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Searching for potential wintering and migration areas of a Danish Barn Swallow population in South Africa by correlating NDVI with survival estimates

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Abstract On the basis of correlation analyses between annual Normalised Difference Vegetation Index (NDVI) values in Africa and the annual survival rate estimated for a breeding population of barn swallows *Hirundo rustica* from Denmark, we identified potential wintering and migration areas in South Africa during December–February and March–May, when barn swallows commonly occur in South Africa. During December–February we identified potential wintering areas only in the western part of South Africa, in the Karoo. Potential areas in the central and eastern parts of the country were only identified during March–May. NDVI values in the Karoo during March–May explained most of the variance in annual adult survival rate of the population. The high ratio of European ringed barn swallows among controlled individuals in the Karoo was similar to the ratio that would be expected based on the number of ringed barn swallows and the population sizes of barn

swallows in north-western European breeding populations. The level of this ratio in the Karoo was higher than in any other locality in the central and eastern parts of South Africa and Botswana, indicating that ringed birds from the eastern flyway are absent to a much smaller extent than ringed birds from the western flyway. This approach shows that the NDVI and survival method can focus ringing efforts to regions and areas that are likely to harbour specific breeding populations, thereby helping to identify potential wintering and migration areas for breeding populations of migratory birds.

Keywords Normalised difference vegetation index (NDVI) · Ringing · South Africa · Swallow · Survival · Wintering areas

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Introduction

During their lifetimes inter-continental migrating birds make use of areas separated by great distances, which may expose them to serious natural and/or direct or indirect man-made environmental influences (Alerstam 1991; Berthold 1993; Greenberg and Marra 2005). These environmental factors include increasing perturbation in regular weather patterns and increasing habitat perturbation (e.g. droughts) in the breeding and wintering areas. Likewise, the journeys, which may be many thousands of kilometres long, can be affected by climate change and large-scale human-induced habitat modification, both of which pose significant threats to migratory species (Marchant 1992; Berthold et al. 1998).

There is an increasing imperative to understand how these species adapt to such environmental conditions, which are highly unpredictable in space and time, and to understand physiological, morphological and behavioural strategies that allow such adaptation (Brown et al. 1999; Crick et al. 1999; Sæther et al. 2000; Møller and Szép 2005). While there have been several detailed

investigations on populations of migrating bird species in their breeding areas in Europe, for only a very few of these populations is there substantive information available on the exact migration routes and wintering grounds (Webster et al. 2002). Without this knowledge it is difficult to explore the potential effects of various environmental factors on migration and the wintering areas of migrant populations and to investigate the interactions among conditions at the breeding, migration and wintering grounds (Marra et al. 1998; Etterson and Shaw 2001; Saino et al. 2004).

The need to have accurate and abundant information – within the very near future – on the migration and wintering areas of a specific breeding population or on the migration and breeding area of a specific wintering population is becoming increasingly important. For most migrating species, the traditional, more than 100-year-old bird ringing method has yielded insufficient data with respect to identifying migration and wintering areas of specific and intensively studied breeding populations (Berthold 2001). A typical situation is the sand martin (*Riparia riparia*) project in eastern Hungary (Szép 1995), in which more than 100,000 breeding individuals of colonies along the Tisza River have been ringed since 1986 – without a single African recovery or re-trap; consequently, the African winter quarters (Del Hoyo et al. 2004) of this population remains unknown. Although novel radio and satellite tracking methods show great promise, particularly for the study of most of the small migrating passerine species that form the majority of migrating birds, the technology will not be applicable for several years or decades because of the weight and short lifespan of potential transmitters (Cochran and Wikelski 2005) and the very high costs involved when working with appropriate sample sizes.

The acceleration of the adverse effects of climate change and man-induced habitat destruction in breeding, migration and wintering areas makes it necessary to develop new methods for identifying migration and wintering areas of focal breeding populations. Potentially promising new tools are methods based on stable isotopes and trace element profiles of feathers moulted in the wintering or breeding areas (Rubinstein and Hobson 2004). In order to use these methods to identify moulting areas, both in the breeding and in the migration/wintering areas, it is essential to carry out large-scale, systematic sampling across whole continents for the specific species for which the migration maps are required (Hobson 2005). However, the spatial resolution of these methods can vary greatly among areas (T. Szép et al. in preparation). Promising results have been obtained using these techniques in North America and Europe for some species (Szép et al. 2003; Hobson 2005), but the cost of these methods when used alone in attempts to identify migration, wintering and breeding areas are extremely prohibitive. It is more likely that such methods could work much more efficiently as hypothesis-testing techniques – if we could first obtain

information on potential migration and wintering areas using other techniques.

A novel Normalised Difference Vegetation Index (NDVI) and survival method (Szép and Møller 2005) that is based on the close positive relationship between annual habitat condition of the migration/wintering areas [measured from NDVI satellite pictures (Pettorelli et al. 2005)] and annual survival rate measured in the breeding area of a specific breeding population is one such tool. This method shows great promise for providing useful information about the location of potential migration and wintering areas as well as the environmental conditions in these areas. Several investigations of long-distance migrating species, from the small sand martin to the large white stork (*Ciconia ciconia*) (Møller 1989; Kanyambwa et al. 1990; Peach et al. 1991; Szép 1995), have shown that the estimated annual survival rate has a significant positive correlation with the amount of rainfall in the migrating/wintering areas and that the survival rate can be effectively modelled using these values. The aforementioned studies used rainfall data from specific areas of Africa; however, the NDVI and survival method uses NDVI satellite images that provide quantitative data on the condition of the vegetation (Pettorelli et al. 2005) for the entire African continent with a high spatial (approx. 8×8 km) and temporal (10-day periods) resolution. These images are available for all years from 1981. The close relationship between habitat condition and survival has allowed us to investigate potential areas of Africa, and potential time periods that produce covariation between annual changes in habitat condition and annual survival rate estimates of the study population. Areas with a high positive correlation between habitat condition and survival rate can be regarded as being potential candidates for migrating or wintering areas of the study population. Such satellite-based data provide a unique opportunity to produce correlation maps that shows regions within the African continent for the given period of the year where the annual condition of the vegetation is statistically significantly correlated with the survival rate. These regions can be regarded as potential migration and wintering areas among which the true migration and wintering areas having a high impact on survival are likely to occur. Due to the large number of areas considered during a correlation study, several areas could show high correlations without a biologically relevant connection to the studied populations, thereby underlining the importance of testing the method in the field.

In the investigation reported here, we used the capture-recapture data collected during the long-term barn swallow (*Hirundo rustica*) project in Denmark (Møller 1994) to identify potential migrating and wintering areas of this population in South Africa, which we subsequently identified using the NDVI and survival method (Szép and Møller 2005). We carried out field surveys and bird ringing in the predicted wintering areas and in the control areas in South Africa where European barn swallows winter. Our aim was to test the validity of the

predictions of this new method with respect to identifying migration and wintering areas in South Africa by using existing data and our own field data collected from 2003 to 2004.

Methods

Estimation of survival rate

Annual survival rate was estimated from capture-recapture data of 1193 adult male and 1270 adult female barn swallows that had been ringed and recaptured by A.P. Møller in a study area of approximately 45 km² at Kraghede (57°12'N, 10°00'E), Denmark, from 1984 to 2003 (see Møller, 1994 for details). The Danish study population returns from spring migration in the period spanning April–June and departs on its autumn migration in the period August–October. Wintering takes place in Africa south of the Sahara, with the Danish study population wintering in southern Africa (Møller 1994). Wintering birds are nomadic, following seasonal rains that give rise to the appearance of swarming termites and other insects (Cramp 1988), although, based on ringing data, the great majority (>85%) of barn swallows tend to remain within an approximate 100-km radius of the roost during single and subsequent wintering seasons (Oatley 2000). None of the ringed birds from the Danish focal breeding population has yet to be recaptured during the winter in Africa. We estimated adult annual survival rates using capture-mark-recapture methods (Lebreton et al. 1992). The goodness-of-fit of the general Cormack-Jolly-Seber model (Clobert and Lebreton 1987) to the data was calculated using the programme RELEASE (Burnham et al. 1987) and the bootstrap function of the program MARK (White and Burnham 1999). Modelling and the estimation of survival and recapture rates were made with MARK (White and Burnham 1999). Model selection among studied models was based on Akaike's Information Criterion by selecting the model with the lowest AICc value (Anderson et al. 1994). The Akaike weight (Anderson and Burnham 1999) and likelihood ratio tests were used for comparing a given model with others within which it was nested (Lebreton et al. 1992).

Estimating environmental conditions in Africa

We estimated environmental conditions during migration and in the African winter quarters of the barn swallow using the NDVI, which is based on satellite images indicating the condition of rainfall-dependent vegetation in space and time (Prince and Justice 1991). NDVI provides an estimate of the amount and vigour of vegetation on the Earth's surface and is directly related to the level of photosynthetic activity (Prince and Justice 1991). The NDVI index is likely to reflect the abundance of insects because insects depend on plant productivity.

This is particularly likely to be the case for species like the barn swallow that rely on swarming insects such as termites in Africa as such insects become active in direct response to precipitation. NDVI has been used as an indicator of relative biomass and greenness of the vegetation (Pettoirelli et al. 2005), precipitation (Schmidt and Karnieli 2000) and quantity and quality of bird habitats (Wallin et al. 1992). NDVI data are available at USGS-EROS Fews-Net for the entire African continent (<http://www.igskmncnwb015.cr.usgs.gov/adds/>), and these images have been calibrated for inter-sensor and intra-sensor degradation for 1982–2004 (Tucker et al. 2006).

NDVI data are available for each pixel that covers an area 8×8 km (i.e. 64 km²). The values are subsequently averaged to obtain a mean estimate for each grid cell of 0.25° latitude by 0.25° longitude. This was done for each period of the annual cycle of the barn swallow in Africa (autumn: September–November; winter: December–February; spring: March–May) using WINDISP v4.0 software (<http://www.fao.org/WAICENT/faoinfo/economic/giews/english/windisp/windisp.htm>). We calculated NDVI data for grid cells for which at least 30% of the pixels had valid data. We only included grid cells in the analyses if there were NDVI data available for each year for which we had survival estimates (1984–2003). This criterion resulted in the exclusion of 15% of the approximate 46,000 grid cells in Africa because of cloud-cover and water surface.

Identifying potential migration and wintering areas

Areas were identified using the Spearman rank correlation coefficient between the time series of survival estimates and the time series of NDVI data for each grid cell (Szép and Møller 2005). For each of the three periods (autumn, winter and spring) we identified grid cells that had a positive correlation between the estimate of annual survival and the NDVI exceeding a critical threshold, $r \geq 0.5$. We only investigated positive correlations because migratory birds have populations that are regulated outside of the breeding season (see Discussion in Szép and Møller 2005). Large numbers of positive correlations between survival and NDVI are unlikely to occur in neighbouring squares by chance, and we considered potential areas that were formed from at least four neighbouring 0.25°×0.25° grid cells, where the correlation, between survival and NDVI values in the given grid cell(s) was greater than or equal to 0.5 (Szép and Møller 2005).

Field survey and ringing in South Africa

During two 3-week periods in January–February 2003 and 2004, we carried out intensive surveys across South Africa by visiting the potential wintering areas in the western part of South Africa, located in the Karoo

(northern Cape region), identified by the NDVI and survival method. We also visited other well-known barn swallow wintering areas [central part (Bloemfontein), eastern part (Durban and Pietermaritzburg) and north-eastern part (Middleburg and Johannesburg) of South Africa] which had not been selected; ringing teams commonly band barn swallows at roosts at these latter locations. In addition to observing barn swallows in these areas, we carried out bird ringing, mainly at roosts but occasionally at foraging sites [the Karoo in 2003–2004, at Meltonwold (Loxton)], and we checked for dead birds and counted the numbers of barn swallows on telephone wires with and without rings in the Karoo in 2004. This was done with the permission of the local nature conservation authority (permit: ODB 2159/2004).

In the focal region of the Karoo, we ringed and checked barn swallows for European rings at the following times and locations: (1) 2003: Tanqua Dam (32°23'S, 19°52'E), Saaipais (32°53'S, 20°37'E), Merweville (32°31'S, 21°13'E); 2004: Meltonwold (Loxton) (31°27'S, 22°45'E), 10-km radius area NE direction from Fraserburg (31°45'S, 21°40'E); 10-km radius area at Vosburg (30°45'S, 22°47'E); 5-km radius area SW direction from Griquatown (29°06'S, 23°09'E). We ringed birds at other control sites at Creighton in 2004 (29°58'S, 29°49'E) and Durban in 2003 and 2004 (29°38'S, 31°05'E) and worked together with ringing teams in Bloemfontein (2003 and 2004) (Nuttall 2003), Pietermaritzburg (2003), Middleburg (2003) (van den Brink 2003), Cape Town (2003) and Johannesburg (2003). In 2003, we were able to catch and ring only 20 swallows in the surveyed part of the Karoo without recaptures of any European ringed individuals.

Population and ringing data

We used the BirdLife/EBCC (2004) data for estimating the size of the breeding barn swallow population for European countries. As an estimate of the population size we used the mid-point between the minimum and maximum values of the population sizes.

The number of ringed barn swallows in the countries was estimated from the mean annual ringing totals for 2003 and 2004, where data were available from published ringing reports (Spina 1998, 2001; Clark et al. 2004, 2005; Anon 2005; Mokwa 2005; Roggeman and Vangeluwe 2005), via the ringing centres (Estonia, Lithuania, Russia) or from the official WWW sites (Swedish annual report: <http://www2.nrm.se/rc/ring-sume.html>; Finnish swallow project: <http://www.fmn.helsinki.fi/english/zoology/ringing/research/swallow.htm>; Dutch Swallow Project 2004: <http://www.nioo.knaw.nl/projects/boerenzwaluw/sitehtml/esp2004.htm>). We used the ringing data from the last year of publication if information for 2003 and/or 2004 was unavailable. In the case of Belarus, we estimated the number of ringed birds by assuming similar values as for Ukraine and Russia (i.e. 500 barn swallows per year).

Results

Survival rate

The basic Cormack-Jolly-Seber model (Φ_{s*t}, P_{s*t}) did not provide an adequate fit to the data ($\chi^2 = 71.842$, $df = 33$, $p < 0.001$; RELEASE). The main reason for the lack of fit was the different capture probabilities of newly ringed and previously ringed adults that were significantly different both for males ($\chi^2 = 32.012$, $df = 18$, $p = 0.022$) and females ($\chi^2 = 39.829$, $df = 15$, $p < 0.001$).

This lack of fit is symptomatic of the different survival rates of newly ringed birds (first breeders) and previously ringed birds (older breeders). As a starting general model, we considered the $\Phi_{ma1*ma2*fa1*fa2*t}, P_{s*t}$ model, with survival rates differing among newly ringed males (ma1), previously ringed males (ma2), newly ringed females (fa1) and previously ringed females (fa2), the addition of an interaction term (*) for time (t) and a recapture rate differing between the sexes and varying with time (s*t). This starting general model fitted the data as measured by the bootstrap goodness-of-fit test (MARK programme, $p = 0.59$; 1000 repetitions). The over-dispersion value (c-hat) was slightly less than 1 (c-hat = 0.951), and so a c-hat = 1 value was used for model selection.

During model selection, we found that in the $\Phi_{ma1+fa1+ma2fa2+t}, P.$ model, the survival rate differed among first-time breeding males (ma1) and first-time breeding females (fa1), being the lowest for first-time breeding females and males and the highest for older breeders (ma2fa2) with a positive correlation with time, while the recapture rate was constant over the study period. This model had the lowest AICc value of all the models studied. We then used this model for modelling the survival rate as a function of NDVI values for wintering and migration areas.

Potential migration and wintering areas in South Africa

In the search for potential wintering and migration areas we used the estimated survival rates of the newly ringed, first-time breeding males (ma1) based on the $\Phi_{ma1+fa1+ma2fa2+t}, P.$ model for calculating correlations between survival rates and NDVI values of various grid cells across Africa. The survival rate of each group varied in parallel over the study period, and as the structure of the selected model shows, the survival rate of each group had the same level and direction of annual variation; consequently, we considered the survival rate of first-time breeding males (ma1) to be appropriate for the NDVI investigation.

We did not find any potential areas in South Africa for the autumn migration period (September–November) (Fig. 1a); i.e. there were no clusters of grid cells with significant correlations (i.e. $p > 0.5$). With respect to the wintering period (December–February), there were

seven potential areas in South Africa, all in the western part of the country, mainly in the Karoo (Fig. 1b). Among these areas there was one large area in the central Karoo (Fig. 1b). For the spring migration (March–May), we found 11 potential areas both in western and eastern South Africa (Fig. 1c). Among these areas were two large ones: one along the eastern coast of South Africa and one in the southern part of the Karoo.

When we considered the NDVI values of the seven areas during the winter migration and the 11 areas during the spring migration to be factors influencing survival rate as the dependent variable, the stepwise regression analysis selected one area in the Karoo during the spring migration (March–May) for which the annual changes of NDVI were significantly related to the estimated survival rate ($p=0.005$). This model accounted for 38% of the variance.

Suggested wintering area and existing recovery and recapture data

With respect to the Danish barn swallow population, there were 28 recoveries (i.e. birds found dead) and recaptures (i.e. birds checked alive and re-released) of individuals that had been ringed in Denmark (data from the EURING Databank Fig. 2). All five Danish recov-

eries in South Africa were found in the central and the eastern part of the country, and none of these were found in the Karoo region. The most western recoveries of Danish barn swallows were from Kimberley.

Ratio of European ringed barn swallows in focal and control areas

The ringing and controlling of barn swallows in the suggested wintering area of the Karoo during January 2004 yielded a 1.1% ratio of European ringed swallows among the controlled birds (Table 1). Of the Europeans ringed swallows found in the Karoo, three British, one Dutch and one Norwegian barn swallow had been ringed during the summer roosts, while three other barn swallows had been ringed during the autumn migration in Spain. The identification of the recovered and controlled barn swallows suggests the presence of breeding populations that mainly use the western flyway and of the north-western European breeding populations to which the Danish population belongs (Fig. 2).

The ratio of European ringed barn swallows among ringed birds in other parts of South Africa was much lower. In Bloemfontein, where the most intensive and regular ringing of barn swallows has taken place since 1999 (Nuttall 2003), the mean recapture rate of

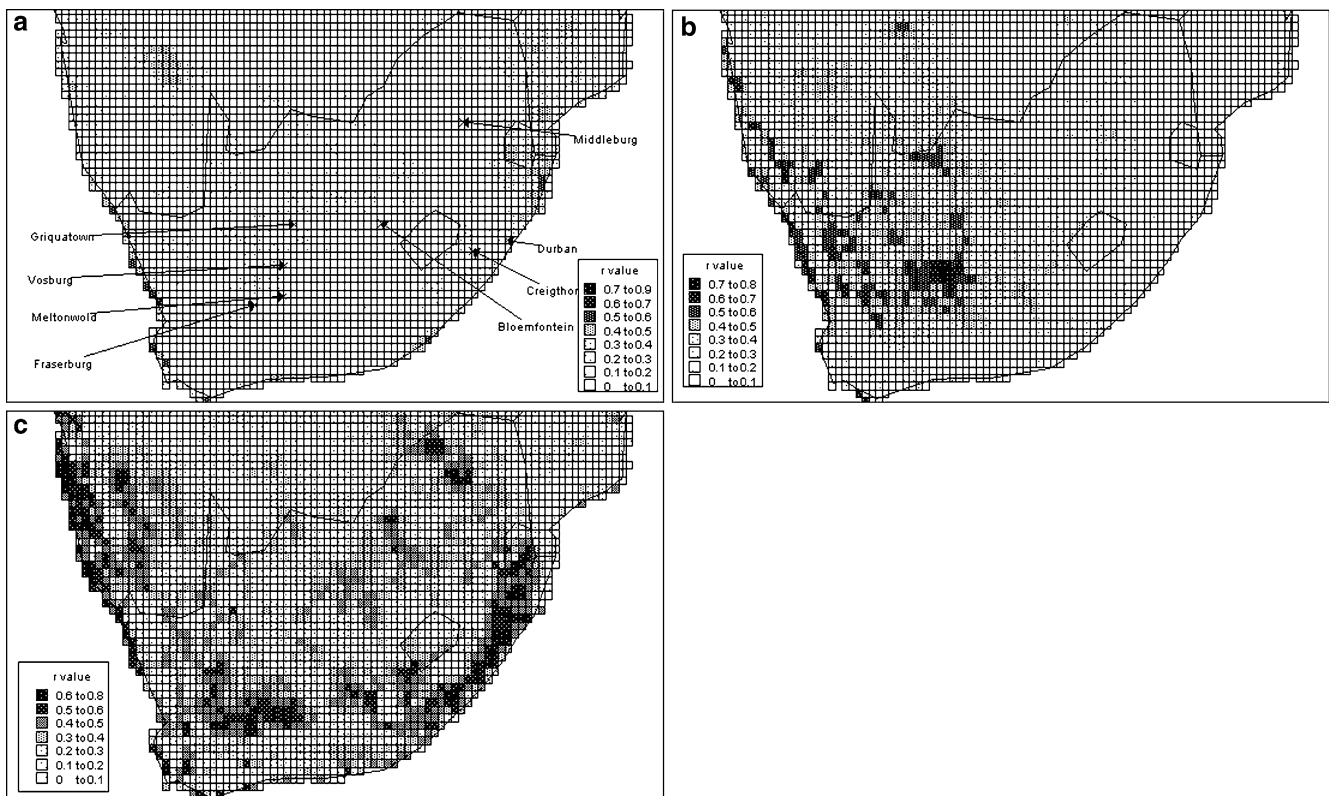


Fig. 1 Correlation between NDVI values of $0.25 \times 0.25^\circ$ squares and survival rate of the Danish breeding population from 1984 to 2003 in South Africa during the autumn (September–November)

(a), winter (December–February) (b) and spring (March–May) (c). Sampling sites are indicated

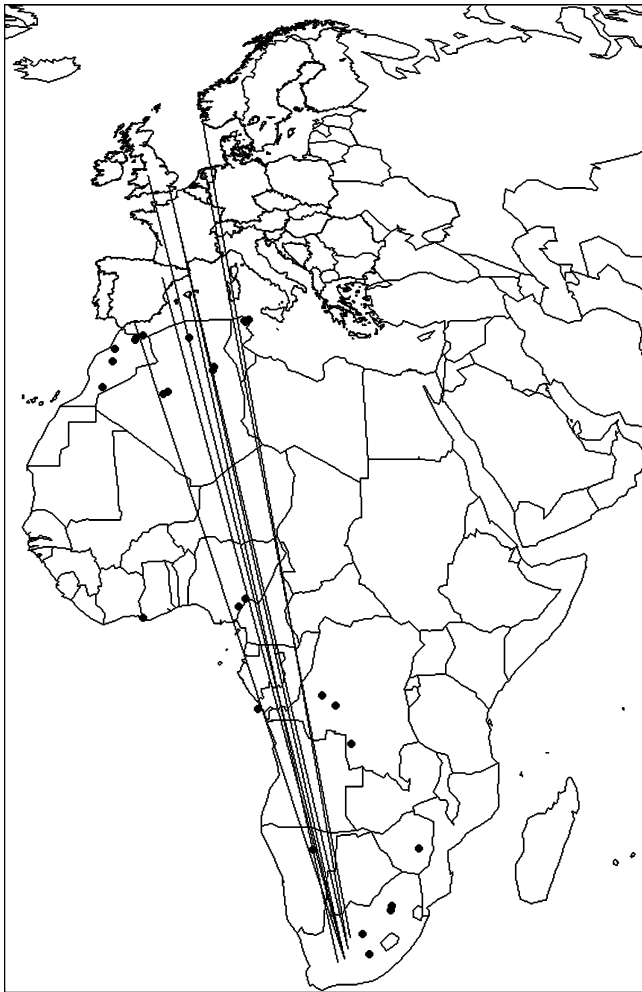


Fig. 2 Sites of recoveries and recaptures of barn swallows in Africa that had been ringed or recaptured in Denmark (black dots). Lines connect the ringing and recapture localities of the eight recaptured barn swallows found in the Karoo in 2004

European ringed barn swallows was 0.45% (SD: 0.237, $n=6$ years) when all data were considered. However this value was lower – 0.35% and had a lower variance (SD=0.136, $n=6$) – when only birds ringed in areas

belonging to the western flyway were included (i.e. ringed birds from Finland and Poland excluded). In 2004 in Bloemfontein, this value was 0.57%; however, only recaptures from the western flyway areas were recorded (Table 2). Intense ringing at a large barn swallow roost in Middleburg (much further to the east) during 2003, organised by Herman and Zephne Bernitz (van den Brink 2003), showed a 0.55% recapture rate when all recapture data were considered, although this value is lower, i.e. 0.26%, when only recaptures from the western flyway were considered (four Finnish-ringed birds excluded). van den Brink (2003) ringed intensively in Botswana at two large barn swallow roosts during 2003 and had a recapture rate of 0.36% from all European ringed barn swallows, although when only data from the western flyway were considered [i.e. excluding birds ringed in Finland (5), Estonia (1), Lithuania (1), Hungary (1) and Israel (1)], this value was only 0.13%.

Ratio of ringed barn swallows and population size in Europe

On the basis of the estimated ratio of ringed barn swallows in various European countries, which are the locations from where the majority of the barn swallows found in South Africa originate (Oatley 2000), the use of the western and eastern flyways is clearly identifiable (Table 2). We can therefore expect that the probability of recapturing a European ringed barn swallow in South Africa is the highest for barn swallows that breed in north-western Europe and use the western flyway, mainly to South Africa. Most barn swallows from this region probably use the western flyway through Spain in both autumn and spring, where the intensive ringing of barn swallows (e.g. 33,700 adults in 2002, Pinilla et al. 2003) mainly at roosts increases the chances of recapturing European ringed barn swallows in South Africa.

The ratio of ringed barn swallows is expected to be much lower in countries from where the majority of individuals use the eastern flyway; the exception being Finland where an intensive ringing of barn swallows, within the framework of the EURING Swallow project

Table 1 Number of European ringed barn swallows and number of controlled barn swallows at the studied sites in 2003 and 2004

Sites	Recaptured individual ^a s	Number of controlled individuals	Ratio of recaptured birds (%)
Karoo 2004	8	763	1.1
Meltonwold 2004 (31° 27' S, 22° 45' E)	4 (2 UK, 2 SP)	462	0.87
Fraserburg area 2004 ^b (31°45' S, 21°40'E)	1 (SP)	100	1.0
Vosburg area 2004 ^b (30°45'S, 22°47'E)	2 (1 UK, 1 N)	101	1.98
Griquatown area 2004 ^b (29°06'S, 23°09'E)	1 (NL)	100	1.0
Bloemfontein 2004 (29°03'S, 26°25'E)	2 (1 N, 1 SP)	350	0.57
Creighton 2004 (29°58'S, 29°49'E)	0	44	0
Durban 2004 (29°38'S, 31°05'E)	0	88	0
Durban 2003 (29°38'S, 31°05'E)	0	98	0

^aUK, United Kingdom; SP, Spain; N, Norway; NL, the Netherlands

^bBarn swallows were controlled by visual observation for rings on the leg and by collecting dead individuals at the same location

Table 2 Estimated population size^a, number of annually ringed barn swallows and ratio of ringed birds^b in European countries where the majority of the breeding barn swallow populations use mainly the western or eastern flyway and winter in South Africa

Country	Population size (mean)	Number of ringed swallow/year ^c	Ratio of ringed swallow (%)	Period ^d
Belgium	50,000	23,000	11.5	2003
Denmark	225,000	4,300	0.48	2004
Netherlands	150,000	11,400	1.9	2003–2004
Norway	45,000	10,000	5.56	1997
Sweden	225,000	1,500	0.17	2003
UK	726,000	39,800	1.37	2003–2004
Western flyway	1,421,000	90,000	1.58	
Belarus	1,250,000	500	0.01	Estimated
Estonia	200,000	1,300	0.16	2003–2004
Finland	155,000	20,000	3.23	2003–2004
Latvia	296,000	600	0.05	1999
Lithuania	225,000	2,400	0.27	2003–2004
Poland	2,250,000	11,500	0.13	2003–2004
Ukraine	1,085,000	500	0.01	1999
Russia	4,750,000	500	0.003	2003–2004
Eastern flyway	10,211,000	37,300	0.09	

^aMean population size calculated on the base of minimum and maximum population size estimates of BirdLife/EBCC (2004)

^bRatio of ringed birds was calculated by dividing the number of ringed barn swallows by the population size multiplied by 4 (one pair: two adults + two juveniles)

^cNumber of ringed birds rounded to hundreds

^dPeriod refers to year(s) for which ringing data were available for a given country. In the case of Belarus, we considered a similar number of ringings as in Russia and Ukraine

(Saurola 2001), has yielded a high recapture ratio (Table 2).

The ratio of European ringed barn swallows among the controlled barn swallows in the focal Karoo region in 2004 was at a level that would be expected on the basis of the number of ringed barn swallows and the sizes of the breeding barn swallow populations in north-western Europe (Table 2).

Discussion

On the basis of the correlation analysis between annual NDVI values and annual survival rate estimates (Szép and Møller 2005) estimated for a specific breeding barn swallow population in Denmark, we have identified potential wintering areas in South Africa. We were not able to find any potential areas for the autumn migration (September–November) when the majority of barn swallows could migrate toward South Africa, but identified only areas in the relevant periods of the year (December–February and March–May) when barn swallows stay in South Africa (Harrison et al. 1997). This result indicates that the NDVI and survival method (Szép and Møller 2005) may provide useful insights into the timing and use of the identified potential wintering areas.

During December–February, when the majority of barn swallows are moulting in Southern Africa (van den Brink et al. 2000) and the level of movement is likely to be at its lowest, we identified potential wintering areas for the Danish population only in the western part of South Africa, with the largest continuous area being in the Karoo (northern Cape). We did not find any potential areas in the central or eastern part of South Africa for

this period. The atlas of southern African birds (Harrison et al. 1997) indicates that the identified region is used by wintering barn swallows, although the density of barn swallows here is lower than in the central and eastern parts of the country. Our field survey showed the density of the barn swallows in the identified area of the Karoo was lower than in the central and eastern parts of the country. We identified potential areas in the central and eastern parts of the country only during March–May, which covers the end of the moulting and the beginning of the spring migration of the barn swallow. When we took all of the identified areas in South Africa into consideration, we found that the area in the Karoo during March–May explained most of the variance in survival rate of the studied Danish breeding population.

It initially appears to be contradictory that areas in the central and eastern parts of South Africa, from where all Danish recoveries came from, should not play a primary role in wintering for this population. However, the ringing of barn swallows in South Africa is highly biased towards the central and eastern parts of the country, potentially leading to a biased distribution of recaptures and recoveries of European-ringed barn swallows. Because of the larger breeding populations and the smaller number of ringed barn swallows in the countries contributing to the eastern flyway than in the countries contributing to the western flyway, the number of recoveries could also be biased. During our field survey in the Karoo, we found that the barn swallow forms small roosts, rarely numbering more than 1000 individuals. It is difficult to find such small roosts, which are far apart and probably highly variable in time and space. Therefore, it is likely to be problematic to ring barn swallows in the Karoo compared to other regions

in the central and eastern parts of the country, where larger, less temporally variable roosts are common and where there are more ringers. This could explain why there was no relevant barn swallow ringing in the identified Karoo region before the present investigation.

The high ratio of European ringed barn swallows among the controlled individuals in the Karoo region is similar to the ratio that would be expected on the basis of ringed barn swallows and the population sizes of barn swallows of the north-western European breeding population to which the Danish population belongs. The level of this ratio in the Karoo is higher than that found at any other locality in the central and eastern parts of South Africa and Botswana during the same years, indicating the much lower influence of admixture of unringed barn swallows from the eastern flyway. This result is consistent with the identified area in the Karoo being important to the Danish population.

The data provided by the long-term study of barn swallows in Denmark (Møller 1994) could assist us in exploring the wintering area, not only for the focal population but also on a larger scale in nearby regions in Europe. In our case, the origin of recaptures and recoveries of European ringed birds in the Karoo shows that the identified wintering area could be important to barn swallow breeding populations in north-western Europe (e.g. UK, the Netherlands, Norway, Sweden and Denmark). Further studies on connectivity could help in identifying the scale at which we can expect similarities in migration and wintering areas among breeding populations.

The present validation study of the NDVI and survival method (Szép and Møller 2005) in South Africa has shown that this method can help identify potential wintering and migration areas for breeding populations and the timing of use of such areas. The area where the majority of the focal Danish breeding population winters can be among those areas with a high positive correlation between NDVI values and survival rates. The predictions formulated using this method with respect to the location of these potential wintering areas may be give the opportunity to be tested directly using field surveys, ringing and stable isotope and trace element analysis. The NDVI and survival method can help focus ringing effort to regions and areas that have much greater impact on the survival of specific breeding populations than earlier studies have allowed.

Zusammenfassung

Auf der Suche nach möglichen Überwinterungs- und Zuggebieten einer dänischen Rauchschnalbenpopulation in Südafrika durch Korrelation von NDVI und Überlebensraten

Mithilfe einer Korrelationsanalyse von jährlichen NDVI-Werten (von Satellitenbildern abgeleitete Vegetationsdichteindizes) aus Afrika und der jährlich

geschätzten Überlebensrate einer dänischen Rauchschnalbenpopulation (*Hirundo rustica*), haben wir mögliche Überwinterungs- und Zuggebiete dieser Population in Südafrika zwischen Dezember und Februar bzw. März und Mai identifiziert. Von Dezember bis Februar fanden wir mögliche Überwinterungsgebiete nur im westlichen Teil von Südafrika, in der Gegend Karoo. Mögliche Gebiete in den zentralen und östlichen Teilen des Landes wurden nur zwischen März und Mai identifiziert. Die NDVI-Werte von März bis Mai aus Karoo erklärten einen Großteil der jährlichen Variation in der Überlebensrate adulter Vögel der dänischen Population. Der hohe Anteil der in Europa beringten Rauchschnalben unter den in Karoo kontrollierten Individuen ähnelt dem Verhältnis von der Zahl beringter Rauchschnalben zur geschätzten Größe der NW-europäischen Brutpopulation. Der Anteil ist in Karoo höher als in jedem anderen Gebiet der zentralen und östlichen Teile von Südafrika und Botswana, was darauf hindeutet, dass Rauchschnalben der östlichen Zugroute gegenüber denen der westlichen Zugroute in der Beringung unterrepräsentiert sind und dort fehlen. Dieser Ansatz zeigt, dass die NDVI- und Überlebensmethode dazubeitragen können, den Beringungsaufwand auf bestimmte Regionen und Gebiete, die spezifische Brutpopulationen beherbergen können, zu fokussieren, indem sie hilft mögliche Überwinterungs- und Zugareale von Zugvogelpopulationen zu identifizieren.

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References

- Alerstam T (1991) Bird migration. Cambridge University Press, Cambridge
- Anderson DR, Burnham KP (1999) Understanding information criteria for selection among capture-recapture or ring recovery models. *Bird Study* 46:S14–S21
- Anderson DR, Burnham KP, White GC (1994) AIC model selection in overdispersed capture-recapture data. *Ecology* 75:1780–1793
- Anon (2005) Copenhagen bird ringing centre, zoological museum. Report at the EURING General Assembly, Strasbourg
- Berthold P (1993) Bird migration. Oxford University Press, Oxford
- Berthold P (2001) Bird migration: A general survey, 2nd edn. Oxford University Press, Oxford
- Berthold P, Fiedler W, Schlenker R, Querner U (1998) 25-year study of the population development of Central European songbirds: a general decline, most evident in long-distance migrants. *Naturwissenschaften* 85:350–353
- BirdLife/EBCC (2004) Birds in Europe: population estimates, trends and conservation status. BirdLife conservation series No. 12, Cambridge University Press, Cambridge

- Brink B van den (2003) Report of European swallow *Hirundo rustica* ringing in Botswana in 2003. *Afr News* 32:51–53
- Brink B van den, Bijlsma RG, van der Have TM (2000) European swallows (*Hirundo rustica*) in Botswana during three non-breeding seasons: the effects of rainfall on moult. *Ostrich* 71:198–204
- Brown JL, Li SH, Bhagabati N (1999) Long-term trend toward earlier breeding in an American bird: a response to global warming? *Proc Natl Acad Sci USA* 96:5565–5569
- Burnham KP, Anderson DR, White GC, Brownie C, Pollock KH (1987) Design and analysis methods for fish survival experiments based on release-recapture. *Am Fish Soc Monogr* 5:1–437
- Clark JA, Robinson RA, Blamer DE, Adams SY, Collier MP, Grantham MJ, Blackburn JR, Griffin BM (2004) Bird ringing in Britain & Ireland in 2003. *Ring Migr* 22:85–127
- Clark JA, Robinson RA, Balmer DE, Blackburn JR, Grantham MJ, Risely K, Adams SY, Griffin BM (2005) Bird ringing in Britain and Ireland in 2004. *Ring Migr* 22:213–253
- Clobert J, Lebreton J-D (1987) Recent models for mark-recapture and mark resighting data: a response to C. Brownie. *Biometrics* 43:1019–1022
- Cochran WW, Wikelski M (2005) Individual migratory tactics of New World *Catharus* thrushes. In: Greenberg R, Marra P (eds) *Birds of two worlds*. Johns Hopkins Press, Washington, D.C.
- Cramp S (ed) (1988) *The Birds of the Western Palearctic* vol 5. Oxford University Press, Oxford
- Crick HQP, Dudley C, Glue DE, Thomson DL (1999) Climate change related to egg-laying trends. *Nature* 399:423–424
- Etterson JR, Shaw RG (2001) Constraint on adaptive evolution to global warming. *Science* 294:151–154
- Greenberg R, Marra P (eds) (2005) *Birds of two worlds. The ecology and evolution of migration*. Johns Hopkins Press, Washington, D.C.
- Harrison JA, Allan DG, Underhill LG, Herremans M, Tree AJ, Parker V, Brown CJ (eds) (1997) *The atlas of Southern African birds*. BirdLife South Africa, Johannesburg, South Africa
- Hobson KA (2005) Flying fingerprint, making connections with stable isotopes and trace elements. In: Greenberg R, Marra P (eds) *Birds of two worlds*. Johns Hopkins Press, Washington, D.C.
- Hoyo J Del, Elliott A, Christie D (eds) (2004) *Handbook of the birds of the world, vol 9. Cotingas to pipits and wagtails*. Lynx Edicions, Barcelona
- Kanyambwa S, Schierer A, Pradel R, Lebreton J-D (1990) Changes in adult annual survival rates in a western European population of the white stork (*Ciconia ciconia*). *Ibis* 132:27–35
- Lebreton J-D, Burnham KP, Clobert J, Anderson DR (1992) Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol Monogr* 62:67–118
- Marchant JH (1992) Recent trends in breeding populations of some common trans-Saharan migrant birds in northern Europe. *Ibis* 134[Suppl 1]:113–119
- Marra PP, Hobson KA, Holmes RT (1998) Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* 282:1884–1886
- Mokwa T (2005) Report of the Gdańsk ringing scheme 2003–2004. EURING General Assembly, Strasbourg, France
- Møller AP (1989) Population dynamics of a declining swallow *Hirundo rustica* L. population. *J Anim Ecol* 58:1051–1063
- Møller AP (1994) *Sexual selection and the barn swallow*. Oxford University Press, Oxford
- Møller AP, Szép T (2005) Rapid evolutionary change in a secondary sexual character linked to climatic change. *J Evol Biol* 18:481–495
- Nuttall R (2003) The Bloemfontein swallow project: 2001–2003. *Afr News* 32:12–15
- Peach WJ, Baillie SR, Underhill L (1991) Survival of British sedge warblers (*Acrocephalus schoenobaenus*) in relation to west African rainfall. *Ibis* 133:300–305
- Pettorelli N, Vik JO, Mysterud A, Gaillard J-M, Tucker CJ, Stenseth NC (2005) Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends Ecol Evol* 20:503–510
- Pinilla J, Frias O, Moreno-Opo R, Gómez-Manzanique A, Hernández-Carrasquilla F (2003) Informe De Actividades De La Central De Anillamiento De Aves Icona. AÑO 2002. SEO/BirdLife, Madrid
- Prince SD, Justice CO (eds) (1991) Coarse resolution remote sensing of the Sahelian environment. *Int J Remote Sens* 12:1133–1421
- Oatley TB (2000) Migrant European swallows (*Hirundo rustica*) in southern Africa: a southern perspective. *Ostrich* 71:205–209
- Roggeman W, Vangeluwe D (2005) Belgian ringing scheme (BLB) Report at the EURING General Assembly, Strasbourg
- Rubinstein DR, Hobson KA (2004) From birds to butterflies: animal movement patterns and stable isotopes. *Trends Ecol Evol* 19:256–263
- Sæther B-E, Tufto J, Engen S, Jerstad K, Røstad OW, Skåtan JE (2000) Population dynamical consequences of climate change for a small temperate songbird. *Science* 287:854–856
- Saino N, Szép T, Ambrosini R, Romano M, Møller AP (2004) Ecological conditions during winter affect sexual selection and breeding in a migratory bird. *Proc R Soc London Ser B* 271:681–686
- Saurola P (2001) The EURING swallow project in Finland years 1999–2000. EURING Newsl 3
- Schmidt H, Karnieli A (2000) Remote sensing of the seasonal variability of vegetation in a semi-arid environment. *J Arid Environ* 45:43–60
- Spina F (1998) The EURING swallow project: results from the first pilot year. EURING Newsl 2
- Spina F (2001) EURING swallow project third newsletter years 1999–2000. EURING Newsl 3
- Szép T, Møller AP (2005) Environmental conditions on migration and the winter quarters and survival of migratory birds. In: Greenberg R, Marra P (eds) *Birds of two worlds*. Johns Hopkins Press, Washington, D.C.
- Szép T (1995) Relationship between West African rainfall and the survival of central European bank swallows *Riparia riparia*. *Ibis* 137:162–168
- Szép T, Møller AP, Vallner J, Kovács B, Norman D (2003) Use of trace elements in feathers of sand martin *Riparia riparia* for identifying moulting areas. *J Avian Biol* 34:307–320
- Tucker CJ, Pinzon JE, Brown ME, Slayback D, Pak EW, Mahoney R, Vermote E, El Saleous N (2006) An extended AVHRR 8-km NDVI data set compatible with MODIS and SPOT vegetation NDVI data. *Int J Remote Sens* (in press)
- Wallin DO, Elliott CCH, Shugart HH, Tucker CJ, Wilhelm F (1992) Satellite remote sensing of breeding habitat for an African weaver-bird. *Landscape Ecol* 7:87–99
- Webster MS, Marra PP, Haig SM, Bensch S, Holmes RT (2002) Links between worlds: unraveling migratory connectivity. *Trends Ecol Evol* 17:76–83
- White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:S120–138