In focus: Stay-at-home strategy brings fitness benefits to migrants

James J. Gilroy, School of Environmental Sciences, University of East Anglia

Abstract:

In this issue, two studies examine the extent to which variation in migratory behaviour influences individual fitness across a population. Lok et al. (2017) examine reproductive success and post-fledging survival in a population of Eurasian spoonbills (*Platalea leucorodia*), comparing individuals that winter in south-west Europe against those migrating to sub-Saharan Africa, while Grist et al. (2017) measure reproductive success in a population of European shags (*Phalacrocorax aristotelis*) breeding in Scotland that either remain resident or migrate to surrounding waters. Both studies find that individuals migrating longer distances tend to show later initiation of breeding attempts. In turn, longer migration correlates with lower reproductive success in both populations. In spoonbills, this effect is most pronounced in older male birds, whilst young individuals show little difference in breeding success with respect to migration distance. In shags, fitness benefits of residence were most pronounced when both individuals of a pair were resident, although there was no evidence of assortative mating. Both studies provide fascinating new insights into the role migratory variability can play in shaping population dynamics.

Main text:

Migration ranks among the greatest spectacles of the natural world, and yet it remains one of the most challenging aspects of animal ecology to study. Partly owing to the difficulty of tracking individuals as they traverse the globe, we still understand relatively little about key aspects of migratory life, including the mechanisms that underpin variation in migration within and between individuals, and how this influences migratory evolution.

For researchers seeking to understand migratory behaviour, fertile ground can be found among species that express multiple migratory strategies within the same breeding population. In particular, partial-migrants - those with both resident and migratory phenotypes – offer opportunities to directly compare fitness consequences between strategies, as well as tease apart factors influencing why individuals adopt one strategy or another (Adriaensen & Dhondt 1990). Partial migration is relatively widespread in nature (Chapman et al. 2011), but researchers have long struggled to collect the detailed data necessary to elucidate the processes underlying emergent patterns. In particular, research has been hampered by the difficulty of measuring migration at the individual scale, and of following individuals for long enough to quantify their subsequent fitness (Marra et al. 1998; Gunnarsson et al. 2006). Such data can only be collected through exhaustive efforts to mark and track individuals across large spatial and temporal scales.

In this issue, two studies report on just such exhaustive efforts, shedding new light on the within-species migratory variability and how it relates to individual fitness. Grist et al. (2017) report on a study of European shags (*Phalacrocorax aristotelis*) breeding on the Isle of May, Scotland, in which the reproductive success of resident individuals is compared against those migrating relatively short distances (up to 100km) to wintering locations in surrounding waters. Lok et al. (2017) use a similar approach to report on fitness differences among Eurasian spoonbills (*Platalea leucorodia*) breeding in the Netherlands, this time comparing shorter-distance migrants (up to 2,000 km) against long-distance migrants that winter in sub-Saharan Africa (c. 4,700 km). Combined, these studies thus provide fascinating insights into migratory variability across a broad swathe of the migratory spectrum.

Strikingly, both studies report similar overall patterns within their study populations (Fig. 1): that individuals performing longer migrations tend to have lower reproductive fitness than those wintering closer to their breeding sites. In shags, resident individuals tended to raise more young, of higher condition than their migratory counterparts, and thus had greater chance of subsequently recruiting young into the breeding population. In spoonbills, that pattern was echoed for short-distance migrants relative to those that cross the Sahara each winter. Increased fitness amongst shorter-distance migrants has been reported previously in several other species (e.g. Adriaensen & Dhondt 1990; Gillis et al. 2008; Anderson et al. 2015), but the new studies in this issue provide unprecedented novel insights into the mechanisms underpinning the emergent pattern.

In both studies, fitness differences among individuals were closely linked to the timing of breeding. Individuals migrating shorter distances (spoonbills) or remaining resident (shags) tended to initiate broods earlier in the season than their more migratory counterparts. As is common throughout the avian world, earlier initiation translates into greater chances of successfully raising young to fledging (Forslund & Part 1995). This could be related to nest site quality – those arriving earliest at the breeding colony have access to the best locations (Kokko 1999) - or optimal timing of breeding in relation to seasonal peaks of resource availability (Both & te Marvelde 2007; Jones & Cresswell 2010). Early fledglings also tend to have greater post-fledging survival chances, often as they have a longer period to feed prior to the onset of more difficult conditions at the end of the breeding season (Naef-Daenzer et al. 2001).

It should perhaps come as little surprise that longer-distance migrants have poorer breeding success – migration is, after all, an arduous feat that can impose significant costs on the condition of those undertaking it (McWilliams et al. 2004). However, this poses an evolutionary conundrum: if longer-distance migration is more costly than residence, why would it persist in the population? Evolutionary models suggest that multiple migration strategies (including residence) can persist if 1) overall fitness benefits are balanced by the two strategies, or 2) if the optimal outcome for an individual varies depending on its phenotype (Lundberg 1988; Kaitala et al. 1993; Chapman et al. 2011).

In both of the new studies, fitness benefits appear to be unbalanced in favour of shorter migration (unless some unmeasured parameter is having a buffering effect), suggesting that condition 1 is not met in these cases. For condition 2 to be the driver underpinning migratory persistence, migration would need to be the best option for at least some of the individuals within each population. This could arise, for example, if individuals with a particular trait are unlikely to survive if they adopt the resident/short distance strategy, despite incurring subsequent costs for reproduction. What might such a trait be?

In the shag population, migratory strategies appear to remain fixed though adult life (Grist et al. 2014), suggesting that migratory 'decisions' do not depend on any condition-dependent phenotypic trait. Grist et al. (2017) also found no influence of sex on the likelihood of individuals adopting a given strategy, nor on its consequent fitness benefits. Interestingly, fitness benefits were maximised if both male and female of a pair were resident, and yet there was no evidence of assortative mating in relation to migratory strategy. Costly migration therefore does not appear to persist due to asymmetric sex-dependent benefits in this case, and the role of other phenotypic traits (e.g. body size) remains unclear.

In spoonbills, Lok et al. (2017) uncover clearer evidence for a trait-dependent fitness cost of migration, relating to age: older long-distance migrants (particularly males) tend to breed significantly later than short-distance migrants of equivalent age, and consequently have lower likelihood of raising young to recruitment. For younger individuals, however, the fitness benefits of long- and short- migration were more similar. Trans-Saharan migration might therefore remain an optimal (or at least break-even) strategy for younger individuals, allowing long-distance migration to persist. Under such a scenario, however, we might expect individuals to switch from longer to shorter migration as they age, and yet spoonbill migratory strategy again typically remains fixed throughout life, just as it does in shags. Condition-dependence therefore seems unlikely to be the principal mechanism allowing more costly long-distance migration to persist in either population.

One possibility is that the relative benefits of different migratory strategies vary over timescales greater than those captured in either study. Both sets of authors consider the possibility that the observed benefits of shorter migration may be counterbalanced by other factors over longer time periods, for example by periodic survival costs incurred among residents when winter conditions are poor (Kaitala et al. 1993).

Another intriguing possibility is that the relative benefits of short-migration/residency have emerged only recently, as a result of environmental change. This seems particularly plausible in the case of the spoonbills, as the numbers of individuals overwintering in Europe have increased significantly over the last 20 years (Lok, Overdijk & Piersma 2013). This could reflect improving conditions for overwintering in Europe following climatic amelioration, or deteriorating conditions in the traditional African winter range. Links between environmental change and altered migratory behaviour are seldom documented, although climate-related patterns of migratory change have been observed in European wildfowl (Maclean et al. 2008), as well as in some shorebirds (Austin & Rehfisch 2005) and passerines (Visser et al. 2009). Grist et al (2017) and Lok et al (2017) both provide compelling evidence that within-population variation in migration distance, and consequent fitness impacts, could be important drivers of population-scale changes in migratory behaviour. Such changes may become increasingly important in future, as migratory species respond to climatic changes occurring in each of the areas they visit during the annual cycle.

Overall, these studies demonstrate the tremendous insights that can be gained from long-term mark-resight studies of migratory variability within populations. Whilst they reveal intriguing commonalities, they also highlight the extent to which species differ in the mechanisms underpinning migratory variability, and their effects on sex- and age-specific fitness. Many questions remain to be answered, including the role of density dependence in regulating the optimality of different strategies (Chapman et al. 2011), as well as the determinants of strategy selection at early life stages. Understanding the mechanistic processes underpinning migratory variation will be fundamental if we are to fully understand how migratory systems evolve, or predict how they will respond to conservation actions under ongoing environmental change.

References

Adriaensen, F. & Dhondt, A.A. (1990) Population dynamics and partial migration of the European robin (Erithacus rubecula) in different habitats. Journal of Animal Ecology, 59, 1077-1090.

Anderson, A.M., Novak, S.J., Smith, J.F., Steenhof, K., Heath, J.A. (2015) Nesting phenology, mate choice and genetic divergence within a partially migratory population of American Kestrels. The Auk, 133, 99-109.

Austin, G. E., & Rehfisch, M. M. (2005). Shifting nonbreeding distributions of migratory fauna in relation to climatic change. Global Change Biology, 11, 31-38.

Both, C., & te Marvelde, L. (2007). Climate change and timing of avian breeding and migration throughout Europe. Climate Research, 35, 93-105.

Chapman, B. B., Brönmark, C., Nilsson, J. Å., & Hansson, L. A. (2011). The ecology and evolution of partial migration. Oikos, 120, 1764-1775.

Forslund, P. & Part, T. (1995) Age and reproduction in birds - hypotheses and tests. Trends in Ecology & Evolution, 10, 374-378

Gillis, E.A., Green, D.J., Middleton, H.A. & Morrissey, C.A. (2008) Life history correlates of alternative migratory strategies in American Dippers. Ecology, 89, 1687-1695.

Grist, H., Daunt, F., Wanless, S., Nelson, E.J., Harris, M.P., Newell, M., Burthe, S. & Reid, J.M. (2014) Site fidelity and individual variation in winter location in partially migratory European shags. PloS One, 9, e98562.

Grist, H., Daunt, F., Wanless, S., Burthe, S. J., Newell, M. A., Harris, M. P., & Reid, J. M. (2017). Reproductive performance of resident and migrant males, females and pairs in a partially migratory bird. Journal of Animal Ecology.

Gunnarsson, T.G., Gill, J.A., Atkinson, P.W., Gélinaud, G., Potts, P.M., Croger, R.E., Gudmundsson, G.A., Appleton, G.F. & Sutherland, W.J. (2006) Population-scale drivers of individual arrival times in migratory birds. Journal of Animal Ecology, 75, 1119-1127.

Jones, T., & Cresswell, W. (2010). The phenology mismatch hypothesis: are declines of migrant birds linked to uneven global climate change?. Journal of Animal Ecology, 79, 98-108.

Kaitala, A., Kaitala, V., & Lundberg, P. (1993). A theory of partial migration. The American Naturalist, 142, 59-81.

Kokko, H. (1999). Competition for early arrival in migratory birds. Journal of Animal Ecology, 68, 940-950.

Lok, T., Overdijk, O. & Piersma, T. (2013) Migration tendency delays distributional response to differential survival prospects along a flyway. American Naturalist, 181, 520-531.

Lok, T., Veldhoen, L., Overdijk, O., Tinbergen, J. M., & Piersma, T. (2017) An age-dependent fitness cost of migration? Old trans-Saharan migrating spoonbills breed later than those staying in Europe, and late breeders have lower recruitment. Journal of Animal Ecology.

Lundberg, P. (1988). The evolution of partial migration in birds. Trends in Ecology & Evolution, 3, 172-175.

Maclean, I., Austin, G. E., Rehfisch, M. M., Blew, J. A. N., Crowe, O., Delany, S., ... & Van Roomen, M. (2008). Climate change causes rapid changes in the distribution and site abundance of birds in winter. Global Change Biology, 14, 2489-2500.

Marra, P.P., Hobson, K.A. & Holmes, R.T. (1998) Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science, 282, 1884-1886

McWilliams, S. R., Guglielmo, C., Pierce, B., & Klaassen, M. (2004). Flying, fasting, and feeding in birds during migration: a nutritional and physiological ecology perspective. Journal of Avian Biology, 35, 377-393.

Naef-Daenzer, B., Widmer, F., & Nuber, M. (2001). Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. Journal of Animal ecology, 70, 730-738.

Visser, M. E., Perdeck, A. C., BALEN, V., Johan, H., & Both, C. (2009). Climate change leads to decreasing bird migration distances. Global Change Biology, 15, 1859-1865.

Figure legend

Figure 1. Schematic showing key effects of within-population variation in migration distance on subsequent breeding success, as documented by a) Lok et al. (2017) in a population of Eurasian spoonbills (*Platalea leucorodia*) breeding in the Netherlands and migrating to south-west Europe or sub-Saharan Africa, and b) Grist et al. (2017) in a population of European shags (*Phalacrocorax aristotelis*) breeding in Scotland and remaining either resident or migrating to surrounding waters.