



Seabirds mated for life migrate separately to the same places: behavioural coordination or shared proximate causes?



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Long-term pair bonds occur in diverse animal taxa, but they are most common in birds, and can last from a few years to a lifetime. In many of these species, after the reproductive season, birds migrate to distant nonbreeding grounds where they remain for several months, and until recently, little was known about whether partners maintain contact during migration. This gap in knowledge was primarily due to past methodological difficulties in tracking long-term, large-scale movements of individuals. However, the development of new animal-borne geolocation devices has enabled researchers to track movements of individuals for a year or more. We tracked the annual migrations of both members of breeding pairs of Scopoli's shearwaters, *Calonectris diomedea*, breeding on Linosa Island (Italy) and found that although they did not migrate together, they did spend a similar number of days travelling to and from similar terminal nonbreeding areas. Although migration destinations were alike, they were not identical. That partners did not appear to travel or spend time together in the nonbreeding season suggests that similarities were not due to behavioural coordination. We performed additional analyses to uncover alternative, potential proximate mechanisms. First, we found that body mass of breeding adults during the chick-rearing period correlated positively with the decision to migrate further south, so conceivably pair members may migrate to similar areas because of shared reproductive costs; however, partners were not of similar body mass. Distances between nonbreeding areas for individuals that nested closer together were smaller than for individuals that nested far apart. As neighbours tend to be more closely related due to high natal philopatry, this suggests that similarities within pairs in migration behaviour may reflect the influence of shared genes on migration strategy.

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Animals form long-term breeding partnerships in diverse species including invertebrates (Seibt & Wickler, 1979), fish (Fricke, 1986) and mammals (Clutton-Brock, 1989), but most commonly in birds (reviewed in Black, 1996). Pair bonds in birds often endure for several years (in ca. 50% of bird orders, 21% of bird families; Black, 1996), and can last for life, particularly in long-lived species (Bried & Jouventin, 2002; Hamer, Schreiber, & Burger, 2002). In these species, losing or changing a mate carries substantial energy and opportunity costs associated with finding a new partner and breeding site (Bried & Jouventin, 2002), and often results in a missed breeding season. Furthermore, breeding attempts of reunited partners tend to be much more successful than those of

new partners (Coulson, 1970; Mills, 1979; Chardine, 1986; Ollason & Dunnet, 1988; Black, 1996, 2001; Van de Pol, Heg, Bruinzeel, Kuijper, & Verhulst, 2006; Limmer & Becker, 2010; Sánchez-Macouzet, Rodríguez, & Drummond, 2014), indicating that experience with the same mate fine-tunes partner compatibility (the 'mate familiarity effect'; Black, 1996). High mate fidelity and behavioural coordination between partners is particularly pronounced in seabirds (Bried & Jouventin, 2002; Hamer et al., 2002) and probably evolved because they live for a long time, and successful reproduction requires biparental care during both incubation and chick rearing (Clutton-Brock, 1991; Wittenberger & Tilson, 1980; Hamer et al., 2002). Seabirds must therefore carefully coordinate key aspects of their behaviour with those of their partner, including the timing of trips to sea (which affects the distances and locations to which they can travel), to ensure the successful execution of reproductive duties that include defending the nest site, incubating eggs or caring for chicks (Clutton-Brock, 1991;

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Hamer et al., 2002). Indeed, more behaviourally synchronized pairs tend to achieve higher breeding success (e.g. Hatch, 1990; Hamer et al., 2002).

Soon after breeding, however, most seabirds leave the breeding colony and migrate long distances to spend the nonbreeding period in regions with seasonally higher prey availability and a milder climate (Berthold, 2001; Hamer et al., 2002; Pulido, 2007). As they have a strong incentive to maintain their pair bond from one year to the next, partners may have an advantage if they could coordinate their migration schedules to travel together, maintain contact in nonbreeding areas, or at least return to the colony at the same time during the prebreeding period. Alternatively, pairs may show similarities in migration behaviour without actively coordinating their behaviour, for example if other shared traits (e.g. genetic or life history) influence migration.

Until recently, however, little was known about whether, in pelagic seabirds, long-term partners travel together, meet in nonbreeding areas or show other similarities in migration behaviour (but see Ens, Choudhury, & Black, 1996). This is mainly because, historically, most migration research depended on ring resighting, a powerful method for mapping the general movements of species and populations but limited in utility for following the detailed movements of individuals. New tracking technology, however, permits the tracking of birds' movements in detail for an entire year or longer, making it possible to follow the migration journeys of both pair members (Phillips, Silk, Croxall, Afanasyev, & Bennett, 2005; Schaffer et al., 2006; Guilford et al., 2009, 2012; Rayner et al., 2012). These data can reveal whether partners depart, travel or return at similar times, or go to the same destinations.

Here we report spatial and temporal characteristics of the annual migration of mated adult Scopoli's shearwaters, *Calonectris diomedea*, in the winters following successful breeding seasons. The aim of our study was two-fold: (1) to determine whether partners show similarities in migration behaviour, and (2) to assess whether any similarities reflect active behavioural coordination, and if not, whether they could be indirect effects of other traits shared by partners, such as similarity in body size or condition, or nest placement in the breeding colony. This is, to our knowledge, the first study to report detailed analyses of similarities among pair members in temporal and spatial aspects of migration, and to investigate the proximate drivers.

METHODS

Instrument Deployment

The Scopoli's shearwater is a pelagic seabird that breeds in the Mediterranean, formerly classified as a subspecies of the Cory's shearwater but now considered to be a separate species (Sangster et al., 2012). Our study population breeds on Linosa island (35°87'N, 12°86'W), which holds the second largest breeding colony of Scopoli's shearwaters in the Mediterranean (ca. 10 000 breeding pairs; see Massa & Lo Valvo, 1986). The nests are located mostly in the crevices of the ca. 1 km long lava formations along the northern coast of the volcanic island, in an area called Mannarazza. Breeding females lay a single egg during the second half of May, chicks hatch around mid-July and fledglings leave the colony around the middle to end of October. Mate fidelity is high in this species (71.4–88.1%: Mougín, Jouanin, & Roux, 2000; Thibault, 1994; Cachia Zammit & Borg, 1986; Swatschek, Ristow, & Wink, 1994). About two-thirds of mate changes are due to an absent mate and only one-third reflect a divorce (Mougín et al., 2000).

We attached light-level global location sensors (MK9 from British Antarctic Survey, Cambridge, U.K., and MK3006 from Bio-track, Dorset, U.K.; hereafter GLS) to leg rings of adult breeding

Scopoli's shearwaters in 2009, 2010 and 2011, during the chick-rearing period (early August). We recovered the instruments at the beginning of the subsequent breeding season (mid-May). We tracked 46 individuals from 31 nests for up to three nonbreeding seasons, which provided 60 complete migrations. Twelve individuals were tracked repeatedly: 10 individuals (six males, four females) for 2 years and two individuals (one male, one female) for 3 years. We obtained paired tracks (i.e. complete tracks from both members of a pair in the same year) at 16 nests; at six of these nests, both pair members were tracked twice or more. All of the tracks were of birds that successfully reared a chick to fledging, i.e. they were of similar breeding status. We distinguished between the sexes using body measurements (Lo Valvo, 2001) and vocalizations.

Analysis of Geolocation Data

The light data were processed using BASTrak software (British Antarctic Survey). We used a light threshold of 2 and a sun elevation angle of -5 , derived from calibration data from five geolocators of the same type left in the colony during the whole migration period. We visually inspected light transitions at sunrise and sunset, and assigned a level of confidence (scored from 1 to 9, with 9 as the highest) based on the slope and smoothness of the light curve; only locations derived from the highest quality transitions (scored as 9, which included more than 95% of transitions) were used in further analysis. Outward migration began in late October (after the autumn equinox) and the return migration ended in early February to mid-March (before the spring equinox), so there was no need to remove positions during equinox periods. Latitude and longitude were calculated from daylength and the timing of local noon, respectively. These geolocators provide two locations per day (at local midnight and noon) with an estimated mean error \pm SD of 186 ± 114 km (Phillips, Silk, Croxall, Afanasyev, & Briggs, 2004).

Migration Parameters

We extracted several parameters that described different aspects of the birds' migration journeys, including the timing of movements, as well as spatial attributes such as locations of nonbreeding areas and distances and duration of travel. Periods of migratory flight were defined as those in which the bird travelled at least 0.8 degrees in one direction for at least three consecutive positions (1.5 days). A threshold value of 0.8 was chosen to identify half days during which birds travelled longer distances, because, in nonbreeding areas, birds moved on average only 0.02 degrees each half day in both longitude and latitude, compared with a mean of >1.5 degrees in longitude or latitude during migrations. Occasionally, birds appeared to travel a distance of >0.8 degrees during the nonbreeding period, which may indicate an excursion or random error in the location data; these could be excluded from the analysis because they did not satisfy the criterion that birds had to travel in the same direction for three consecutive positions.

The total time spent in transit during migration was the sum of all periods of flight during the migration period. Nonbreeding periods were defined as those in which birds ceased rapid directional flight for at least 3 days. We defined the number of days spent in nonbreeding areas as the time away from the colony that was not spent in transit. The final nonbreeding location was the last nonbreeding area in which birds spent time before they initiated the return (spring) migration. We determined the date and approximate time \pm ca. 6 h (as there are two locations per day) when birds (1) initiated migration in autumn (date of departure), (2) arrived at the first nonbreeding area, (3) initiated the return migration to the breeding colony from the

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