

Migratory connectivity in barn swallows and other hirundines

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Environmental indicators such as the Normalized Difference Vegetation Index (NDVI) (Petty et al. 2005) provide important insights into spatial and temporal patterns of primary productivity and hence food availability for many different organisms, including barn swallows *Hirundo rustica* (Saino et al. 2004a, b). Based on this observation, Szép and Møller (2005) argued that when time series of survival estimates were available for a migratory bird population, this time series could be correlated with time series for environmental indicators such as NDVI, particularly in

areas where the given population was wintering, provided that mortality mainly occurred outside the breeding season as is commonly the case in migratory birds (review in Szép and Møller 2005). Therefore, this novel approach to identification of potential wintering grounds of migratory bird populations opened up the possibility for further tests based on stable isotope, trace element or genetic marker profiles. A number of caveats and underlying assumptions of this approach were discussed in detail by Szép and Møller (2005). Recently, Szép et al. (2006) extended this approach in an attempt to identify potential wintering grounds for a Danish barn swallow population that had been subject to a long-term population study since 1984, thus providing information on annual survival rates. Szép et al. (2006) used correlations between NDVI and adult survival rates, but also information on the frequency of ringed barn swallows in different parts of South Africa, and the actual South African recovery sites of breeding birds from Denmark, to identify potential wintering grounds of the specific population. We are currently investigating the extent to which trace element and stable isotope profiles from barn swallows from different areas in South Africa match the profiles from breeding birds from the Danish breeding population.

Underhill (2007; LGU hereafter) has criticized our approach on a number of different grounds, namely that: (1) we attempted to “demonstrate” that the Danish population wintered in Northern Cape; (2) we should have asserted that there is a fine-scale one-to-one link between breeding areas and non-breeding areas; (3) “the fine-scale one-to-one link between breeding areas and non-breeding areas...does not change through the passage of decades”; (4) there is no evidence of segregation of migratory populations of

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barn swallows in Africa; (5) the redistribution of birds in South Africa in response to changes in rainfall patterns prevents any evidence of connectivity; (6) we made no attempt to test if a “large number of positive correlations between survival and NDVI are unlikely to occur in neighboring squares by chance”; and (7) spatial autocorrelation in rainfall would produce a large number of similar correlations simply by chance. Although we have not made several of these postulated claims, or we have already made the tests and published the results (Szép and Møller 2005; Møller and Hobson 2004; Saino et al. 2004a, b), we examine each of these assertions below.

1. According to LGU, we should have attempted to demonstrate that the Danish population wintered in Northern Cape. This is incorrect because no claim can be further away from our philosophy of science. We had no intention of demonstrating anything. What we did was to produce a number of hypotheses about connectivity, carefully making predictions, and to test these in a hypothetico-deductive manner, as is commonly done by evolutionary ecologists. It is well known that attempts to make demonstrations lead nowhere (Popper 1972). That was also reflected by our information-theoretic model selection approach (Burnham and Anderson 2002).
2. We should have asserted that there is a fine-scale one-to-one link between breeding areas and non-breeding areas. Again, we have never made such a claim in Szép et al. (2006), nor in the paper originally describing the method (Szép and Møller 2005). We made no statements whatsoever about the scale of connectivity. While connectivity has been the subject of intense scientific interest for some time (e.g., Webster et al. 2002), we carefully avoided making any specific statements about the scale of such effects. Saino et al. (2004a, b) have shown for an Italian population of barn swallows that there is a good match between NDVI in a part of Central Africa, where the population winters according to extensive ringing recoveries, and life history, morphology and parasite load of individuals from that population. This provides evidence of the scale of connectivity effects being of the order of hundreds of kilometers, and Saino et al. (2004a, b) carefully investigated that question by changing the scale of NDVI information used for their analyses. Furthermore, Møller et al. (2006) have shown, using stable isotope analysis, that barn swallows in Ukraine mainly winter in eastern South Africa, but in the sink population around Chernobyl they originate from a larger area as reflected by the increased variance in isotopes. Thus, source–sink dynamics can affect variance in isotopic profiles and, by inference, the spatial range of winter sites contributing to a local population.
3. “The fine-scale one-to-one link between breeding areas and non breeding areas...does not change through the passage of decades”. We have made no claims about temporal stability of connectivity beyond the duration of the study on adult survival rates. It would be erroneous to make such a claim on long time scales because changes in rainfall patterns over ecological and geological time scales would have necessitated changes in distributions of wintering populations, as already discussed extensively by Moreau (1972). In fact, there is empirical evidence for the barn swallow, showing that a specific breeding population has changed its distribution locally in the wintering areas in South Africa (Mead 1970). This observation indicates that (1) wintering grounds can change, but also (2) that the winter recoveries of such a breeding population remain concentrated in a specific area despite changes in rainfall causing changes in distribution.
4. LGU claims that there is no evidence of segregation of migratory populations of barn swallows in Africa, following information published by Rowan (1968) and Oatley (2000). Neither Rowan (1968) nor Oatley (2000) made any statistical analyses of connectivity, and their studies thus do not have any empirical bearing on the issue of connectivity. R. Ambrosini, A. P. Møller and N. Saino (unpublished manuscript) have recently developed a new method to quantify connectivity and objectively delineate clusters of recoveries that can be said to be statistically identifiable and unique, relying on randomization procedures and Mantel correlation coefficients. Using the more than 3,000 recoveries of barn swallows from Africa, Ambrosini et al. demonstrated that there was highly significant clustering, with evidence of four different clusters that basically corroborated Moreau’s (1972) suggestions. Among these clusters, there was one in southwestern Africa with its main breeding grounds in the United Kingdom, the Netherlands and Denmark, and a second cluster in southeastern Africa with its main breeding grounds in Sweden, Finland, the Baltic countries and further east. Consistently, Møller and Hobson (2004) have shown for the Danish barn swallow population, which is the subject of

this paper, that it consists of at least two isotopically distinct populations, presumably wintering in different areas, where the single annual molt takes place. The common and the rare isotopic groups also differed in morphology and reproduction despite breeding sympatrically. T. Szép, M. Reviego, F. de Lope and A. P. Møller (unpublished manuscripts) have similarly identified sympatric populations of sand martins *Riparia riparia* in Hungary and house martins *Delichon urbica* in Spain that breed in neighboring colonies, but differ in trace element profile, timing of arrival, morphology, reproduction and temporal pattern of adult survival. These findings suggest that connectivity is a common phenomenon in barn swallows in particular and in hirundines in general.

5. The redistribution of birds in South Africa with changes in rainfall patterns prevents any evidence of connectivity. The redistribution of hirundines in Africa in relation to rainfall is a classical fact of ornithology (Rudebeck 1957). However, that does not prevent connectivity from being present, as we have shown above. We suggest that redistribution is not the same as mixing, and that birds from different populations still remain segregated despite redistribution. This suggestion is supported by extensive analyses of stable isotope and trace element profiles of feathers from barn swallows captured at roosts along a gradient from west to east across South Africa (T. Szép, K. A. Hobson, J. Vallner, S. E. Piper, B. Kovács, D. Z. Szabó and A. P. Møller, unpublished manuscript). That study shows that 60% of all individuals can be correctly assigned to roosts based on discriminant function analyses of feather contents of stable isotopes and trace elements. If there had been both frequent redistribution and mixing from different roosts, such high levels of correct classification would have been unfeasible.
6. Szép et al. (2006) made no attempt to test if a “large number of positive correlations between survival and NDVI are unlikely to occur in neighbouring squares by chance”. Contrary to this claim, we have explicitly tested whether a large number of positive correlations between survival and NDVI are unlikely to occur in neighboring squares by chance, using a number of different scenarios and assumptions (Szép and Møller 2005, p. 393). We did not repeat these tests and assumptions in Szép et al. (2006), because they had already been presented elsewhere. However, we did cite our previous paper and referred readers to that source for further information.

7. Spatial autocorrelation in rainfall would produce positive correlations between survival and NDVI in neighboring squares (in fact, not squares because they are $0.25^\circ \times 0.25^\circ$ cells) by chance alone. We are fully aware of the effect of auto-correlation in rainfall patterns, because we have already specifically analyzed and published information on this issue based on NDVI information from South Africa (Szép and Møller 2005). These spatial autocorrelation analyses showed that the scale of such correlation is in the order of up to a couple of hundred kilometers (Szép and Møller 2005, pp. 396–397). Thus, we can dismiss this factor as accounting for large clustering of squares with significant correlations between NDVI and adult survival that we have reported (Szép and Møller 2005; Szép et al. 2006).

In conclusion, we suggest that the method that we have developed (Szép and Møller 2005; Szép et al. 2006) provides important and useful information about connectivity in migratory birds. Such information can form the basis for specific studies attempting to test whether isotope or trace element profiles of genetic markers from a given area in the winter quarters coincide with those obtained at the breeding grounds. Clearly, this method is superior to just sampling randomly across Africa to identify specific wintering grounds. Furthermore, we strongly believe that the way forward for the scientific study of migratory birds is by accumulation of knowledge and explicit tests of underlying assumptions and predictions, as done by Szép and Møller (2005) and Szép et al. (2006). Finally, we argue that our method provides an important basis and incentive for collaboration between ornithologists in Europe and Africa, as shown by Szép et al. (2006).

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