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IN FOCUS

Exploration and refinement of migratory routes in long-lived birds

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Abstract

In Focus: Campioni L, Dias MP, Granadeiro JP, Catry P (2019). An ontogenetic perspective on migratory strategy of a long-lived pelagic seabird: Timings and destinations change progressively during maturation. *Journal of Animal Ecology*, 00:1-15. <https://doi.org/10.1111/1365-2656.13044>

How migration routes develop in long-lived migratory animals remains poorly understood. Campioni et al. (2019) tracked the migration of immature and breeding Cory's shearwaters and found that the timings and routes gradually changed with age. Young birds followed more exploratory routes at first, but gradually shortened and defined them as they matured, and they returned to the breeding grounds progressively earlier. These findings suggest that long-lived species start by exploring potentially suitable areas for the non-breeding season and progressively refine their migration route as they age.

Keywords: migration, exploration-refinement, immature, seabirds, learning

Migration is a key event in the annual cycle of many animals, from insects to turtles, fish, birds and mammals (Berger, 2004; Broderick, Coyne, Fuller, Glen, & Godley, 2007; Brodersen et al., 2012; Brower, 1996; Newton, 2008). How migration routes establish is a central question in animal ecology, and essential to understanding the evolution of animal migration. In some species such as geese and

23 cetaceans, young individuals learn their migration route by following parents or family groups
24 (Harrison et al., 2010; Mueller, O'Hara, Converse, Urbanek, & Fagan, 2013; Valenzuela, Sironi,
25 Rowntree, & Seger, 2009). Others, including numerous small passerines, genetically inherit a
26 migratory distance and direction (Liedvogel, Akesson, & Bensch, 2011). Migration in these species is
27 however not entirely genetically controlled, and learning occurs as animals repeat their routes, as
28 evidenced by the fact displaced juveniles on their first migration cannot correct for their displacement
29 while adults can (Perdeck, 1958; Thorup et al., 2007, p. 2007). However, these two mechanisms of
30 cultural and genetic inheritance do not apply to all species. Some do not accompany their young during
31 migration, or follow complex migration routes which vary greatly between individuals, making genetic
32 encoding unlikely. How migration strategies develop in these species remains poorly understood.

33 A third alternative mechanism called exploration-refinement was recently proposed for the
34 development of migration routes in long-lived species (Guilford et al., 2011). Long-lived animals may
35 repeat their migration route dozens of times over their lifetime, so there is scope for learning to take
36 a central role. Furthermore, breeding is often deferred for several years, so immature individuals may
37 experience less pressure to return to their breeding grounds in their first spring—instead they may
38 benefit from spending more time acquiring skills for future breeding. In the exploration-refinement
39 hypothesis, young animals spend their first few years exploring potential wintering grounds, and
40 gradually refine their migration route as they age. Their migration would therefore not be under
41 genetic or cultural control but rather rely on learning, experience, and memory. Tracking the
42 movements of young animals over long periods of time is difficult and so evidence supporting the
43 exploration-refinement mechanism remains so far mostly limited to the gradual improvement of
44 migratory schedule—and to a lesser extent, migratory routes—in a raptor (Sergio et al., 2014), indirect
45 evidence from a long-lived seabird with dispersive migration patterns which cannot be explained by
46 genetic or cultural control but suggest individual learning (Fayet et al., 2016; Guilford et al., 2011), and
47 a tendency for exploration in the foraging movements young seabirds (Votier et al., 2017).

(Campioni, Dias, Granadeiro, & Catry, 2019) provides the most convincing evidence to date in support of the exploration-refinement hypothesis. They tracked the non-breeding movements of known-age immature Cory's shearwaters *Calonectris borealis*, long-lived North Atlantic seabirds which defer breeding for up to 9 years, and compared them between ages and with those of adult birds. Their first key finding is that immature birds travelled longer distances over the entire year and followed more spatially diverse routes than adults. For example, over a third of young immatures visited the North-West Atlantic on their migration to the wintering grounds but this proportion steadily decreased with age. This supports the hypothesis that birds explore wider areas in their youth and reduce this exploratory behaviour over time. A second key finding of the study is that most migration timings gradually advanced and migration routes progressively shortened with age (in duration and distance) until reaching the levels of adult birds. On the southward migration to the wintering grounds, birds departed at similar times, but younger birds made more stopovers and their journey lasted longer. On the northward migration to the breeding grounds, birds left earlier, shortened their route and arrived earlier as they became older. These findings show that birds progressively refined their migration routes with age.

Campioni et al.'s findings represent robust support for the development of migration route by a mechanism of exploration and refinement in long-lived birds. Most characteristics of their shearwaters' migration evolved over time, including the timing of departure and arrival, the duration and distance covered during the journey, and the number of stopovers. In other words, birds continued to improve the timing and efficiency of their migration route until it reached those of adults, presumably optimal for breeding. This gradual improvement of migratory schedule is also seen in long-lived terrestrial migrants (Sergio et al., 2014), but without the exploratory tendency of Cory's shearwaters, perhaps because of a higher cost of going off course to inhospitable regions. In both studies, young birds could travel at similar speeds as adults, therefore the delay in migratory timings of younger individuals is not linked to slower flight speed. It more likely suggests a lower ability to fine tune one's internal clock from environment cues to adjust the timing of departure, or to cope with

unfavourable conditions. Wind in particular is crucial for long-distance flights in both terrestrial and marine birds (Shamoun-Baranes, Liechti, & Vansteelant, 2017), and young birds less able to cope with adverse wind conditions could be delayed (Sergio et al., 2014). Alternatively (or additionally), young birds may also have inferior navigation skills (e.g. a less accurate sun compass), although evidence of this is limited (Gagliardo, Ioalè, Odetti, & Bingman, 2001). An alternative explanation for the late arrival of immatures at the breeding ground is that young birds may purposefully delay their migration to avoid competition with adults (Kokko, 1999). This seems to be the case in some passerines (McKinnon, Fraser, Stanley, & Stutchbury, 2014) but is unlikely to apply to the shearwaters in this study, because timings progressed gradually rather than following a step-change between immatures and first-time breeders.

Interestingly, Campioni et al. (2019) did not find any gradual shift or higher diversity in the wintering destinations of immature birds and the main migration corridors between breeding and wintering areas. These were broadly similar among ages and both adults and immatures showed high fidelity to their wintering site. This suggests that the migratory destination of Cory's shearwaters is either under genetic control, learned culturally by following older birds (departure dates from the colony of fledglings and adults overlap) or is settled on after exploration in the very first years of life (before the start of the study). The multiple wintering areas used by both immature adults Cory's shearwaters in the study and the fact that adults are known to switch destinations between years (Dell'Ariccia et al., 2018) makes a genetic control of migratory destination unlikely, but a convincing answer can only be obtained by tracking the very first few migrations of birds. High mortality in the first winter makes this a challenge however, as it requires deploying hundreds of data loggers—and only recovering devices from survivors—or using expensive and larger satellite transmitters. Few studies have attempted this yet, but interestingly, and contrary to our predictions for Cory's shearwaters, emerging results suggest that wintering destination may be in fact genetically controlled, even in those species which refine their routes with age (Péron & Grémillet, 2013; Weimerskirch et al., 2013). The most striking evidence to date comes from tracking the first migration of streaked shearwaters *Calonectris leucomelas* and

honey buzzards *Pernis apivorus*. In both species, fledglings share the same wintering area as adults but reach it more or less in a straight line from their natal colony, crossing a major ecological barrier in the process (a mountain range in Japan and the Mediterranean Sea, respectively), while adults take a detour around these barriers (Hake, Kjellén, & Alerstam, 2003; Yoda et al., 2017). The genetic control of migratory destination may depend on the availability and directional spread of appropriate wintering grounds, combined with the opportunity for social learning of migratory routes.

The results of Campioni et al. (2019) significantly advance our understanding of the ontogeny of migratory routes in long-lived birds, and establish robust support for exploration and refinement to be a third mechanism, besides genetic and cultural inheritance, by which young birds may learn and develop a preferred migration route during their pre-breeding years. The prevalence of high individual consistency in migration route in adult birds, a strong indication of learning, suggests that it is a common mechanism in long-lived birds (Conklin, Battley, & Potter, 2013; Fayet et al., 2016; Sergio et al., 2014). The important study by Campioni et al. (2019) will hopefully inspire more studies testing for this mechanism in a wide range of species. Further research is also needed to investigate the detailed mechanisms by which exploration and refinement of migration routes is achieved, identify the particular skills which immatures hone over time to reach their final migration strategy, and measure the extent by which some aspects of migration remain socially learned or genetically controlled.

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Figures

Figure 1. A schematic figure illustrating how the migration routes of Cory's shearwaters develop over time during spring migration. As birds become older (from light grey to black), their routes are less exploratory and more direct, they depart from the wintering grounds earlier and arrive at the colony earlier. This figure does not represent the different routes and wintering grounds Cory's shearwaters use in reality and was simplified to a single wintering ground for clarity.