, marginal Hoopoe population

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8.1 Abstract

1. Preserving marginal populations may become a key conservation issue given continuing habitat fragmentation. Often small and isolated, such populations are likely to have developed specific local adaptations that might enhance the overall ability of a species to cope with the new evolutionary challenges imposed by rapid environmental change. Preserving this evolutionary potential may become crucial as these populations are more vulnerable to stochastic events and therefore more prone to extinction.

2. We studied in the Swiss Alps a small, marginal population of the Hoopoe (*Upupa epops*), a declining migratory insectivorous farmland bird. We first investigated the effect of weather variation on food provisioning to chicks by Hoopoe parents. Second, while accounting for density-dependence we tested the extent to which breeding success is governed by weather circumstances and assessed the possible consequences on population growth.

3. Provisioning rate and provisioned prey biomass were negatively affected by adverse weather (cool, rainy days), were higher in males and also increased with brood size. Much smaller proportions of molecrickets (*Gryllotalpa gryllotalpa*, the most profitable prey locally, constituting 93% of chicks' food biomass), were provisioned on days with adverse weather conditions, irrespective of brood size.

4. Density affected both nestling survival (range: 72.2 – 86.6% according to year) and reproductive output (3.97 – 5.51 fledglings/brood*year). Rainfall prior to hatching and – to a lesser extent – during the first days of chicks' lives had a negative impact on their survival, and there was a positive effect of temperature on chick survival just before fledging. Reproductive output was negatively affected by precipitation during the hatching period, but was enhanced by warm temperature just before hatching and in the last days before fledging. The variable reproductive output can potentially have a strong impact on the population growth.

5. A succession of adverse, rainy springs – as foreseen for Central Europe by many future climatic scenarios – would impact negatively upon Hoopoe demography and thus population growth. This case study confirms that conservation efforts may be obliterated if risks linked to increasing climate variability are not properly accounted for in the management of small marginal populations.

Keywords: Bird conservation • Density-dependent regulation • Food provisioning • Insectivorous birds • Reproduction vs. climate variation • Species conservation • Trophic ecology

8.2 Introduction

Species conservation has long focused on habitat protection and restoration (Young 2000; Fazey et al. 2005). New globally emerging threats, such as climate change, may obliterate habitat management efforts, in particular when a species' demography is sensitive to environmental stochasticity (Sala et al. 2000; Parmesan & Yohe 2003; Thomas et al. 2004). Wide-scale range shifts of species have been predicted in the long term due to progressive changes in temperature and precipitation regimes (e.g. Huntley et al. 2008). Under a scenario of rising climate variability (Easterling et al. 2000), however, marginal populations (here defined as geographically peripheral or close to altitudinal range border) may sooner suffer from environmental stochasticity. This is because ecological conditions prevailing at distribution border are already naturally suboptimal (Lawton 1993; Jacquemyn et al. 2007). In addition, marginal populations are often small and isolated, which theoretically renders them more susceptible to gradual environmental change, demographic stochasticity and catastrophic events (Caughley 1994; Nathan et al. 1996; Nantel & Gagnon 1999; Inchausti & Halley 2003; Antonovics et al. 2006). The contention that marginal populations are more prone to extinction has, however, been refuted by some researchers (Lomolino & Channell 1995; Channell & Lomolino 2000). Irrespective of this, the strength of decline or the probability of extinction of the species as a whole could be further exacerbated by the loss of possible specific adaptations to local conditions (Brown 1984; Hoffmann & Blows 1994; Lesica & Allendorf 1995). Marginal populations could thus potentially buffer against loss of a species' overall evolutionary aptitude in the face of a rapidly changing environment (Lesica & Allendorf 1995; Reznick et al. 1997; Hendry & Kinnison 1999; Crandall et al. 2000). They should therefore be a primary focus of conservation biology (Lesica & Allendorf 1995).

One of the most important demographic parameters is recruitment (Sæther & Bakke 2000), which, all else being equal, depends primarily on the number of offspring produced (Crick, Gibbons & Magrath 1993; Newton 1998). This is especially true in short-lived species. In several such species, the number of offspring depends to a large extent upon seasonal weather circumstances during reproduction (e.g. Siikamäki 1996; Veistola, Lehikoinen & Eeva 1997; Newton 1998; Rodriguez & Bustamante 2003, Geiser et al. 2008). Weather often impacts food availability, but due to its strong stochasticity food availability remains mostly unpredictable for individuals engaging in reproduction (Cucco & Malacarne 1996a,b; Mills et al. 2008). Food availability depends firstly on fluctuations in prey populations (either seasonal or inter-annual), secondly on prey detectability (partly determined by the prey activity pattern), and thirdly on prey accessibility. Although the latter may be hampered by variations in foraging habitat structure (Schaub 1996), weather affects all three factors above. Species that feed on insects are primarily concerned since endothermic organisms reduce their overall activity in bad weather conditions, thereby becoming unavailable to predators (Taylor 1963; Avery & Krebs 1984; Cucco & Malacarne 1996a; Veistola et al. 1997). Birds that have population strongholds in lower latitudes would thus be more likely to suffer from weather and climate variation when occurring at range margins in cooler climates (e.g. in the North or close to their upper altitudinal limit), although this remains controversial (Sagarin & Gaines 2002). For ground-feeding insectivorous birds, very few studies have documented the impact of weather conditions on both food provisioning performance to chicks by parents and reproductive output (Radford et al. 2001, Geiser et al. 2008).

The Hoopoe (*Upupa epops,* Linnaeus 1758) is presently among the most endangered bird species in Central and Western Europe (Hustings 1997). It has been suggested that Hoopoes are particularly sensitive to climatic conditions, in particular precipitation during reproduction (Glutz von Blotzheim 1980; Cramp 1985; Rehsteiner 1996). This may explain why western European populations, where rainfall tends to be high due to exposure to depressions coming from the West, seem to fluctuate more than Mediterranean and eastern populations (Bussmann 1950; Cramp 1985; Rehsteiner 1996). Yet, the mechanism by which weather and climatic conditions affect population dynamics and determine long-term modification of distribution range in this species remains unknown (Laiolo, Bignal & Patterson 1998; Radford & Du Plessis 2003). This study aims to unravel that mechanism.

The Hoopoe is red-listed in Switzerland and is among the fifty bird species for which conservation action plans are currently under development (Keller et al. 2001). About 100 breeding pairs remain, mostly on the plain of the upper Rhône valley (Schmid et al. 1998), where a small population is monitored since 1979 (Arlettaz 1984, Arlettaz et al. 2000). The Valais Hoopoe population is marginal as the plain of the upper Rhône is flanked in the North and in the South by two major mountain ranges culminating at more than 4000 m. There is therefore not only a discontinuity to the next populations in Italy and France (situated hundreds of kilometres away in the South), but also a very continental climate with frequent cold spells during the breeding season due to the proximity of the mountains. As the Valais Hoopoes were continuously declining, a tailored conservation programme was launched in 1998 (Arlettaz et al. 2000), based on conservation recommendations drawn by Fournier & Arlettaz (2001). The implementation of these measures has led to a progressive recovery of the population, which, however, remains small (Arlettaz, Fournier & Zbinden 2000).

In this study, we first looked at the impact of weather variation on the efficacy of food provisioning to chicks by parents. Second, we attempted to test to which extent reproductive performance is affected by weather and/or density-dependent regulation; the latter had to be accounted for because our population has recently been expanding. We then assessed the potential impact of weather variation on the Hoopoe population dynamics. This information will be crucial not only for the long-term conservation management of the Valais Hoopoes, but also to predict species' response to future climate change and weather variation.

8.3 Material and Methods

The study was carried out in 2000–2006 on the plain of the Upper Rhône Valley (Central Valais, south-western Swiss Alps; 46°2' N, 07°4' E). The plain (460–520 m altitude) is primarily devoted to industrial farming, in particular dense dwarf fruit tree plantations, vegetables and vineyards. Our study population uses nestboxes almost exclusively as nest sites. Nestboxes (*n* ~ 700) were checked every second week during the breeding season, from mid April to late July. Those containing broods were additionally checked every second to third day for close tracking of the course of breeding.

8.3.1 Food provisioned to chicks

In 2001, 26 broods were filmed for three entire days each during the chick feeding period – which lasts 26–29 days in the Hoopoe (Cramp 1985) – in order to collect data on nestlings' diet and parents' foraging ecology. The first filming (brood stage I) took place when chicks were 11–15 days old, the second (brood stage II) when they were 16–20 days old and the third (brood stage III) at 21–25 days. We did not film at an earlier age because the mother covers the chicks until they start to thermoregulate by themselves and thus does not deliver food to the young. The video systems consisted of a camera with an automatic iris (Videotronic, CCD-7012P, Neumünster, Germany) coupled with a time-lapse video recorder (Sanyo, SRT 7168P, Osaka, Japan). The focus and sharpness of the images were controlled with a small portable monitor (Sony, GV-D800, Tokyo, Japan). A generator (Honda EU 10I, Tokyo, Japan) was used for power supply. Video-monitoring lasted from approximately 6:00 to 21:00. The chicks were counted at the beginning and at the end of a filming session. Adult Hoopoes were mist-netted and ring-marked at nesting sites when chicks were 5-10 days old. Sex-specific codes were drawn with markers on parents' head feathers; clearly visible on the video-tapes this marking enabled gender recognition so as to assess sex-specific provisioning activity.

For each feeding event, the following variables were noted from video sequences: time, sex of provisioning adult, prey type (we distinguished molecrickets *Gryllotalpa gryllotalpa* L., caterpillars, and other prey) and item size. Dry biomasses were estimated based on Arlettaz & Perrin (1995). For molecrickets we recognized three size classes, including larvae (2 sizes, with an estimated average biomass of 0.36 g and 0.46 g per item, respectively) and imago (0.68 g). Average dry weight of caterpillars and other prey were set to an average of 0.08 g

(Arlettaz & Perrin 1995). We calculated feeding frequency and estimated provisioned biomass per hour. Hoopoes are single prey loaders (they provision only one prey item at a time), which facilitated prey identification.

From a principal component analysis (PCA) run with four weather variables (sunshine duration per day, mean daily temperature, daily amount of rainfall, and mean daily relative humidity, all recorded in the core of the study area, at Sion meteorological station; 46.2°N, 7.4°E; on-line database MeteoSwiss) we obtained a proxy of daily weather conditions throughout the season (*n* = 50 days), which consisted of the first factor of the PCA (explaining 63% of the overall model variance). The first factor correlated positively with temperature (r = 0.60) and sunshine duration (r = 0.90) and negatively with rainfall (r = -0.70) and humidity (r = -0.93). Thus, positive values correspond to “nice” days (warm and dry), whilst negative values describe “bad” days (cool and rainy).

Using structurally equal statistical approaches with the same independent variables, we analysed feeding rate (number of parental food provisioning events per hour), biomass delivered to nestlings per hour and the proportion of molecrickets among all delivered food items by appyling linear mixed models (lmer, R Development Core Team 2006). Brood identity was considered a random factor. The fixed factors were sex, brood stage, brood size and weather. To test whether the potential impacts of sex and weather changed with brood stages, we also included the two-way interactions sex*brood stage and weather*brood stage. We fitted 24 candidate models (all possible combinations of fixed effects) and ranked them according to their support by the data with the Akaike Information criteria (AIC_c; Burnham & Anderson, 2002).

8.3.2 Reproductive success vs. weather variation and population density

Data on reproductive output (number of fledglings per brood) and nestling survival (percentage of hatched young that fledged) from 2000–2006 were used to test whether reproductive success for each single brood was related to variation in weather conditions (*n* = 514 broods). Only broods with at least one egg hatching were considered in the analysis. In the case of a rapidly increasing population, the impact of density-dependent regulation is more likely to operate towards the end of the time series, which should be discernible mostly as a decrease in the number of young fledged per brood and as an increase of nestling mortality over time. One would expect, however, a comparatively less pronounced directional chronological change in nestling survival as this parameter would be more responsive to environmental stochasticity (weather variation) and, as a corollary, more robust to potential density-dependent effects typical in fast recovering populations.

As weather variables we used daily mean ambient temperature and daily amount of rainfall, recorded by the meteorological station Sion. Rain (r) and temperature (t) values were averaged over five day periods (pentades, p), such that the hatching day for each single brood was the last day of pentade 0 (i.e. r_0 corresponds to the average rainfall of the pentade p_0 starting on the fourth day before hatching and ending with the day of hatching, being day 0). Average values were calculated for three consecutive pentades, starting on the first day after hatching and ending 15 days later (r_1 = average of days 1–5 after hatching, r_2 = average of days 6–10 after hatching, r_3 = average of day 11–15 after hatching; similar calculations were made for temperature, t_0 through to t_3).

We used an information-theoretic approach (Burnham & Anderson, 2002) for model ranking and to identify whether temperature and rain impact on breeding performance, and if so which pentade(s), in terms of temperature and rain, play(s) the most crucial role. We applied linear mixed effect modelling (lmer) implemented in the program R (R Development Core Team 2006). With an abbreviated model selection procedure (to reduce model complexity) and according to the $dAIC_c$, we defined the best model describing the influence of rain and temperature on the reproductive success of our local Hoopoe population (Fig. 1). Rain and temperature values, as well as breeding density (which increased over time) and hatching date were treated as fixed effects, whereas the location of the brood (nestbox site) was treated as a random effect in order to avoid pseudoreplication. Hatching date was only included in the models for reproductive output, but not for the survival of the hatchlings as we assumed that it is not influenced by the time of breeding. For the calculation of reproductive output the data was assumed to reflect a Poisson distribution, while for the nestling survival, the response variable was assumed binomial.

8.3.3 *Population growth*

To assess the importance of the impact of weather at the population level, we calculated the population growth rate (λ) using a simple population model. In this model we assumed adult survival (S_{ad}) to be 0.4, first year survival (S_1) to be 0.18 and the proportion of females conducting a second brood (p_2) to be 0.4. The values of S_{ad} and p_2 stem from our population (own unpublished results), S_1 was chosen in such a way that the population growth is ~1. We further assumed that the population is closed geographically. The growth rate of the population is then $\lambda = S_{ad} + S_1(1 + p_2)F/2$, where F is the reproductive output of a brood. We used the predictions of F for the various weather variables as obtained from the analyses above.

8.4 Results

8.4.1 Nestling diet

The video footage comprised 78 tapes (*n* = 26 broods, with 3 days of filming each; 1’172 h). In total, 5’454 prey items were recorded; they consisted of 59.3% molecrickets, 20.3% Lepidoptera larvae, and 4.9% other prey (Aranaeidea, Coleoptera, Formicidae, Diptera larvae – mostly Tipulidae); 15.5% items could not be identified (Fig. 2). From a dry biomass point of view (total biomass = 2’226.4 g), molecrickets were estimated to make up 93% of the overall diet, Lepidoptera larvae and unidentified prey 3% each, and other prey items about 1% (Fig. 2).

8.4.2 Food provisioning by parents

Variation in the hourly feeding rate (mean ± SE) could be explained by sex, weather and brood size (Table 1a), and there was some uncertainty regarding brood stage. Hourly feeding rates increased with brood size (by 0.32 ± 0.12 feedings/h per nestling) and with the weather factor (by 0.17 ± 0.09 feedings/h per score); it was also higher in males (2.69 ± 0.23) than in females (1.84 ± 0.20; Fig. 3).

The prey biomass delivered to chicks was affected by the same variables as feeding rate (Table 1b). It increased with brood size (by 0.21 ± 0.03 g/h per nestling) and favourable weather conditions (by 0.12 ± 0.04 g/h per score; Fig. 4). Males delivered, on average (± SE), more biomass per hour (1.23 ± 0.08 g) than females (0.68 ± 0.08 g; Fig. 3). Again there was some uncertainty regarding the brood stage (Table 1b). The interaction terms were not important, indicating that the relationships between delivered biomass and sex, and between biomass and weather remained the same irrespective of brood stage (Figs. 3 and 4).

The proportion of molecrickets among all delivered food items differed between sexes and brood stages (Table 1c). The proportion was affected also by weather and by brood size, as well as by the interaction of sex and brood stage (Table 1). Males delivered a higher proportion of molecrickets (0.90 ± 0.04 of the prey items per hour) than females (0.82 ± 0.06 of items/h; stage I). The proportion of molecrickets was highest at the first brood stage (0.90 ± 0.04) and decreased slightly thereafter (stage II: 0.85 ± 0.04; stage III: 0.84 ± 0.06; males, Fig. 3). Finally, the proportion of molecrickets in chicks' food increased when good weather conditions prevailed (slope on the logit scale: 0.21 ± 0.03) and with increasing brood size (slope on the logit scale: 0.29 ± 0.09).

8.4.3 Reproductive success vs. weather conditions

Mean annual reproductive output (2000-2006) varied between 3.97 and 5.51 fledglings per brood (overall mean ± SE: 4.71 ± 2.31), and mean nestling survival between 72.3% and 86.6% (79.3% ± 0.31; only broods with at least one hatchling were considered, *n* = 514). Concerning reproductive output, r_0 and r_1 (rainfall in pentades 0 and 1) and t_0 and t_3 (temperature in pentades 0 and 3) were included in the best model (Table 2). The number of fledglings was positively associated with temperature, while rainfall exerted a negative influence on this parameter. It was also negatively associated with breeding density and hatching date. Nestling survival was negatively affected by r_0 and r_1, whilst t_3 had a positive effect and t_2 a negative one (Table 3). The estimate for breeding density in the best model for nestling survival was highly positive.

8.4.4 Population growth

The predicted minimum and maximum values of the reproductive output for the weather variables t_0, t_3, r_0 and r_1 (Fig. 5) were used to calculate the potential population growth rate under this range of weather conditions. The ranges of the population growth rates were large (t_0: 0.89 – 1.02; t_3: 0.85 – 1.07; r_0: 1.01 – 0.79; r_1: 0.99 – 0.83) indicating that weather variation can potentially have a strong impact on Hoopoe population growth, even if only reproductive output is affected.

8.5 Discussion

This study supports the hypothesis that an important component of Hoopoe population dynamics is sensitive to weather variation. It further establishes the mechanism involved in the demographic process: cool, rainy days actually affect the efficiency of food provisioning by parents to chicks, which lowers reproductive success. One might argue that this is indeed not very surprising, knowing the mostly Mediterranean distribution of the species in Europe. Given a rapid generation turnover in this species (own unpublished data from mark-recapture), Hoopoe population dynamics appears to be driven principally by recruitment. A sustained drop in productivity, as could be experienced under a succession of rainy springs (a prediction of most climatic scenarios for the Alps; Easterling et al. 2000) can lead to population declines within short time.

Adverse weather conditions resulted in reduced feeding activity, i.e. a drop in the total biomass of provisioned prey caused primarily by a diminished proportion in the diet of the most profitable prey, molecrickets (Fournier & Arlettaz 2001). This indicates that molecrickets are more difficult to find when the weather conditions are bad. Adults then switch to other prey types such as caterpillars (Fournier & Arlettaz 2001), yet because these prey items are smaller, Hoopoes cannot fully compensate as they are single prey loaders. The low availability of molecrickets during bad weather must be due to reduced activity, detectability or accessibility at low temperature and during rainfall. It might well be that the terrestrial foraging habits of Hoopoes render them more susceptible to adverse weather than non-terrestrial insectivorous birds, which were the focus of the majority of previous studies on the impact of weather on reproduction in insectivorous birds (e.g. Cucco & Malacarne 1996b; Pellantova 1981; Veistola et al. 1997; Radford et al. 2001).

Feeding rate did not vary notably between the three chick stages, but there was some evidence that the biomass supplied decreased as chick age advanced. As we filmed nestlings only from age 11 days onwards, i.e. after 35-45% of the duration of chick stay at nest had elapsed, we have no quantitative data about the earlier feeding patterns. However, as the female covers the young until they thermoregulate by themselves (until about 8-10 days of age), our brood stage I actually corresponds to a burst of provisioning activity, which also matches the period when chick growth rate is maximum and (Fournier & Arlettaz 2001), incidentally, chick mortality highest (this study). A progressive decrease in food provisioning before asymptotic growth is common in birds (e.g. Turner 1983).

Male investment in food provisioning during chick rearing, counted as either number of prey items or biomass, was higher than that of female in all stages. Moreover, Hoopoe males have to feed their partner during incubation and then contribute to the entire prey supply during early chick stages when the female still broods. Males and females differ thus markedly in their parental tasks: incubation relies totally on the female, whereas chick rearing is primarily the male's responsibility. We predict that male provisioning efficiency correlates with territory quality (i.e. molecricket availability at the study site), the acquisition of which will depend on male hierarchical status (Martín-Vivaldi et al. 1999). The drop in feeding effort by females in later stages may also be due to the fact that a large proportion of them leave their brood before the young have fledged, in order to engage into a new breeding trial, often with a different male to the previous partner (own unpublished data).

Population density affected both nestling survival and productivity. The carrying capacity of the study population remains unknown, but its demographic recovery after the implementation of corrective conservation measures was rapid, resulting in approximately a five-fold increase in the number of breeding pairs within 10 years (Arlettaz et al. in prep.). This further supports the view of a very rapid generation turnover in this species. Actually, most other European populations have not shown a similar increase in the meantime, with the notable exception of a German population where similar conservation measures as in Valais have been implemented (Stange & Havelka 2003).

Our data on food provisioning by parents, combined with a modelling approach which allowed the effects of density regulation to be separated from weather factors, suggests that a reduced amount of delivered biomass (especially molecrickets) in bad years greatly affects productivity. Adverse weather around hatching time impacted upon both survival and productivity, whilst warm, sunny and dry weather before hatching and during the last nesting phases boosted productivity. The sensitivity of Hoopoes to limited food availability has been discussed by Martín-Vivaldi et al. (1999) in relation to the brood reduction hypothesis. These authors established that Hoopoes lay optimistic clutch sizes in order to raise as many chicks as possible. Parents appear not to feed smaller chicks as long as the larger ones are begging (Martín-Vivaldi et al. 1999), which biases mortality toward the youngest chicks. As less profitable prey is fed under unfavourable weather (this study), weather appears to be the ultimate factor responsible for a brood reduction strategy.

In general, population dynamics of short-lived species like that of Hoopoes is highly reactive to variations in factors regulating reproductive output (Sæther & Bakke 2000). Yearly adult survival is only around 40% (own unpublished data from capture-recapture modelling). Broods laid early in the season frequently produce 8-9 young in Valais, with the fittest adults even capable of undertaking three broods a year. Hoopoe demography therefore reacts extremely sensitively to environmental change in the breeding area. Thus, we believe that the fluctuations and patterns of range extension/retraction reported for western, central and northern European Hoopoe populations during the 20th century may actually have been caused by periodic climatic cycles, e.g. series of good or bad years in a row (Glutz von Blotzheim 1980; Cramp 1985; Rehsteiner 1996). This study also provides some support to the long-term predictive model of range shift by Huntley et al. (2008).

Any future Hoopoe conservation programme in western and central Europe should bear this weather issue in mind, especially in small populations. Of course, nestling survival and number of fledglings are two among several vital parameters potentially affected by weather variation. It is for instance likely that post-fledging survival is also affected by weather circumstances. Future population dynamics modelling based on extensive capture-recapture data may contribute to unravelling the relationship between post-nesting survival and weather conditions.

Sensitivity to weather variation, as illustrated here, could be a serious impediment to the protection of marginal, endangered animal populations (Lessica & Allendorf 1995). It might indeed annihilate costly local conservation efforts. One may expect this problem to become more acute in the face of continuing habitat fragmentation and climate change. The direction of these changes remains difficult to predict with accuracy, due for example to the subtle interplay between temperature and precipitation variation. Most current climate scenarios, however, foresee an augmentation of extreme weather events, i.e. greater variability of local climate can be anticipated (Easterling et al. 2000). This may only further exacerbate the impact of environmental stochasticity upon population demographic trajectories and even masks the long-term, gradual changes caused by global warming in terms of range shifts (Huntley et al. 2008). This problem should be accounted for in any species preservation scheme, especially of small, marginal populations.

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Table 1 Influence of sex, brood stage, brood size and weather, as well as interactions of brood stage with sex and weather, a) on feeding rate (n/h), b) biomass delivered per hour (g) and c) proportion of molecrickets in chicks' diet, evaluated by a model selection procedure (24 candidate models; see Fig. 1). Only results of the best models are presented in the tables. Given are the model selection criteria (ΔAIC_c: difference in the small sample size adjusted Akaike's Information Criterion between the best and the current model; AIC_c w: Akaikie weight; Deviance) and the effects.

a) Feeding rate

	Best model		2nd best model		3rd best model	
	Estimate	SE	Estimate	SE	Estimate	SE
Model selection criteria						
ΔAIC_c	0.00	-	1.18	-	2.87	-
AIC_c w	0.44	-	0.24	-	0.10	-
Deviance	599.59	-	602.95	-	598.03	-
Effects						
Intercept	1.219	0.607	1.252	0.598	1.289	0.672
Sex[1]	-0.875	0.261	-0.875	0.266	-0.875	0.261
Bd. stage II	-	-	-	-	0.246	0.324
Bd. stage III	-	-	-	-	-0.186	0.341
Weather	0.173	0.094	-	-	0.131	0.099
Brood size	0.317	0.118	0.310	0.116	0.295	0.119
Sex[1] * Bd. stage II	-	-	-	-	-	-
Sex[1] * Bd. stage III	-	-	-	-	-	-

b) Biomass delivered

	Best model		2nd best model		3rd best model	
	Estimate	SE	Estimate	SE	Estimate	SE
Model selection criteria						
ΔAIC_c	0.00	-	2.03	-	4.85	-
AIC_c w	0.66	-	0.24	-	0.06	-
Deviance	312.96	-	310.55	-	308.81	-
Effects						
Intercept	0.264	0.159	0.402	0.184	0.311	0.199
Sex[1]	-0.545	0.112	-0.545	0.111	-0.363	0.192
Bd. stage II	-	-	-0.108	0.137	-0.013	0.191
Bd. stage III	-	-	-0.219	0.140	-0.038	0.196
Weather	0.117	0.035	0.109	0.037	0.109	0.036
Brood size	0.208	0.030	0.202	0.030	0.202	0.030
Sex[1] * Bd. stage II	-	-	-	-	-0.190	0.268
Sex[1] * Bd. stage III	-	-	-	-	-0.362	0.274

c) Proportion of molecrickets in diet

	Best model		2nd best model		3rd best model	
	Estimate	SE	Estimate	SE	Estimate	SE
Model selection criteria						
ΔAIC_c	0.00	-	2.82	-	9.16	-
AIC_c w	0.79	-	0.19	-	0.01	-
Deviance	731.67	-	729.86	-	743.09	-
Effects						
Intercept	0.714	0.606	0.787	0.612	2.112	0.435
Sex[1]	-0.696	0.150	-0.693	0.151	-0.698	0.150
Bd. stage II	-0.451	0.135	-0.462	0.140	-0.491	0.134
Bd. stage III	-0.382	0.164	-0.441	0.171	-0.629	0.147
Weather	0.210	0.034	0.214	0.066	0.188	0.034
Brood size	0.289	0.085	0.274	0.086	-	-
Sex[1] * Bd. stage II	-0.068	0.195	-0.065	0.196	-0.081	0.195
Sex[1] * Bd. stage III	-1.217	0.227	-1.218	0.227	-1.133	0.225
Weather * Bd. stage II	-	-	0.056	0.092	-	-
Weather * Bd. stage III	-	-	-0.058	0.085	-	-

[1] estimate for females; Bd. stage = brood stage

Table 2 Best three models out of 103 candidate models for reproductive output. Given are the model selection criteria (ΔAIC_c: difference in the small sample size adjusted Akaike's Information Criterion between the best and the current model; AIC_c w: Akaikie weight; Deviance) and the effects. See Fig. 1 for further details on model selection and the methods for the meaning of the variables.

	Best model		2nd best model		3rd best model	
	Estimate	SE	Estimate	SE	Estimate	SE
Model selection criteria						
ΔAIC_c	0.00	-	0.33	-	0.99	-
AIC_c w	0.09	-	0.09	-	0.07	-
Deviance	700.56	-	702.95	-	699.48	-
Effects						
Intercept	3.163	0.263	2.936	0.217	3.004	0.257
t_0	0.048	0.031	-	-	-	-
t_1	-	-	-	-	0.053	0.032
t_2	-	-	-	-	-0.052	0.034
t_3	0.071	0.026	0.068	0.025	0.086	0.028
r_0	-0.079	0.022	-0.081	0.022	-0.070	0.023
r_1	-0.050	0.021	-0.048	0.021	-0.047	0.022
Breeding density	-3.244	3.406	-4.433	3.324	-3.736	3.356
Hatching date	-0.010	0.002	-0.008	0.001	-0.009	0.002

Table 3 Best three models out of 59 candidate models for nestling survival. Given are the model selection criteria (ΔAIC_c: difference in the small sample size adjusted Akaike's Information Criterion between the best and the current model; AIC_c w: Akaikie weight; Deviance) and the effects. See Fig. 1 for further details on model selection and the methods for the meaning of the variables.

	Best model		2nd best model		3rd best model	
	Estimate	SE	Estimate	SE	Estimate	SE
Model selection criteria						
ΔAIC_c	0.00	-	0.89	-	0.99	-
AIC_c w	0.23	-	0.15	-	0.14	-
Deviance	1388.09	-	1384.85	-	1387.02	-
Effects						
Intercept	1.350	0.311	1.408	0.312	1.362	0.311
t_2	-0.287	0.080	-0.261	0.077	-0.286	0.076
t_3	0.286	0.074	0.272	0.074	0.282	0.074
r_0	-0.276	0.053	-0.288	0.054	-0.279	0.054
r_1	-0.217	0.055	-0.224	0.055	-0.221	0.055
r_2	-	-	-0.071	0.059	-0.062	0.059
r_3	-	-	-0.084	0.056	-	-
Breeding density	11.774	9.201	9.919	9.245	11.484	9.206

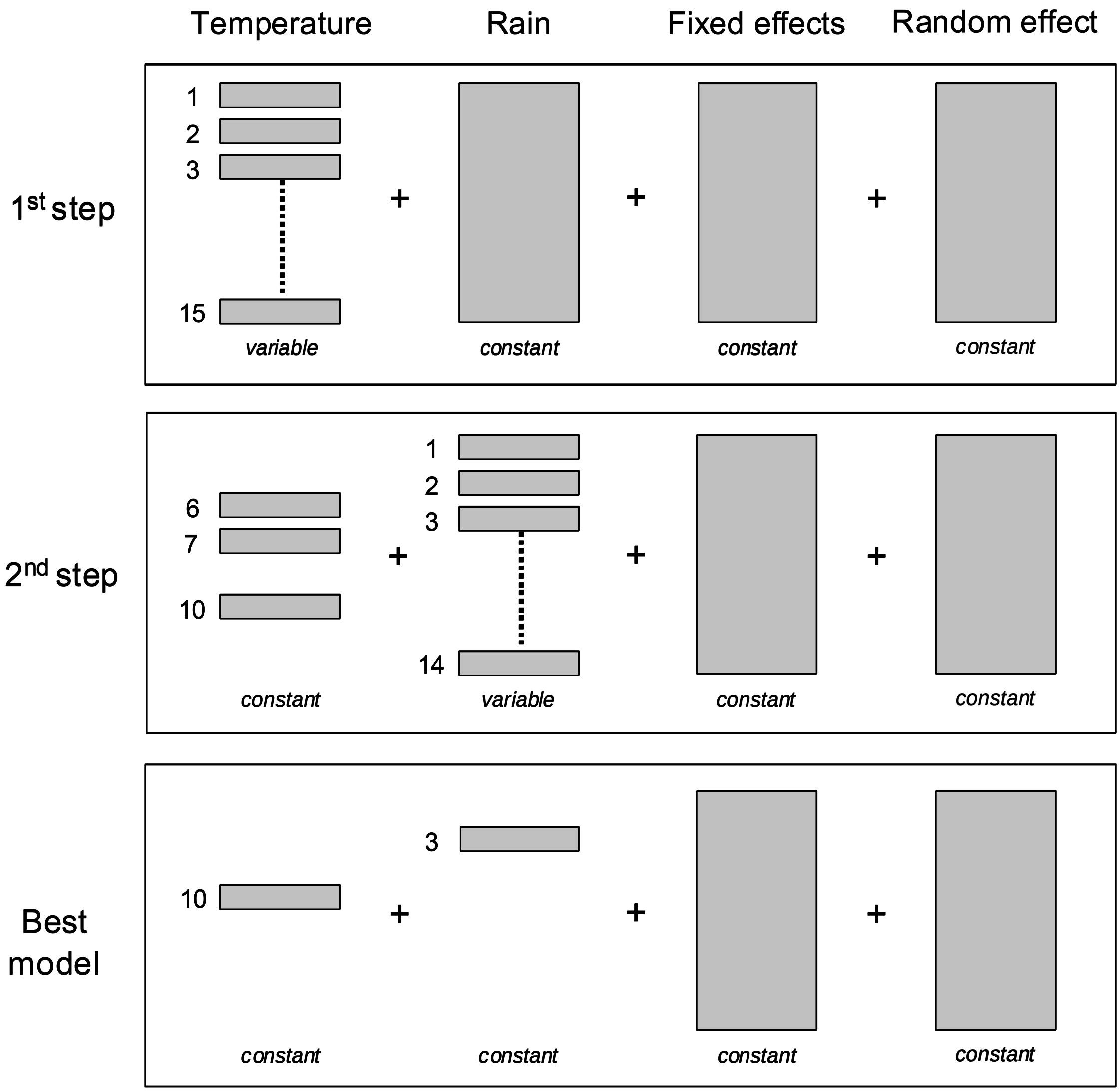

Figure 1 Overview of the abbreviated modelling procedure adopted here to reduce model complexity for the analysis of the relationships between reproductive success and environmental factors. First step: only the four temperature variables ($t_{0\text{-}3}$, see *Material and Methods* for nomenclature) were varied in all possible combinations (resulting in 15 different models), with rain put in the model as «full model» ($r_{0\text{-}3}$) and the other effects held constant (fixed effects: breeding density and hatching date [the later only in reproductive output modelling]; random effect: breeding site [nestbox]). Second step: Based on AIC_c (threshold for further selection $dAIC_c < 2$), the best models with varying temperature were chosen and held constant, whilst the rain parameters ($r_{0\text{-}3}$) were sequentially added to the best models from step one, also in all possible variations (14 different models per fixed temperature variable). Again, other effects were held constant. Third step: from this abbreviated model selection procedure followed the best models that described the influence of weather on reproductive success. It did not matter to the outcome for the best model whether to first vary the temperature parameters, or rain parameters.

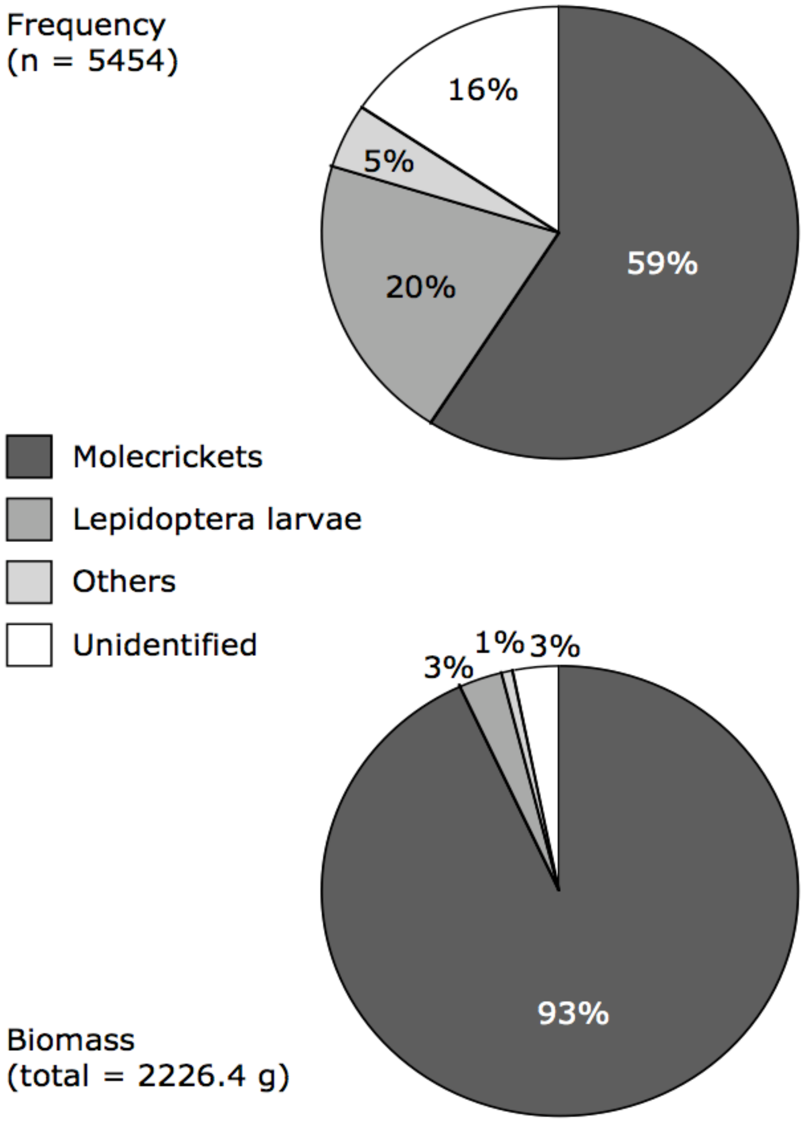

Figure 2 Frequency (*n*) and biomass (g) of prey categories entering the diet of Hoopoe chicks.

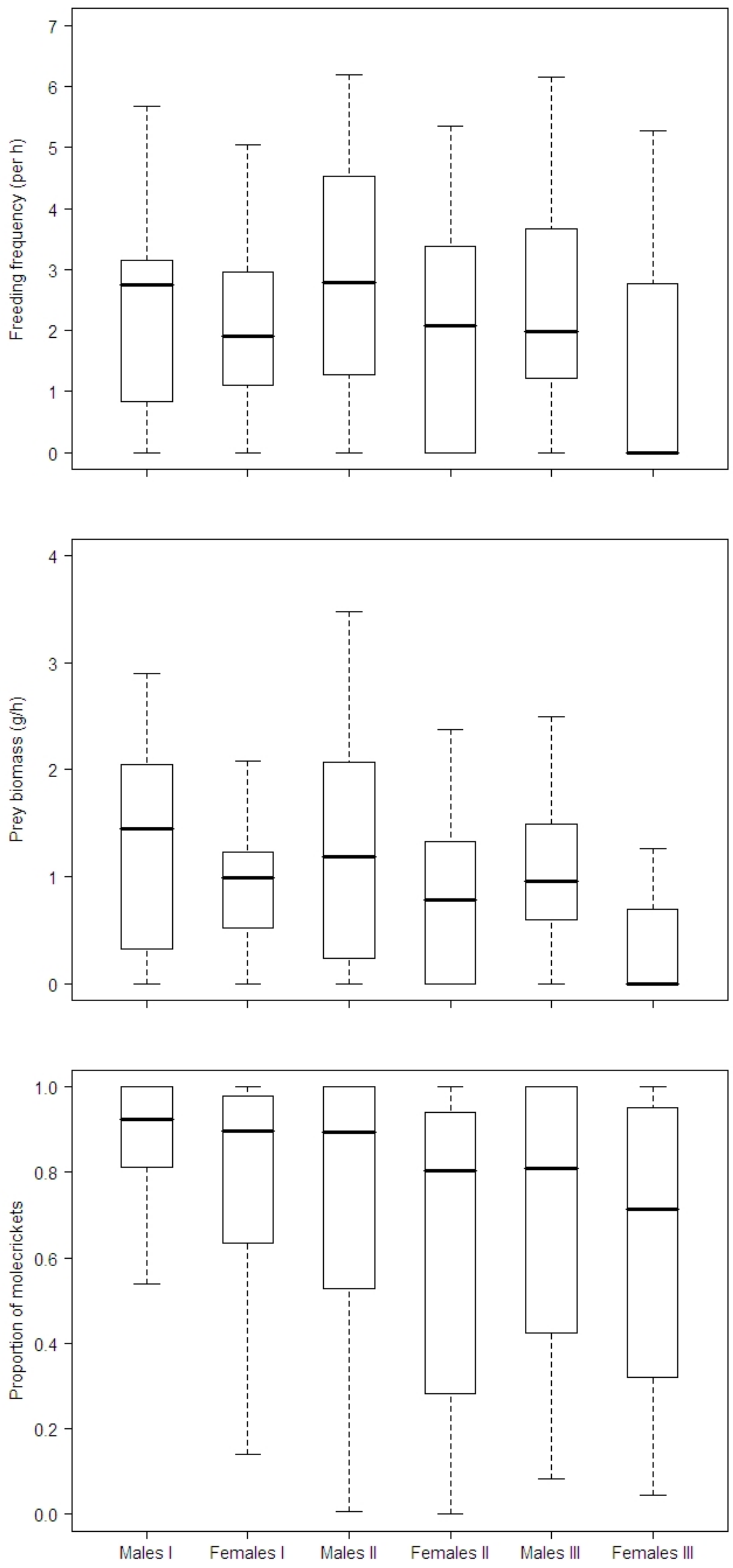

Figure 3 Box plot of feeding frequency (h-1), prey biomass (g) provisioned per hour and proportion of molecrickets derived at 26 Hoopoe breeding sites with respect to chick stage (I-III) and sex of parents.

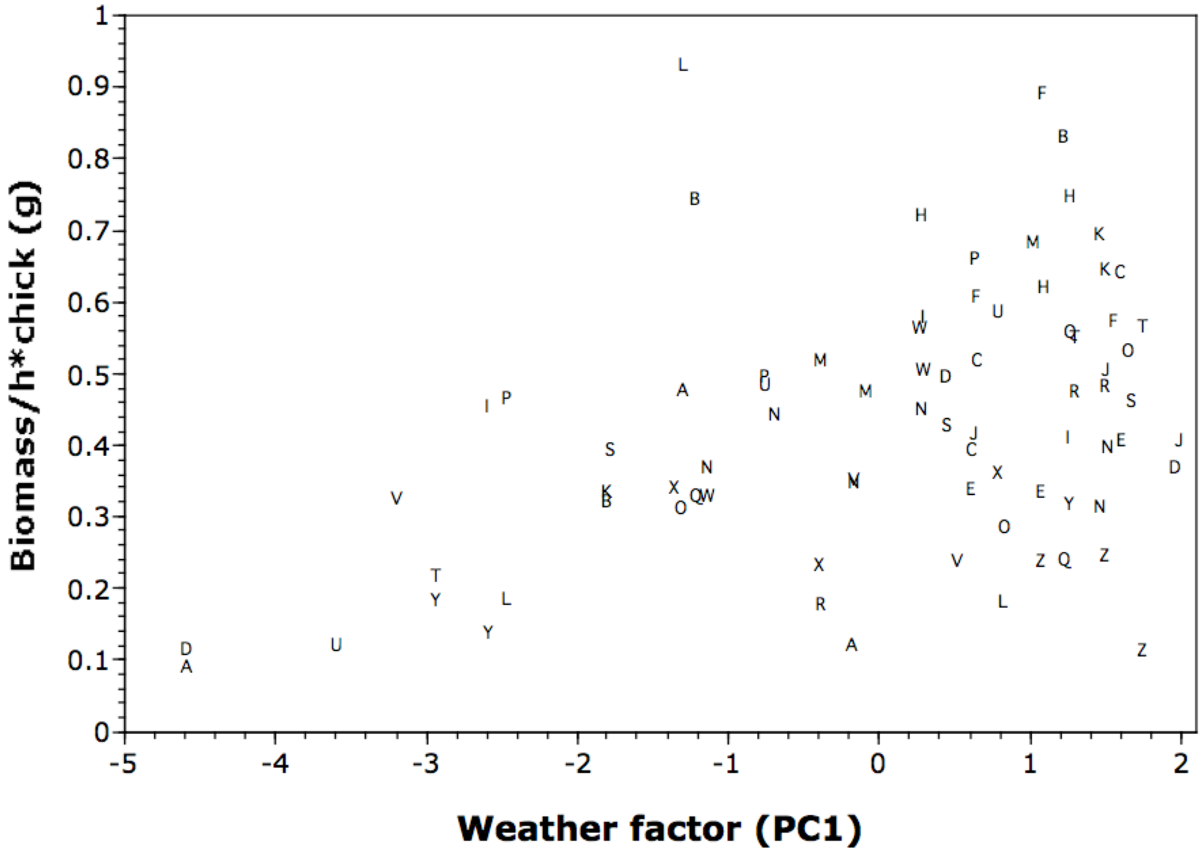

Figure 4 Mean prey biomass provisioned per chick and hour (g) at 26 breeding sites in relation to weather factor. Each brood is depicted by a different letter (3 video filming sessions took place per brood, at stages I, II and III, respectively).

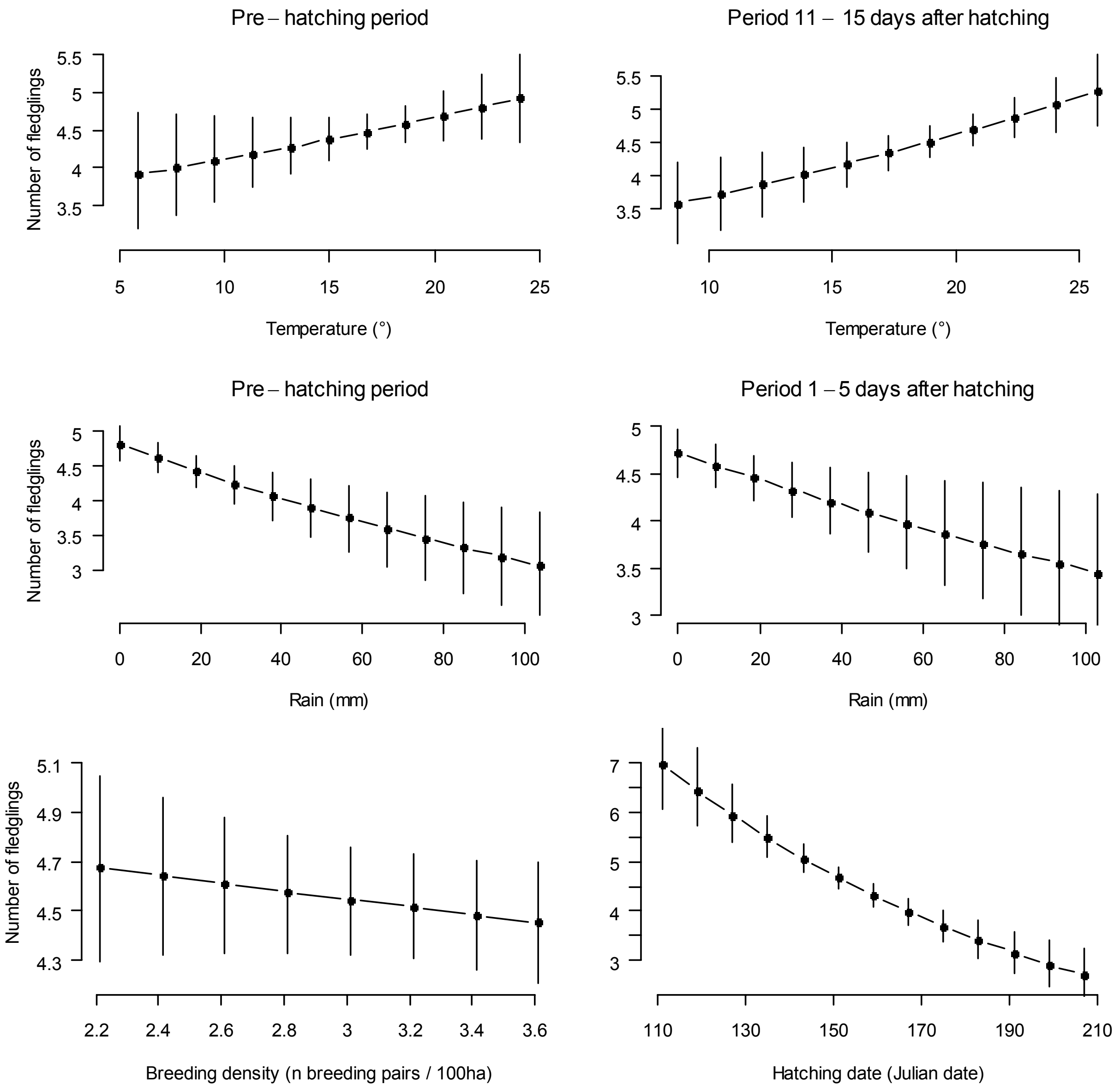

Figure 5 Reproductive output predictions for best model. Number of fledglings in relation to parameters in best model, means ± SE of 1000 bootstrap iterations.

9

Immigration is crucial for the persistence of two endangered, sympatric cavity-nesting migratory birds of Central Europe

Immigration is crucial for the persistence of two endangered, sympatric cavity-nesting migratory birds of Central Europe

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9.1 Abstract

1. Demographic analyses of endangered populations that aim at formulating sound conservation guidelines should first identify and rank vital rates contributing most to changes in population growth rate. Second, the factors affecting the most crucial vital rates should be recognized to propose adequate mitigation actions capable of enhancing population growth.

2. The exchange of individuals within a system of spatially structured populations has strong implications for the dynamics of open, local populations. Yet, the estimation of immigration remains one of the greatest challenges for demographers. Newly integrated population models using a Bayesian framework enable simultaneous estimations of survival, fecundity and immigration, and provide information about the temporal variation of these demographic rates. Retrospective perturbation analysis allows the variation of the population growth rate to be decomposed into relative contributions of the different demographic rates.

3. We applied this novel integrated analytical framework to scrutinize the demography (2002–2008) of two populations of long-distance cavity-nesting migratory birds, the Hoopoe *Upupa epops* and the Wryneck *Jynx torquilla,* which breed sympatrically in south-western Switzerland.

4. The annual population growth rate was positive in the Hoopoe (mean annual increase of 13%), but negative in the Wryneck population (-2%). Survival (both juvenile and adult) and fecundity differed only slightly between the two species, but immigration was about three times higher in the Hoopoe than in the Wryneck. In both species, the temporal variation of immigration contributed most to the changes in population growth rate, with a more pronounced relative contribution in the Hoopoe. The second most important contribution to growth rate was juvenile survival in hoopoes and adult survival in Wrynecks.

5*. Conclusions* This study provides the first assessment of demographic rates for the Hoopoe and the Wryneck, two threatened species of Central Europe. The finding that immigration is in both species the factor impacting most on population growth rate calls for international conservation programmes which seek to favour productive, source populations in order to reinstate an operational system of spatially structured populations.

Keywords: Bayesian • Fecundity • Integrated modelling • *Jynx torquilla* • Life table response experiment • Survival • *Upupa epops*

9.2 Introduction

All conservation actions for declining species are targeted at augmenting population size, which requests recognizing the factors limiting population growth rate (Caughley 1994; Sibly & Hone 2002). Understanding the components of a species' population dynamics may provide decisive insights into the mechanisms involved in decline (Newton 2004; Norris 2004). Improving those demographic rates whose impact on population growth is high is essential. Ranking the impact of various vital rates onto population dynamics is thus often prerequisite to the development of any action plan for endangered populations ('declining population paradigm', Caughley 1994).

The focus of conservation is often a specific population that is geographically open, i.e. characterized by complex patterns of immigration-emigration events (Baguette & Stevens 2003). In species exhibiting a high dispersal capacity such as birds (Paradis et al. 1998), there is increasing evidence that the exchange of individuals between populations has a strong impact on local population dynamics (Newton & Marquiss 1986; Ward 2005; Lampila et al. 2006; Schaub et al. 2006). Of course, other demographic rates such as juvenile and adult survivals (Robinson et al. 2004; Schaub et al. 2006) or fecundity (Seamans et al. 2002) may also play a crucial role.

The main obstacle in demographic analyses of open populations is the estimation of immigration rates. From capture-recapture data and data on fecundity, it is easy to estimate local recruitment through estimates of fecundity and apparent juvenile survival, as well as the probability to survive and remain in the population. Thus all losses in the population (death, emigration) can be specified, but only part of the gains (i.e. local recruitment) is known, which does not allow a complete assessment of the population dynamics. This difficulty is often overcome by assuming that emigration equals immigration (Reid et al. 2004), which renders it impossible to quantify the relative contributions of the two processes to population dynamics. Other approaches have considered that all newly identified individuals in the population are recent immigrants (Møller 2002) or that all locally born individuals were marked (O'Hara et al. 2008). Due to imperfect detectability, the former assumption is in most situations wrong: newly detected individuals might have immigrated into the study population at variable times prior to detection. It is also unlikely that all locally-born young were marked as the breeding sites cannot all be found. A recently developed integrated population model (Abadi et al. in prep.) allows estimating immigration without relying on these strong assumptions. This novel framework thus enables studying in detail all demographic components impacting population growth, which represents a major advancement for demographic analyses in conservation biology.

The population sizes of many long-distance migratory birds are declining (Berthold et al. 1998), but only in a few cases have the main demographic parameters involved in the decline been identified (corncracke, Green 2008; black-tailed godwit, Gill et al. 2001). Studies of migratory birds have often focused on single demographic rates (Sæther et al. 2006) that were not necessarily the most relevant for population dynamics (e.g. Schaub et al. 2005). Studying the demography of migrants is also complicated by large scale movements and reliance on different types of environments during the various stages of their life cycle. As the spatio-temporal pattern of migratory journeys remains poorly known for the vast majority of migratory birds it remains difficult to link seasonal demography with local environmental conditions (Webster et al. 2002). Notwithstanding this general limitation, accurate assessment of population dynamics can be further complicated by of carry-over effects (Norris 2005) and variable density-dependent mechanism taking place at the different staging areas (Ratikainen et al. 2008).

The present study compares the population dynamics of two long-distance migratory birds, the Hoopoe *Upupa epops* and the Wryneck *Jynx torquilla*, both of which have experienced population declines over the last decades in Central Europe. These two species share several life history characteristics: they are insect specialists which search for prey on the ground in sparse vegetation (Hoopoe: molecrickets, Fournier & Arlettaz 2001; Wryneck: ants, Freitag 1996); both are secondary cavity breeders; they overwinter in savannahs of the Sahelian belt in Africa (Glutz von Blotzheim & Bauer 1966; Reichlin et al. 2009); finally, they are relatively productive and start to reproduce at the age of one year. Knowledge about their demography is restricted to crude estimates of their life spans (4-6 years, Glutz von Blotzheim & Bauer 1966) and to the finding that adverse weather affects reproductive success (Geiser et al. 2008; Arlettaz et al. in prep. a).

We studied the population dynamics of Hoopoes and Wrynecks in the Upper Rhône valley (Valais, SW Switzerland) in the Central Alps. The Valais Hoopoe population has dramatically increased recently (Arlettaz et al. in prep. b), while the Valais Wryneck population seemed to have remained more or less stable. Our goal was to identify (i) which demographic rates have contributed most to the population growth rate, (ii) if species-specific differences in these rates could account for the divergent demographic trends that are currently observed, and, finally, (iii) how environmental factors influence the temporal variation of these vital rates. This required first a simultaneous estimation of all demographic rates as well as an assessment of their temporal variability. The temporal variability of the demographic rates was then tested as a function of environmental covariates roughly expressing food availability in the breeding and non-breeding areas. We used integrated population models fitted in the Bayesian framework to estimate all relevant demographic parameters simultaneously (survival, fecundity, immigration) from our two local, open populations, and to model them as a function of environmental covariates. In order to obtain estimates of the temporal variation of the demographic rates, we extended this model to a hierarchical formation, where we assumed that the annual vital rates are the realization of a random process with a mean and a variance that were estimated based on the data at hand. Using these estimates we then partitioned the variance of the population growth rate contributed to by the different demographic rates within and between species ('life table response experiment' *sensu* Horvitz et al. 1997; Caswell 2000; Oli & Armitage 2004). This approach enables a fine-grained recognition of the interplay between the components of population demography and some environmental factors, leading to some better appreciation of the necessary underlying species-specific conservation requirements.

9.3 Material and Methods

9.3.1 Study species and study site

The Hoopoe and the Wryneck are two small-sized (approx. 75 g and 35 g, respectively) birds of semi-open farmland that are red-listed in Switzerland (Keller et al. 2001). Breeding starts in April and is usually completed in August. Many Hoopoes conduct two regular broods in a breeding season, while this is less frequent in the Wryneck. The study area (62 km^2) is situated on the plain of the Rhône valley in the canton of Valais (SW Switzerland, 46° 14'N, 7° 22'E; ca 500 m altitude). The area is dominated by intensive agriculture, with numerous orchards and vineyards. More than 700 nestboxes were sequentially installed in small agricultural shacks between 1998 and 2001/2002 in an attempt to restore a relictual Hoopoe population (Arlettaz et al. 2000). Although the provided nestboxes have a large cavity size to suit Hoopoes' needs, they were also occupied by breeding Wrynecks. Local Hoopoes are exclusively dependent on these nestboxes as there are virtually no other cavities of suitable size available in the study area. This is different for the Wryneck that also uses smaller cavities beyond our control in the study area (e.g. crevices under the roof of agricultural shacks or in piles of wood and poles).

9.3.2 Demographic data

From 2002–2008 we collected three types of demographic data: capture- recapture data (CMR), data on fecundity and population survey data. To obtain capture-recapture data, we ringed all nestlings from nestboxes (ringed nestlings: $n_H = 3161$, $n_W = 1565$; here after n_H and n_W are for Hoopoe and Wryneck, respectively) and all adults that we managed to catch (mistnets, traps, or taken directly from nestboxes after hatching) (individuals: $n_H = 642$, $n_W = 620$). Because Wrynecks react strongly to the song of conspecifics and in order to increase sample size, we additionally mist-netted Wrynecks in the pre-breeding phase (April) with the help of tape-luring. Adult Hoopoes were sexed in the field based on the conspicuous uropygial gland, which is filled with a dark liquid in females only (n_{male} = 304, n_{female} = 338). Adult Wrynecks were sexed genetically (n_{male} = 250, n_{female} = 252), but 118 adults remained unsexed. Unsexed individuals and their offspring were not considered for estimating the demographic parameters. A subsample of nestlings of both species (n_{H} = 207; n_{W} = 152) were sexed genetically based on blood samples. The sex ratio of nestlings was balanced for both species (Hoopoe: 53% females, χ_1^2 = 0.82, df = 1, p = 0.37; Wryneck: 49% females, χ_1^2 = 0.11, df = 1, p = 0.75). Thus, we assigned unsexed nestlings to a sex keeping the overall yearly sex-ratio 1:1 (Nichols et al. 2004).

To obtain data on fecundity, we tightly monitored all broods in nestboxes. Because both species regularly conduct two broods in a season, we calculated for each female the total number of fledglings she produced in a given year (fledged nestlings of known females: Hoopoe: $n_{\text{nestlings}}$ = 2858, n_{females} = 330, involved in 622 broods; Wryneck: $n_{\text{nestlings}}$ = 1268, n_{females} = 170, involved in 220 broods). This avoids the need to estimate the frequency of second broods, which can be difficult. Thus, the estimated fecundity is an estimate of the total number of fledglings a female is producing in a season, not the number of fledglings per brood.

As a measure of population size, we relied on indices obtained from population surveys. For the Hoopoes we used the maximal number of simultaneous broods taking place in the nestboxes in a year. For Wrynecks, a relative population index was calculated as the proportion of occupied territories in a given year on total number of visited territories in the same year in the whole Canton of Valais (breeding bird programme, Swiss Ornithological Institute: mean number of controlled territories per year 189 ± 17.5, range = 171–210; for details on the method see Schmid et al. 2001). The reason why we opted for that crude index, which provides only approximate information about population trend, is that the apparent decrease in number of broods during the course of the study could have been caused by a progressive abandonment of the nestboxes by Wrynecks due to a suboptimal cavity design: remember that the nestboxes were designed for Hoopoes, not for the smaller Wrynecks.

9.3.3 Environmental covariates

Several environmental covariates were used for our analysis, some directly (abundance of main food), others as surrogates for food availability both on the breeding and wintering grounds. Variation of temperature and precipitation has been shown to induce variability of food availability for insectivorous birds during the breeding period (Leech & Crick 2007;

Arlettaz et al. in prep. a), thus potentially impacting fecundity. As correlates of food availability during the non-breeding season we used the Normalized Difference Vegetation Index (NDVI) and the North Atlantic Oscillation (NAO) index. The NDVI is a measure of the primary production recorded through remote sensing techniques (Tucker et al. 2005; US National Oceanic and Atmosphere Administration, NOAA): high values indicate high primary production and are thus likely to reflect the abundance of insects (Pettorelli et al. 2005; Szép et al. 2006). While Wrynecks from Valais are likely to winter in the western Sahelian belt, Hoopoes might also winter in its eastern part (Reichlin et al. 2009, Reichlin et al. in prep. a, Reichlin et al. in prep. b). Therefore we calculated a NDVI for the two areas – with the divide situated at the borders between Chad and Central African Republic (Appendix 1) – for each year as the average values for the months October-February. We only considered NDVI from savannah areas, as this is the preferred habitat of both species (Glutz von Blotzheim & Bauer 1966; Reichlin et al. 2009). The NAO describes the redistribution of atmospheric mass between the Azores and Iceland, as these mass movements strongly impact winter weather conditions in Europe (Hurrell 1996). A positive phase of winter NAO (December – March, wNAO) is associated with stronger-than-average surface westerlies (stronger winter storms), which cause warm and wet winters in northern and coastal Europe, but drier-than-normal conditions in central and southern Europe including the Mediterranean (Hurrell 1995; Hurrell et al. 2003; Bechet & Johnson 2008). Because both indices could have an effect on survival, we expected lower survival when NDVI is low and/or NAO is high (e.g. Grosbois & Thompson 2005). In addition, the African NDVI may have a delayed impact on fecundity (*f*) or immigration (*i*) during the next breeding season, because of possible carry-over effects (e.g. Norris & Taylor 2006). We thus also expected higher fecundity and immigration when the NDVI in the preceding winter was high. Finally, a last possible carry-over effect on fecundity due to adverse weather during migration could be indicated by a negative relationship between fecundity and the wNAO phase, although the response wNAO among species is not unidirectional (Jonzén et al. 2002).

Weather data for the breeding area were obtained from MeteoSwiss (Sion station in the core of the study area). For each year, the mean daily temperatures and total amount of rainfall from May – July were averaged. NDVI data were obtained from http://igskmncnwb015.cr.usgs.gov/adds/datatheme.php (accessed 22 November 2008), and the wNAO index from http://www.cgd.ucar.edu/cas/jhurrell/indices.data.html (accessed 15 December 2008).

For the Wryneck, we also directly measured food availability through an annual estimate of ant nest density based on surveys conducted in 2003–2007 in orchards. Orchards represent the favoured foraging habitat for Wrynecks in Valais (Weisshaupt 2007). Ant nest censuses were conducted on random plots with 5 replicates per plot, in orchards of the study site in the years 2003-2007. We calculated mean annual ant nest density per m^2 corrected for detection probability (nest detection depended on temperature, percentage of bare ground, and vegetation height). More details about the sampling design are provided in Mermod et al. (in prep.). The annual variability of all environmental covariates is shown in Appendix 2. Because covariates were measured in different units, they were standardized (mean = 0, SD = 1) in order to compare directly their effects on vital rates.

Because our time series consists of only seven years of data, the statistical power to detect relationships between demographic rates and environmental covariates remains low (Grosbois et al. 2008). We thus expected only covariates having a strong impact on population dynamics to emerge from the analysis.

9.3.4 Integrated population model

We used integrated population modelling in order to estimate demographic parameters. This model combines the different sources of demographic information into a single model, resulting in an improvement of the precision of the parameter estimates, and the ability to estimate demographic parameters for which no explicit data have been sampled (Besbeas et al. 2002; Brooks et al. 2004; Schaub et al. 2007; Abadi et al. in prep.). Recently, this model was extended to estimate immigration rate, which renders the model particularly useful for our purpose (Abadi et al. in prep.).

The implementation of the integrated population model requires the formulation of the likelihoods of the different data sources (capture-recapture, population survey, and fecundity data). In brief, the likelihood of the capture-recapture data was constructed by assuming that each cohort of released individuals follows a multinomial distribution. This is the well-known Cormack-Jolly-Seber (CJS) model (Lebreton et al. 1992). Fecundity was estimated using a Poisson likelihood, in which the number of fledglings followed a Poisson distribution with the product of the fecundity rate and the number of breeding females as the Poisson parameter.
The likelihood of population survey data is constructed using a state-space model (Besbeas et al. 2002; De Valpine & Hastings 2002), which consists of a state and an observation processes. The state process is described by a female-based, pre-breeding matrix projection model (Caswell 2001) with two age classes. We assumed that reproduction started at one year of age, and that the sex ratio was even. The number of individuals that are one year old ($N_{1,t+1}$) in year *t*+1 is given by

$$N_{1,t+1} = Po\left(\left(N_{1,t} + N_{2+,t}\right)\frac{f_t}{2}\phi_{ju,t}\right)$$

and the number of individuals older than 1 year ($N_{2+,t+1}$) is given by

$$N_{2+,t+1} = Po\left(\left(N_{1,t} + N_{2+,t}\right)\left(\phi_{ju,t} + i_t\right)\right)$$

where $\phi_{ju,t}$ and $\phi_{ad,t}$ are the juvenile and adult apparent survival rates at time *t* (probability that an individual survives and does not emigrate permanently between year *t* and *t+1*), f_t is the fecundity rate at time *t*, i_t is the immigration rate, defined as the number of immigrants in year *t* per individual in the population in year *t-1*. We used Poisson distributions to model the population sizes, which directly accounts for demographic stochasticity.

The observation process links the data from the population survey (y_t) in year *t* to the true population trend, i.e. $y_t = \left(N_{1,t} + N_{2+,t}\right) + \eta_t$, and $\eta_t = N\left(0, \sigma_y^2\right)$, where σ_y^2 is the variance of the observation error terms.

Assuming independence between the different data sources, the joint likelihood of the integrated model is obtained by multiplying the likelihood of the different data sources (Besbeas et al. 2002; Brooks et al. 2004). A concern in implementing the integrated population model is the violation of the assumption of independence since individuals of the local population are often involved in two or more data sets. However, a recent simulation study has shown that this violation exerts only a minimal impact on the accuracy of the parameter estimates (Abadi et al. in prep.). The likelihood of the capture-recapture data of the males were constructed in the same way as that for the females, but was not part of the joint likelihood, unless the sexes were constrained to be identical (see below).

We used the Bayesian approach *via* a Markov Chain Monte Carlo (MCMC) simulation technique for model selection and parameter estimation (Gilks et al. 1996). This approach required defining prior distributions for all model parameters. We specified non-informative priors: a normal ($N(0,10^4)$) prior for regression coefficients, a $N(100,10^4)$ prior truncated to positive values for age-specific population sizes, and a uniform ($U(0,10)$) prior for the standard deviation of the error terms. We assessed the convergence of the MCMC simulations to the posterior distribution using the convergence diagnostic ($\hat{R}$) (Brooks & Gelman 1998). The $\hat{R}$ values were <1.02 for all parameters after running three parallel chains of length 30,000, discarding the first 20,000 as burn-in. These results suggested the convergence of the MCMC algorithms. We finally ran a single chain for 500,000 iterations, discarding the first 100,000, and thinning every 400th observation. We used the deviance information criterion (DIC; Spiegelhalter et al. 2002; van der Linde 2005), which is a Bayesian equivalent of Akaike information criterion (AIC), for model selection. The model with lowest DIC was considered to be the best among the candidate models. The analyses were performed in WinBUGS (Spiegelhalter et al. 2004) and facilitated by using the R2WinBUGS package (Sturtz et al. 2005) in R 2.7.1 (R Development Core Team 2008).

9.3.5 Hierarchical formulation

To get estimates of the temporal variability of the demographic rates that are not inflated by sampling variability, we used a hierarchical formulation of the integrated model (also called random effect model, Burnham & White 2002). In this formulation, the annual estimates are thought to originate from a random process with a common mean and a temporal variance. For the logit of survival rates, we used

$$\operatorname{logit}(\phi_t) = \beta_0 + \varepsilon_t,\ \varepsilon_t \sim N\left(0, \sigma^2_{L\phi}\right),$$

where β_0 is the mean and $\sigma^2_{L\phi}$ is the temporal variance of the logit of survival. We used the log scale to model fecundity and immigration, thus

$$\log(f_t) = \alpha_0 + \varepsilon_t,\ \varepsilon_t \sim N\left(0, \sigma^2_{\log F}\right), \text{ and}$$

$$\log(i_t) = \gamma_0 + \varepsilon_t,\ \varepsilon_t \sim N\left(0, \sigma^2_{\log i}\right).$$

Again, the α_0 and γ_0 are the means and $\sigma^2_{\log F}$ and $\sigma^2_{\log i}$ are the temporal variances of the log of fecundity and immigration.

9.3.6 Model selection

Our goal was to make inference from a simple model. We always kept temporal variation in the models, because this variability was a crucial component. However, we were not sure whether survival and recapture rates also differed between sexes. We thus compared 16 different models, in which we kept the structure of fecundity and immigration rates as time dependent, but included sex effects in survival and recapture rates. We treated possible time-dependence of the recapture rate as fixed effects to simplify the models. We also included models in which recapture rate was constant.

9.3.7 Life table response experiment

We used a random effects life table response experiment (LTRE) to assess the contribution of the variation of demographic rates to the variation in the population growth rate (λ) (Horvitz et al. 1997; Caswell 2000). Generally, the contribution of the variance of the demographic parameter θ is given by the sensitivity of λ to changes in θ ($\frac{\partial\lambda}{\partial\theta}$) and its temporal variability (σ^2_θ) as $\sigma^2_\theta\left(\frac{\partial\lambda}{\partial\theta}\right)^2$. Since the estimates of the temporal variability of the demographic rates are obtained on the logit or log scale, they need to be back-transformed to the original scale.

We further used the fixed effects LTRE approach to examine the contribution of the difference of the demographic rates between the two species ($\theta^h - \theta^w$; where superscripts *h* and *w* are for Hoopoes and Wrynecks, respectively) to the difference in population growth rates ($\Delta\lambda$) (Horvitz et al. 1997; Caswell 2001). An approximate formula for calculating fixed effects LTRE is given by $\Delta\lambda = \lambda^h - \lambda^w \approx (\theta^h - \theta^w)\left(\frac{\partial\lambda}{\partial\theta}\right)$. The sensitivities are evaluated at the average of the mean vital rates of the two species (i.e. at $\left(\frac{\theta^h + \theta^w}{2}\right)$).

9.3.8 *Assessing the impact of environmental covariates*

We constructed models in which a demographic rate θ is a function of an environmental covariate X. We used again the hierarchical formulation, and thus

$$g(\theta_t) = \beta_0 + \beta_1 X_t + \varepsilon_t \text{, and } \varepsilon_t \sim N\left(0, \sigma^2_{X,g(\theta)}\right).$$

Here, the β's are the regression coefficients, $\sigma^2_{X,g(\theta)}$ is the temporal variance of parameter $g(\theta)$ after correction for the linear trend with X, and g is the appropriate link function.

9.4 Results

9.4.1 *Temporal patterns in vital rates and testing for sex effect*

The model selection procedure established that, for both species, the best model included no effect of sex on estimates of survival rates, while recapture rate was constant (model 9; Table 1). Overall, the mean demographic rates of the two species were rather similar: Hoopoes produced, on average, slightly more fledglings than Wrynecks, and their adult survival was slightly lower (Table 2). The most striking difference between the vital rates of the two species was in immigration, which was more than three times higher in Hoopoes compared to Wrynecks. The population growth rates also differed markedly: the Hoopoe population increased on average by 13% per year, while the Wryneck population declined by 2% per year. The mean population growth rate obtained through our population indices drawn from raw counts (see Methods) was 1.147 and 0.982 for Hoopoes and Wrynecks, respectively. They were slightly higher than the estimates yielded by the integrated analyses (Fig. 1). The temporal pattern of demographic rates showed a strong decline in Hoopoe fecundity during the course of the study (Fig. 1). A comparison of the coefficients of variation of the vital rates indicated that immigration was the most variable parameter in both species (Table 2).

9.4.2 Contribution of demographic rates to the variation in growth rate

The LTRE analyses revealed that the variation of immigration rate contributed most and the variation of fecundity least to the observed variation in population growth rate in both species (Fig. 2). For Hoopoes, variation of juvenile survival contributed second most to the observed changes in population growth rate, while for Wryneck the variation of adult survival contributed second most.

In a second analysis we compared the contribution of the difference of the demographic rates between the two species to the differential growth rates. The difference between immigration rates of the two species contributed more than twice to the species-specific population trends compared to the differences evoked by other demographic rates (Fig. 3). Their absolute contributions were more similar.

9.4.3 Explained temporal variation by covariates

The estimated slopes of the environmental covariates on the demographic rates are given in Table 3. None of them were significantly different from 0, as evidenced by the inclusion of 0 within all credible confidence intervals. Compared to the slope, the credible interval was smallest for the impact of rain on fecundity in both species, suggesting that the amount of precipitation during the breeding season may have a negative impact on fecundity.

9.5 Discussion

Our study revealed that the temporal variation of the immigration rate had a strong impact on the dynamics of two local populations of Hoopoe and Wryneck, while the temporal variation of fecundity had virtually no effect at the population level. The impact of apparent survival was intermediate and differed markedly between the two species according to age class: variation in adult survival contributed much to variation in growth rate in the Wryneck, whereas variability in juvenile survival was a major component of population growth in the Hoopoe.

Integrated population dynamic models are very useful as they can provide detailed and accurate information, especially as regards immigration, which was so far in most cases assessed based on untested assumptions such as perfect capture rate (Møller 2002). The reliance on a hierarchical formulation further enabled us to estimate the temporal variance of the demographic rates, which was crucial for the decomposition of the variance components with respect to population growth. Contrastingly, in fixed effects models, the observed fluctuation of the demographic rates from year to year is assumed to be determined entirely by mechanistic differences among years, without considering that they were also subject to sampling variation (variation stemming from the fact that only a subset of the population is sampled). In that case, only approximations have been used to separate temporal from sampling variation (Gould & Nichols 1998; Burnham & White 2002). Notwithstanding this, even with our applied hierarchical models, there remains the problem of the relatively short time series (7 years), which weakens the precision of the demographic rate estimates.

The main outcome regarding the crucial role of immigration can be explained by a high sensitivity of the two bird population growth rates to changes in immigration and/or by the large temporal variation of the immigration rate. Moreover, differences in immigration rates appear to be the main demographic reason why the two species show opposite population trends, with the Hoopoes having increased dramatically during the course of the study, while the Wryneck population slightly decreased.

The population growth rates of both species would be similar if no immigration had occurred ($\lambda = \phi_{juv*}f + \phi_{ad}$, Hoopoe: 0.92; Wryneck: 0.91). These values well below 1 suggest that both populations would not be self-sustainable without immigration, meaning that they theoretically function as sinks (Dias 1996). Yet, true juvenile survival is probably higher than estimated here (Hoopoe: 0.090 – 0.168; Wryneck: 0.098 – 0.135), i.e. closer to what is observed in birds of similar body size (~0.2, Siriwardena et al. 1998; see also Scherner 1989). This indeed suggests that a large fraction of the juveniles emigrate from the local populations. The proportion of emigrants can roughly be estimated under the simplistic assumption i) that young but not adults settle outside our local populations (Greenwood & Harvey 1982), i.e. that the observed adult survival is the true survival (0.41 and 0.46, for Hoopoes and Wrynecks, respectively); and ii) that immigration is absent. As population growth rate is then a mere function of adult survival (known, see above) plus fecundity (known, see Table 2) multiplied by juvenile survival, we can calculate the latter, which is the only unknown parameter in the equation. Under this fictive scenario, juvenile survival must be 0.21 and 0.17 for local Hoopoes and Wrynecks, respectively, to obtain the actual, observed population growth rates (1.13 and 0.98, for Hoopoes and Wrynecks, respectively, Table 2). This would result in an emigration probability of juveniles of 0.38 in Hoopoes (1-0.13/0.21) and 0.29 in Wrynecks (1-0.12/0.17). This suggests that our populations may actually function as sources. Although true emigration rates cannot be assessed definitely, the two Hoopoe and Wryneck populations appear to be part of an open-recruitment system, in which an important part of the recruited breeding birds were not produced locally. Such a system seems to be frequent in spatially structured bird populations (Stacey & Taper 1992; Lambrechts et al. 1999; Baillie et al. 2000; Murphy 2001; Franklin et al. 2004; Schaub et al.

2006). Assessing sink-source dynamics in such a complex, large-scale system of spatially structured populations would require detailed knowledge of the demographic performance of several single local populations, which is currently out of scope due to obvious logistic constraints.

The study of immigration within a population is complicated by issues of spatial scale. Decisive are the extension of the study population and study area, and the spatial discreteness of the latter; finally, the dispersal potential of the species is an essential component. Unfortunately, the natal dispersal distances observed within our study area (Hoopoe: mean = 5.9 km, range = 0–28 km, *n* = 224; Wryneck: mean = 4.1 km, range = 0.3–11 km, *n* = 38) contributes little to the actual dispersal capacity of the species. Still, we think, that due to the relative large size of our study area (62 km^2) the reported great importance of immigration is no artefact of the study design. Our two bird populations are geographically and topographically isolated from others (especially Hoopoes, see below), thus forming a discrete study patch: they are situated on the plain (ca 500 m altitude) of a deep Alpine valley flanked by high mountain ranges.

Despite the common finding about the importance of immigration for the dynamics of our two sympatric bird populations, there are noticeable species-specific differences despite the similar life histories and habitat requirements of two species have. As already mentioned, the study Hoopoe population is very much isolated. Indeed, it is much more isolated than our Wryneck population; the next Hoopoe populations of comparable size are 250 to 350 km farther away (Trento, Italy; Kaiserstuhl, Germany). In between, there are only scattered breeding pairs. We furthermore have a good control of the Valais breeding population because Hoopoes occupy almost exclusively nestboxes (contrary to Wrynecks, see below), which are systematically controlled since years. Indeed, it is the installation of hundreds of nestboxes which has boosted the local population to increase dramatically during the last decade (Arlettaz et al. in prep. b). As immigration plays such an important role it is likely that nestboxes have retained numerous birds which regularly cross the area during spring migration. However, the origins of these immigrants remain unknown, as analyses of stable isotopes in feathers have not found any differences in isotopic values between local birds and possible immigrants (Reichlin et al. in prep. a). The recent stabilisation and even slight population size decrease of Valais Hoopoes may be due to density-dependent population regulation affecting fecundity (Fig. 1, see also Arlettaz et al. in prep. a). As the Hoopoe population has probably reached its carrying capacity, we expect immigration in the future to fall well below the average rate obtained during the phase of demographic expansion. The situation is different for Wrynecks, essentially because they also breed in nesting places other than nest boxes. This is also why the Valais Wryneck population, which historically never reached as low critical population levels as local Hoopoes, did not show a similar rapid response to the sudden availability of nestboxes. Moreover, our Wryneck population is less isolated than the Hoopoe population because there are scattered pairs breeding in the immediate surroundings. Our estimates of immigration may hence be influenced by artefacts induced by more frequent dispersal events occurring on a local scale: from other cavities towards nestboxes and from adjacent breeding areas into our study population. This interpretation is corroborated by a study of feather stable isotopes in the same Wryneck population: Reichlin et al. (in prep. b) demonstrated that individuals caught in the study area for the first time (possible immigrants) showed similar isotopic values to individuals stemming from the study area, which suggests a very close if not identical geographic origin.

Besides immigration, variation of apparent survival also contributed to variation of population growth. The importance of recruitment to population dynamics is usually distinctive for short-lived species (Sæther & Bakke 2000). In the Hoopoe, juvenile apparent survival – i.e. a component of local recruitment (local recruitment = fecundity * apparent juvenile survival) – was important, but not adult survival. In contrast, in the Wryneck, it is the variation of adult survival which contributed more to population growth, almost reaching the contribution of immigration, whilst juvenile survival was marginal. From a conservation viewpoint it would be essential to identify the factors impacting on species- and age-specific survival. Unfortunately, our analyses could not discern any effects of environmental covariates. This may be due in part to the relative short duration of the time series (7 years), i.e. to low statistical power and rather imprecise estimates of demographic rates. Note that the same holds true for the causes of the temporal variability in immigration. Longer time series are needed to identify causal mechanisms driving population dynamics.

Although both species were very productive and fecundity fluctuated markedly over time, the variation in the number of fledglings did only weakly contribute to the variation of the population growth rates. Most probably this is because many of the fledged individuals emigrated from the populations. This does not mean, however, that local reproduction is completely unimportant. The locally produced young that emigrate from the local population are the immigrants to other populations, which may be a very central component for the latter population. Thus, local reproduction is important to stabilize the system of spatially structured populations, but not so much for the local population.

This study establishes that the population dynamics of two endangered sympatric species exhibiting similar life histories was strongly dependent on immigration, which was about three times higher in Hoopoes compared to Wrynecks. The Hoopoe population, which was on the brink of extinction before the start of our study, has been rapidly recovering after corrective measures were implemented since 1999, i.e. increasing the number of nest sites, the most limiting factor locally (Fournier & Arlettaz 2001). In contrast, the Wryneck population seems to have remained relatively stable. The level of immigration found in the Wryneck would thus be typical of spatially structured, but saturated populations, whilst in the Hoopoe the immigration rate would reflect a colonizing phase. It is striking how quickly the local Hoopoe population could recover: this shows that population reservoirs pre-existed, from which individuals readily and opportunistically colonized suitable habitats as soon as available. This is certainly a good sign for future species conservation, but demonstrates again the paramount importance of maintaining and/or restoring habitat of suitable quality for species persistence. This study also confirms that effective conservation of populations actually requires accounting for the large scale dimension beyond local demographic processes. It finally suggests, yet, that focusing conservation action on large-sized populations is not always the best option: relictual populations can quickly develop once local limiting factors have been eliminated, becoming then key components of a broader system of spatially structured populations.

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Table 1 Model selection based on the deviance information criterion (DIC) for the best pattern of vital rates in the analyses of Hoopoe and Wryneck data. The model deviance, the effective number of parameters (PD), and the difference between the DIC of the current model and the best model (ΔDIC) are provided. Φ_{juv} and Φ_{ad} are juvenile and adult survival rates, respectively, *p* is the recapture probability, *f* is the fecundity rate, *i* is the immigration rate, (*t*) stands for year-specific rates, (.) for constant, and (*s*) for the sex effect.

		Hoopoe			Wryneck		
Model No.	Model	Deviance	PD	ΔDIC	Deviance	PD	ΔDIC
1	$\Phi_{juv}(t)$, $\Phi_{ad}(t)$, $p(t)$, $f(t)$, $i(t)$	251.33	134.60	30.20	265.93	119.10	7.10
2	$\Phi_{juv}(t)$, $\Phi_{ad}(t)$, $p(t+s)$, $f(t)$, $i(t)$	257.52	147.60	49.30	271.89	124.20	18.20
3	$\Phi_{juv}(t)$, $\Phi_{ad}(t+s)$, $p(t)$, $f(t)$, $i(t)$	256.02	136.80	37.10	271.33	129.60	23.10
4	$\Phi_{juv}(t)$, $\Phi_{ad}(t+s)$, $p(t+s)$, $f(t)$, $i(t)$	263.27	120.40	27.80	276.69	141.70	40.50
5	$\Phi_{juv}(t+s)$, $\Phi_{ad}(t)$, $p(t)$, $f(t)$, $i(t)$	257.15	115.40	16.70	271.64	137.20	30.90
6	$\Phi_{juv}(t+s)$, $\Phi_{ad}(t)$, $p(t+s)$, $f(t)$, $i(t)$	263.01	121.20	28.50	276.94	157.20	56.20
7	$\Phi_{juv}(t+s)$, $\Phi_{ad}(t+s)$, $p(t)$, $f(t)$, $i(t)$	261.13	157.70	63.00	277.21	138.80	38.10
8	$\Phi_{juv}(t+s)$, $\Phi_{ad}(t+s)$, $p(t+s)$, $f(t)$, $i(t)$	267.85	119.90	32.00	283.73	137.00	42.90
9	$\Phi_{juv}(t)$, $\Phi_{ad}(t)$, $p(.)$, $f(t)$, $i(t)$	228.95	126.90	0.00	240.11	137.80	0.00
10	$\Phi_{juv}(t)$, $\Phi_{ad}(t+s)$, $p(.)$, $f(t)$, $i(t)$	232.54	146.60	23.40	245.35	141.90	9.30
11	$\Phi_{juv}(t+s)$, $\Phi_{ad}(t)$, $p(.)$,$f(t)$, $i(t)$	233.56	142.20	20.00	245.37	145.20	12.70
12	$\Phi_{juv}(t+s)$, $\Phi_{ad}(t+s)$, $p(.)$,$f(t)$, $i(t)$	238.63	121.00	3.80	251.32	133.50	7.00
13	$\Phi_{juv}(t)$, $\Phi_{ad}(t)$, $p(s)$, $f(t)$, $i(t)$	234.63	131.50	10.30	245.93	137.30	5.40
14	$\Phi_{juv}(t)$, $\Phi_{ad}(t+s)$, $p(s)$, $f(t)$, $i(t)$	240.21	122.30	6.70	251.72	129.50	3.30
15	$\Phi_{juv}(t+s)$, $\Phi_{ad}(t)$, $p(s)$, $f(t)$, $i(t)$	240.74	125.40	10.30	251.97	132.70	6.80
16	$\Phi_{ju}(t+s)$, $\Phi_{ad}(t+s)$, $p(s)$, $f(t)$, $i(t)$	244.76	135.30	24.30	257.22	138.50	17.80

Table 2 Estimates of posterior mean with standard deviation (sd), temporal variance ($\hat{\sigma}^2$), and coefficient of variation ($CV = \hat{\sigma} / mean$) of vital rates obtained from the best model (Model 9, Table 1) for both species.

	Hoopoe				Wryneck			
Vital rates	mean	(sd)	$\hat{\sigma}^2$	CV	mean	(sd)	$\hat{\sigma}^2$	CV
Juvenile survival	0.1311	(0.0231)	0.0023	0.3658	0.1211	(0.0290)	0.0012	0.2861
Adult survival	0.4129	(0.0315)	0.0021	0.1110	0.4564	(0.0940)	0.0348	0.4087
Fecundity	6.7046	(0.4096)	0.6430	0.1196	6.1729	(0.3566)	0.4602	0.1099
Immigration	0.2111	(0.1650)	0.0804	1.3432	0.0641	(0.1377)	0.0461	3.3496
Growth rate	1.1287	(0.0311)	-	-	0.9752	(0.0341)	-	-

Table 3 Standardized regression coefficients of environmental covariates on vital rates, along with 95% credible intervals. The slopes are shown on the logit scale for survival and on the log scale for fecundity and immigration rates.

	Juvenile survival			Adult survival			Fecundity			Immigration		
Predictor	Slope	Lower	Upper	Slope	Lower	Upper	Slope	Lower	Upper	Slope	Lower	Upper
Hoopoe												
wNAO	-0.0994	-0.6934	0.4898	-0.1343	-0.4451	0.1524	-0.0545	-0.2060	0.0944	-1.0728	-7.7876	4.4424
NDVIe	-0.0770	-0.6004	0.4557	-0.1766	-0.4381	0.1002	-0.0489	-0.1821	0.0878	-1.6674	-7.8350	2.9003
NDVIw	-0.1434	-0.6440	1.0711	-0.0772	-0.4209	0.2763	-0.0329	-0.2268	0.1251	0.3817	-5.8709	8.1881
Temperature	-	-	-	-	-	-	0.0561	-0.0996	0.1961	-	-	-
Rain	-	-	-	-	-	-	-0.0747	-0.1758	0.0271	-	-	-
Wryneck												
wNAO	0.2266	-0.3040	0.7609	-0.1937	-1.3201	1.0891	-0.0624	-0.2215	0.1276	1.1306	-7.6539	8.0415
NDVIw	0.3120	-0.1021	0.7971	0.0581	-1.1391	1.1611	-0.0680	-0.2143	0.0553	3.7983	-3.5720	9.6345
Ant density	-0.0214	-0.5200	0.6166	0.2263	-1.1095	1.6191	-0.0107	-0.1965	0.1555	2.3829	-4.7601	9.0176
Temperature	-	-	-	-	-	-	0.0489	-0.1340	0.2081	-	-	-
Rain	-	-	-	-	-	-	-0.0904	-0.2134	0.0477	-	-	-

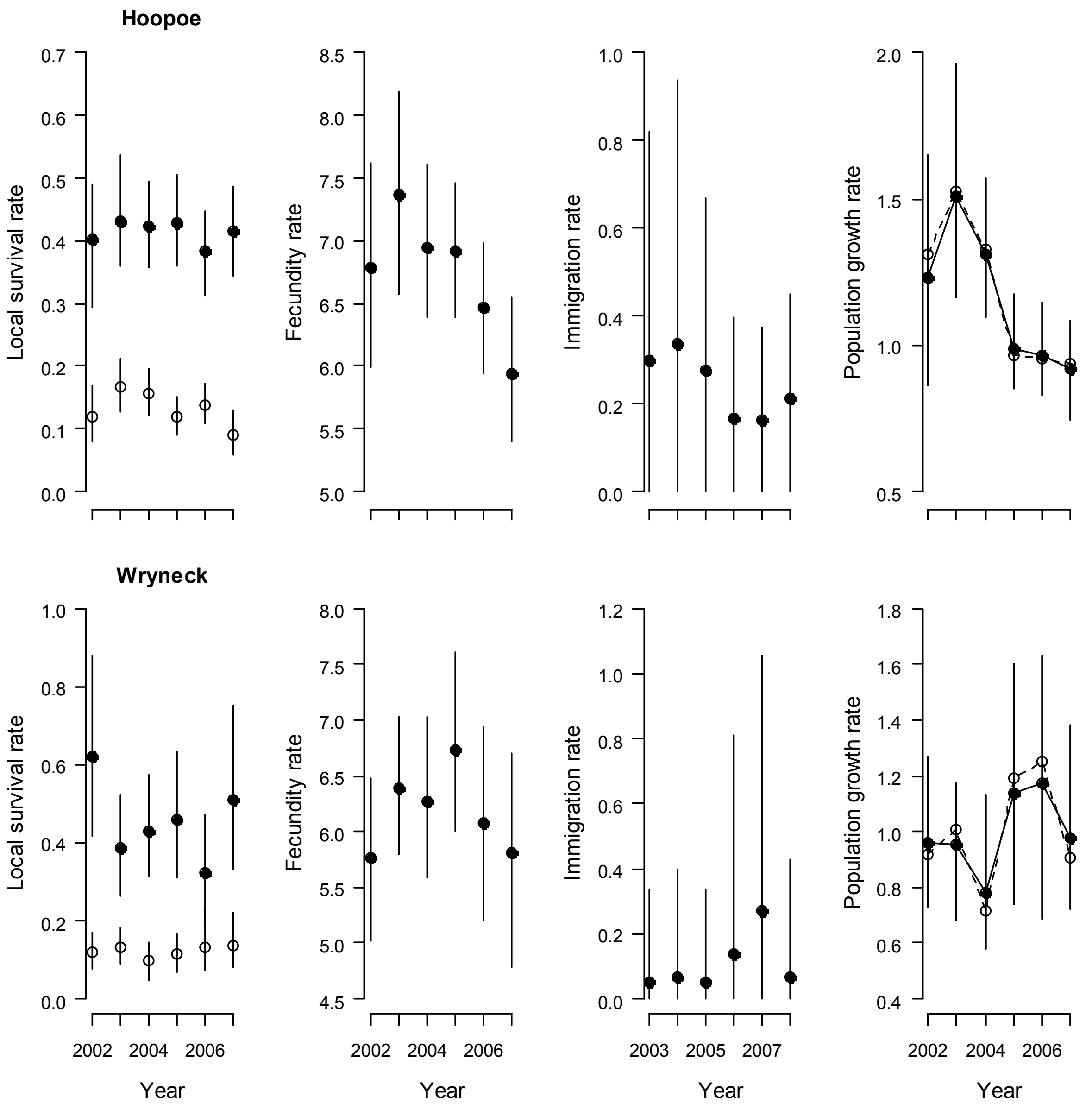


Figure 1 Estimates of annual demographic and population growth rates obtained from the best model (Table 1) along with 95% credible intervals for Hoopoe (upper panel) and Wryneck (lower panel). For survival the *open symbols* refer to juveniles and the *filled symbols* to adults. The population growth rates obtained from the observed counts and integrated model are depicted by *open* and *filled symbols*, respectively.

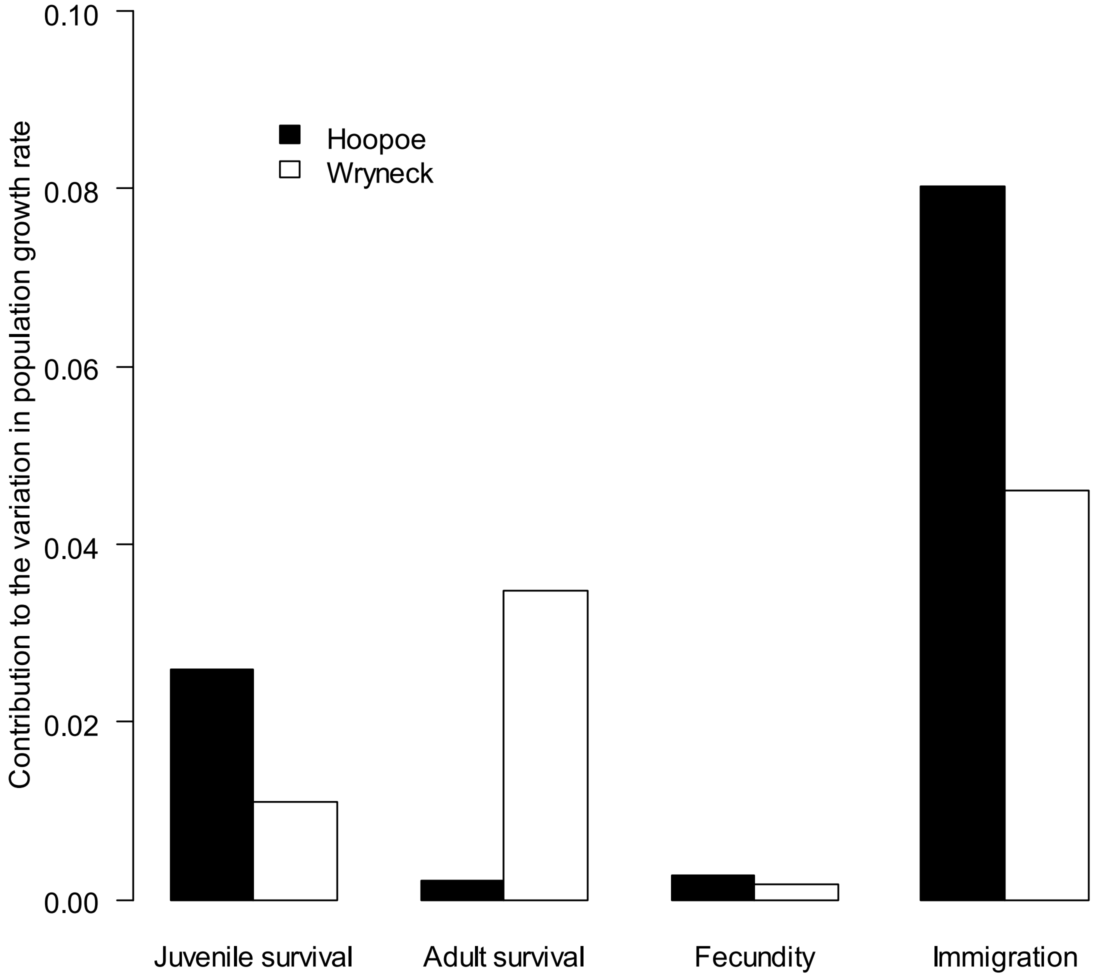


Figure 2 The contributions of each of the vital rates to the variation in the population growth rate for Hoopoe (*black*) and Wryneck (*white*).

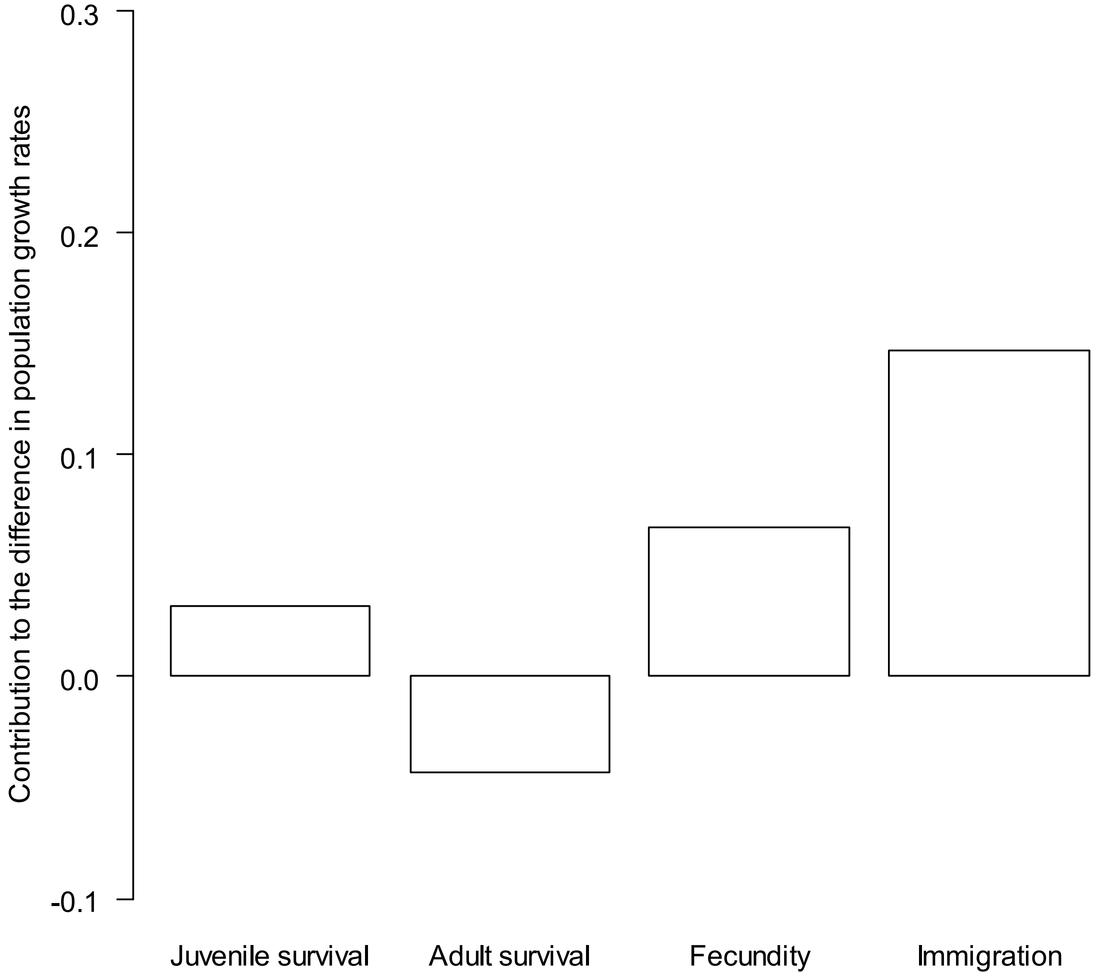
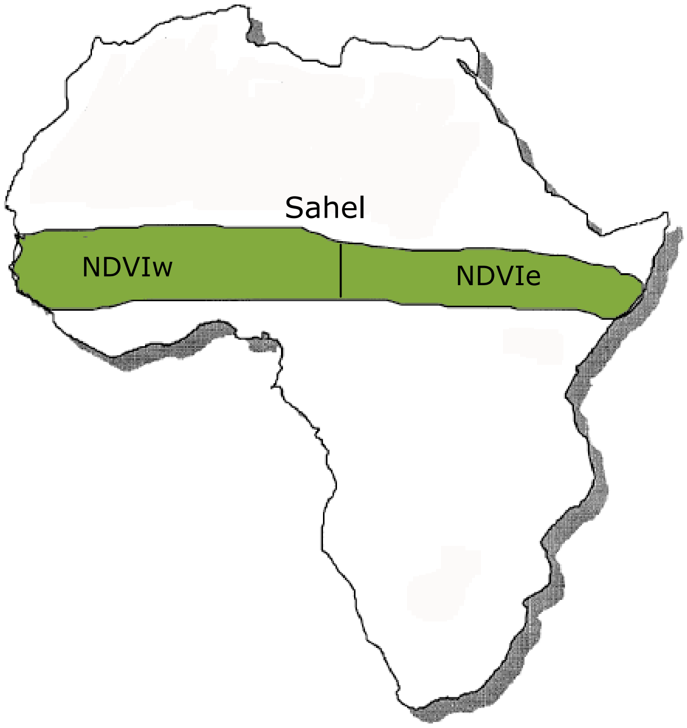
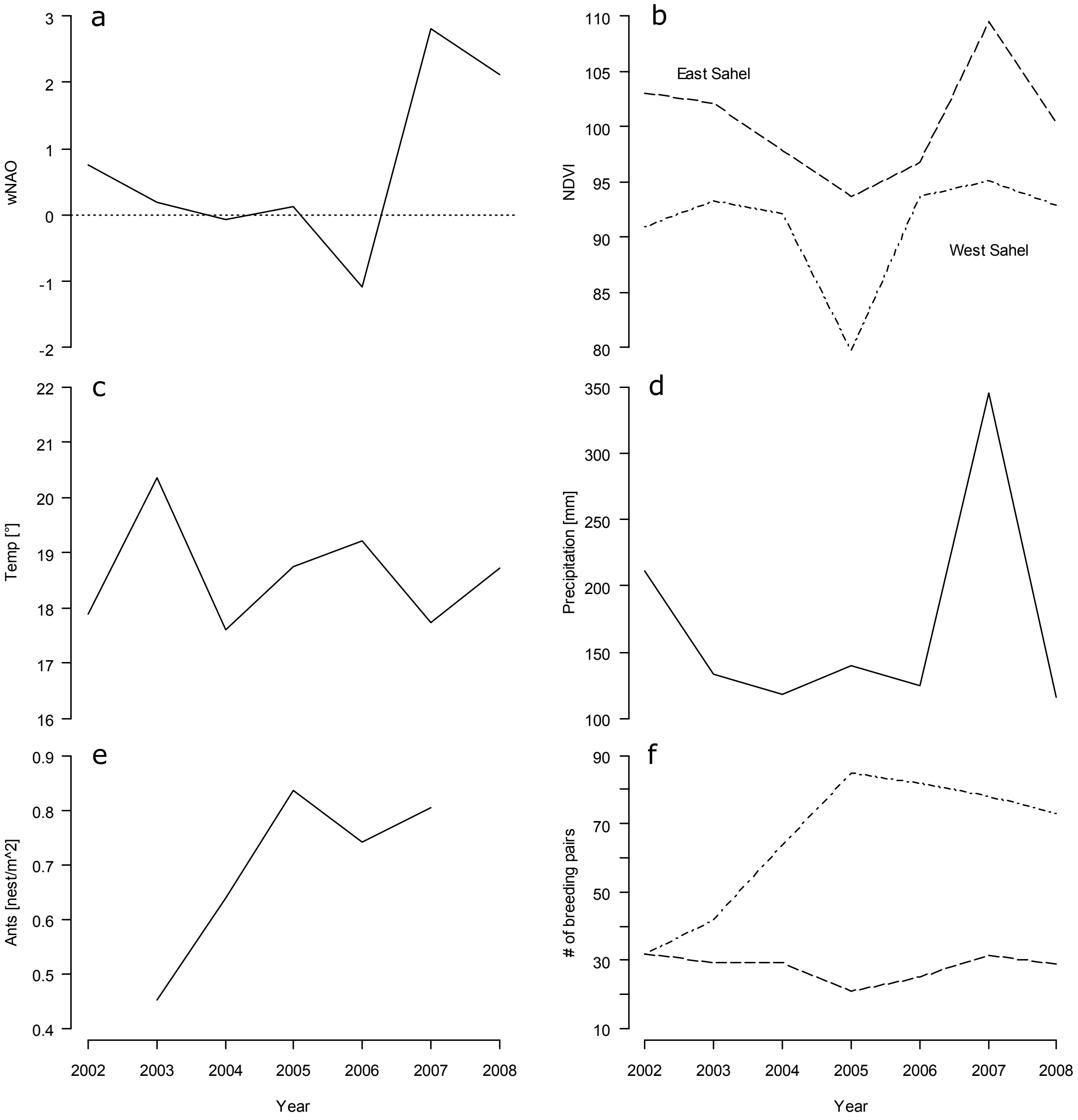


Figure 3 The contributions of the difference between the vital rates of the two species to the difference of the population growth rates between the species.



Appendix 1 Map of Africa, showing the areas of savannahs in the Sahel (*green*) from which NDVIw (West Africa) and NDVIe (East Africa) were calculated.



Appendix 2 Temporal variation of the environmental covariates and population size indices used in this study: a) wNAO, b) NDVI of savannahs in the Sahel: *dashed line* East Sahel, *dotdash line* West Sahel, c) average temperature in the study site for months May–July, d) total amount of precipitation in the study site, e) ant nest density in the study site, f) population index: *dotdash line* for Hoopoes, *dashed line* for Wrynecks.

10

General Conclusions

This work studied the demography of nestbox-breeding Hoopoe and Wryneck populations in south-western Switzerland (lower part of Valais) from a biological conservation perspective: both species have undergone dramatic declines over the past few decades in Central Europe, including Switzerland. The results highlight various aspects of their population ecology, especially the subtle interplay between environmental conditions, life histories, spatio-temporal distribution and demographic rates, which all need to be considered when analyzing the population dynamics of endangered species.

10.1 Outlook

The delineation of wintering areas of hoopoes and wrynecks, essential for linking population growth rate changes to environmental conditions, brought forward several methodological issues. We had to face the fact that, despite the relatively large numbers of ringed hoopoes and wrynecks, only a few birds (ring-bands) were recovered on the African continent and even none in the 'from literature presumed' wintering quarters south of the Sahara desert. In the second approach to delineate wintering areas, we learned the limitations of stable isotope analysis when assigning feathers to a place of origin. (i) Adequate discrimination factors must be determined when trying to link stable isotope values of feathers to a geographical origin. Moreover (ii), the spatial resolution of isoscapes of Africa, on which assignment of feathers to an origin hinges, is unfortunately low compared to Europe (or in the Nearctic's migration system). And last (iii), the widely applied, but crude map approach used in this study might bear some possible sources of errors as pointed out by several authors (Inger & Bearhop 2008; Wunder & Norris 2008). Suggestions for future improvements of the method are made; for instance, likelihood-based assignment could be used to study animal migration (Royle & Rubenstein 2004; Hobson & Wassenaar 2008). The two approaches for the determination of winter quarters of Hoopoes and Wrynecks nonetheless yielded converging results. We accounted for one seminal source of error by calculating the discrimination factors for feathers of known origin (based on modelled isotopic surfaces, Bowen et al. 2005), these obtained factors happened to matched very closely the widely applied values published in the literature. Furthermore, we found independent confirmation for the location of African wintering quarters through an analysis of the isotopic feather values from museum birds collected in these regions. Hence, the stable isotope analysis proved to produce invaluable information, especially for these small-sized birds, for which high precision tracking techniques (e.g. satellite tracking) are still not available. The reliance on other tracking techniques, such as the use of archival geolocation tags (e.g. 'geolocators', Phillips et al. 2007) could eventually challenge our results of wintering quarters of Swiss hoopoes and wrynecks.

Population dynamical modelling stressed the importance of immigration to the two nestbox populations in Valais. However, changes in vital rates and hence changes in population growth rate could not be linked to environmental conditions, at least regarding large scale climatic variation. Reasons for this could be that seven years of demographic data is not enough to pick up any signal of the studied environmental conditions, or that the signal is too subtle to be recognized by the model (i.e. changes of vital rates are not large enough to be explained by covariates in the models). On the one hand, large scale phenomena might not be suited to explain local population changes in these species, which may be more susceptible to adverse local weather (rainy periods) as shown for some demographic parameters in the present thesis (Wang et al. 2002). Even though the variation of immigration contributed most to the observed population change (retrospective perturbation analysis, Caswell 2000), the population may be more sensitive than expected to changes in juvenile survival (as in a prospective analysis, not performed here), which was the vital rate more strongly influenced by climatic conditions. This is usually distinctive for short lived species, for which local recruitment (local recruitment = fecundity * juvenile survival) plays a key role in population dynamics (Sæther & Bakke 2000).

10.2 Relevance for conservation

This study could for the first time estimate the vital rates of Hoopoes and Wrynecks, two endangered cavity-nesting, insectivorous birds of Central Europe. The study highlighted some key ecological features which appear essential for their persistence: (i) availability of sufficient and suitable nest sites, (ii) richly structured landscapes providing accessible foraging patches for these ground-foraging insectivores, (iii) existence of a system of spatially structured populations with source populations capable of providing immigrants for the focal populations. In our study area, Hoopoes and Wrynecks survive in intensively cultivated fruit plantations, where natural tree cavities are almost totally absent. These plantations, however, have open ground habitats below fruit trees that offer optimal foraging opportunities. The installation of nestboxes could compensate for the lack of suitable breeding cavities, enabling the species to survive in a rather monotonous landscape. Corrective measures have thus been successfully implemented locally (Arlettaz et al. in prep.), but it remains now to ensure the existence of good source populations beyond the study area so as to maintain a sustainable immigration rate. The conservation of Valais Hoopoes and Wrynecks seems thus to call for international conservation programmes aiming at restoring source populations on a large scale across Europe. This could be achieved primarily through efforts to improve habitat quality in places with remaining (small) populations. Suitable breeding places can easily be offered in the form of dedicated nestboxes. Optimal foraging micro-habitats are more difficult to obtain, however. Patches of bare ground could be created in orchards and fruit plantations by mechanically (or, in controlled situations, chemically) removing ground vegetation so as to enhance accessibility to arthropod prey (Schaub et al. 2008): such loosely vegetated areas are a key habitat feature for both species. Such targeted conservation actions for Hoopoes and Wrynecks would additionally benefit several declining species of animals inhabiting farmland, including other emblematic birds (e.g. Common Redstart *Phoenicurus phoenicurus*).

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Erklärung

gemäss Art. 28 Abs. 2 RSL 05

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Leiter der Arbeit:	**Prof. Dr. R. Arlettaz** **PD Dr. M. Schaub** **PD Dr. L. Jenni**

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