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A Review of Philopatry in Seabirds and Comparisons with Other Waterbird Species

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Abstract.—Belief that most seabirds return to breed where they had been reared as chicks and exhibit high levels of philopatry and, by implication, have low levels of gene flow, is untenable. In the past, estimates of philopatry have been exaggerated because of the comparative ease of finding individuals returning to their natal area and the difficulty in locating those that have moved away. Measures of philopatry in seabirds obtained from unbiased data show wide between-species variation, and overall it is much lower than was formerly believed. While philopatry is obviously low in species that nest in and move between temporary habitats, it can also be low in colonial species that use the same nesting sites for many years (e.g., cliff-nesting species). Comparisons of the extent of philopatry in other waterbird species show similar variation to those found in seabirds. The expression of philopatry is probably variable within a species and is influenced by environmental conditions and population pressures and so should not be considered a constant for individual species. *Received 28 January 2016, accepted 5 March 2016.*

Key words.—banding recoveries, natal dispersal, philopatry, seabirds, waterbirds.

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There are advantages and disadvantages for animals remaining in the same place during their lifetime. Staying or returning to the same locality results in the accumulation of knowledge about the immediate environment, such as food and water sources, competitors and the threats from predators. Species that persist in any given area testify to its suitability, not only in the past, but also the likelihood of it being so in the immediate future. However, disadvantages arising from remaining at the same place include pressures caused by high population densities, adverse effects of inbreeding and seasonal variations in available food. Persistent breeding at or close to where individuals were reared prevents pioneering and exploiting new breeding areas as well as severely restricting gene flow, all of which can adversely influence the viability of a species, particularly in a changing environment.

The introduction of bird banding in the early part of the 20th century soon produced evidence of individuals returning to breed at or near where they had been reared and was called philopatry. It included species that migrate annually to distant wintering areas, yet return to their natal areas. As banding recoveries accumulated, it was soon believed that this return was the normal situation (Thomson 1936). However, much of the data in support of this relied upon recaptures by the same persons who had originally marked the individuals and who concentrated their efforts within intensively studied but restricted areas and did not search extensively elsewhere. This pattern is well illustrated by the pioneer and intensive banding study that produced many instances of Common Terns (*Sterna hirundo*) returning to breed where they had hatched at Cape Cod, Massachusetts, USA (Austin 1932, 1949), but individuals moving to breed elsewhere were probably missed. This is but one of many studies that could have overestimated the extent to which individuals return to breed near to where they had hatched.

Harris (1984) stated that "Most seabirds return to breed in the colonies where they were born," while Hamer *et al.* (2001) wrote that "many populations [of seabirds] are highly philopatric with little dispersal," and Nelson and Baird (2001) claimed that "the majority of seabirds return to their natal colony" and also that "many species of alcids and larids show marked . . . philopatry." None of these generalizations were supported by evidence. Lloyd *et al.* (1991) were less dogmatic and wrote that ". . . a few may even settle and breed in a colony other than their natal one."

This paper reviews the evidence of the intensity of philopatry (*sensu stricto*) and natal dispersal in waterbirds and concludes that the extent of philopatry varies extensively between waterbird species. For many years, the term philopatry was consistently used and related to the place individuals had hatched (e.g., Mayr 1963; Greenwood 1980; Shields 1982), but more recently some have widened its use, making it synonymous with returning or homing at any age and, in so doing, dropping the link with the natal area (e.g., "the tendency of an organism to stay in, or return to, its home area") (Lawrence and Henderson 1989). Philopatry was also used to describe breeding site fidelity by adults (Ehrlich *et al.* 1988; Frederick and Ogden 1997). In its original sense, a high degree of philopatry implied very limited gene flow, but the more recent use of the term no longer relates it to the place of hatching, often because where the individual birds had hatched was unknown.

In an attempt to avoid ambiguity caused by the modified definition, *natal philopatry* was introduced (despite it being tautology), and then subsequently other adjectives preceded philopatry, including *breeding*, *breeding-site*, *lifetime*, *colony* and *wintering philopatry*, in scientific publications. Some authors then avoided using the term philopatry because of confusion as to its meaning, preferring *natal dispersal*, which tends, in part, to be the compliment of philopatry.

In this paper, *philopatry* is used in its original and strict sense to describe the return of animals to breed in the area where they were reared, while *nest-site fidelity* is used to describe adults returning to the same nesting area in successive years.

METHODS

Searches were made for both published and unpublished estimates of the intensity of philopatry in seabirds based on marked individuals. Each estimate was critically evaluated and many excluded from further consideration because they were heavily biased in favor of records from the natal area. Most studies on several burrow-nesting seabird species and those breeding in inaccessible areas were excluded because of the difficulty in detecting marked individuals that had moved to other areas, e.g., studies on Humboldt Penguin (*Spheniscus humboldti*), Jackass Penguin (*Spheniscus demersus*), Cory's Shearwater (*Calonectris diomedea*), and Black Guillemot (*Cepphus grylle*) (Randall *et al.* 1987; Thibault 1993; Fredericksen and Petersen 1999; Simeone and Wallace 2012). Studies on albatrosses were also excluded because access to many colonies is difficult and also because of taxonomic confusion (Burg and Croxall 2001, 2004). For example, the intensive banding studies on the Laysan Albatross (*Phoebastria immutabilis*) made at Midway Atoll (Fisher 1976) were not accompanied by searches for banded individuals moving to many of the other breeding sites.

A previously unused source of information exists in recoveries of waterbirds banded in Britain and Ireland under the British Trust for Ornithology scheme, where summary data for many species were presented for banded nestlings that were later found dead or dying during the breeding season when old enough to breed (Wernham *et al.* 2002). The data were divided into those that had been found under or over 20 km from their natal sites. This separation was an arbitrary decision applied consistently to all species and was a compromise to partially avoid misclassification of individuals that died while on feeding trips or whose bodies had drifted down rivers or on sea currents. The great majority of these recoveries used were reported by the public and not the persons who banded them in the first place.

Measures of adult nest-site fidelity between successive years have been gleaned from many unpublished and published sources and are presented only for comparison with the extent of philopatry determined for the same species.

RESULTS

Difficulty of Measuring Philopatry

Realistic estimates of the extent of philopatry in many waterbird species can be difficult to obtain and problems encountered in the past are best illustrated by studies on two species.

Common Murre. The population dynamics of the Common Murre (*Uria aalge*) have been investigated in several long-term studies (Tuck 1961; Birkhead and Hudson 1977; Swann and Ramsey 1983; Hudson 1985; Nettleship and Evans 1985; Harris *et al.* 1996), and all reported that the Common Murre is highly philopatric. A similarly high level of philopatry was also claimed for the closely related Thick-billed Murre (*Uria lomvia*) (Steiner and Gaston 2005). None of these studies reported individuals breeding away from their natal colonies.

In a long-term study on Skomer in Wales, up to 20% of Common Murres marked as young subsequently returned there to breed (Birkhead and Hudson 1977), but these were considered too few to replace the annual loss of adults and to contribute to the increasing colony. The shortfall was assumed to be compensated by the movement to the island of unmarked young birds from other colonies. As the study continued, higher proportions of marked young returned to Skomer, and these were then considered to be sufficient to maintain and increase numbers without requiring immigration (Hatchwell and Birkhead 1991; Meade *et al.* 2013). This appears to assume all of the recruits show high philopatry and T. R. Birkhead (pers. commun.) has confirmed that this is his interpretation of the situation for Common Murres breeding on Skomer.

In a similar study on Common Murres on the Isle of May, Scotland, Harris *et al.* (1996) suggested that up to half of the surviving chicks probably bred in other colonies, but this proportion was later reduced to 25% (Harris and Swann 2002) and then to "small numbers" recruiting into colonies away from where they were hatched (Harris *et al.* 2015).

No marked young from Skomer or the Isle of May were reported breeding in other colonies. The lack of inter-colony movement could be genuine or caused by the difficulties of reaching many less accessible colonies and then finding color-banded individuals because the high density of incubating adults often concealed the legs of banded individuals.

In the Baltic Sea of Europe, where breeding Common Murres are more easily observed, both Lyngs (1993) and Olsson *et al.* (2000) found several young Common Murres that had moved away from their natal colonies to breed, with one individual moving many hundreds of kilometers. More recently, additional examples of young Common Murres moving to breed in other colonies have been reported in Norway (Harris *et al.* 2015). While undoubtedly some individual Common Murres are intensely philopatric and return to breed in the same subcolony where they were reared (Harris *et al.* 1996), the extent and possibly the variability of between-colony movements in this species remain to be reliably evaluated.

Studies of the DNA composition of Common Murres from different geographical areas within the Atlantic Ocean (Cadiou *et al.* 2004; Riffaut *et al.* 2005) and the cline in the proportions with the 'bridled' eye rings (Southern 1938) can both be interpreted as evidence of gene flow extending over large areas and hence the movement of individuals between colonies, but such studies do not permit estimates of the extent of inter-colony movements.

Black-legged Kittiwake. In a study in the 1950s and 1960s, nestling Black-legged Kittiwakes (*Rissa tridactyla*) were color-banded on the Farne Islands, Northumberland, and when old enough to breed were searched for in all colonies within 50 km of the natal colony. As a result, 91% were found within 200 m of where they had hatched and few had moved elsewhere (Coulson 2011). This led to the (premature) conclusion that this species exhibited a high degree of philopatry.

Later, this conclusion proved to be at variance with a study where every chick reared in a colony at North Shields in northeast England was marked for 35 consecutive years, but only 9% of female and 36% of male recruits were philopatric and the remainder had emigrated to another colony. Two individuals that bred there had been banded as chicks 600 km away in southern Norway (Coulson and Coulson 2008; Coulson 2011). Marking nestlings in the colony with brightly colored bands, each with a unique engraved alpha-numeric inscription that could be read at a distance, produced a series of reports from others recording individuals moving to breed in other colonies and up to 1,000 km away.

Analyses of British Trust for Ornithology banding returns revealed that the distances kittiwakes of breeding age moved from their natal colonies was bimodal (Fig. 1),

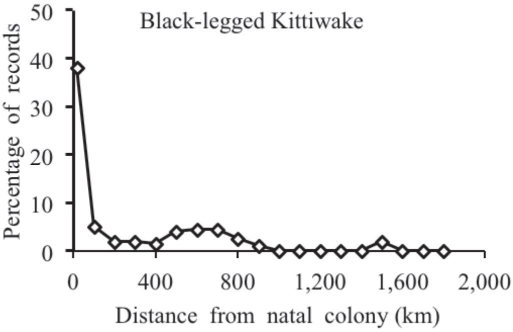

Figure 1. The distance Black-legged Kittiwakes (*Rissa tridactyla*) nested from their natal colonies. Based on Coulson and Neve de Mevergnies (1992) with additions. Note the bimodality of the distribution.

with a peak formed by those returning to the natal colony, then very few moving to nearby colonies within 100 km and then a second (and unexpected) peak of individuals between 200-1,000 km away (Coulson and Neve de Mevergnies 1992). The few moving short distances to other colonies agreed with the initial conclusion, but the second peak formed by long distant movements had not been initially indentified and explained why the early conclusion was anomalous.

Bias in Published Estimates of Philopatry

The effort needed to detect individuals that have moved from their natal colony and to avoid biased results has rarely been appreciated. A search for Black-legged Kittiwakes within 1,000 km of the natal colony in Britain would require visits to over 200 colonies annually for several years – an impossible task for one person. Similarly, finding individuals of an inland breeding seabird that had moved within a radius of 100 km of the natal site would require searching over 31,000 km^2. Detecting movements of a waterbird species restricted to coastlines, e.g., European Shag (*Phalacrocorax aristotelis*) or American Oystercatcher (*Haematopus palliatus*), would involve searching at least 200 km of coastline. The need for cooperative effort to obtain reliable estimates of the intensity of philopatry and natal dispersal is evident.

Use of Banding Recoveries

Table 1 presents data from 13 published studies on species where bias when estimating the intensity of philopatry has been considered to be relatively low. These show a wide spread of values for differences between species. Another source of basically unbiased information exists in banding recoveries of British seabirds, and these have been extracted from the species-by-species accounts in the *Migration Atlas* (Wernham *et al.* 2002) and summarized in Table 2 for 18 seabird species breeding in the United Kingdom and Ireland. As in Table 1, they

Table 1. Estimated levels of philopatry in seabirds from studies that have made efforts to detect the number of individuals that have moved from their natal areas.

Common Name	Scientific Name	Percent Philopatric	Source
Common Eider	*Somateria mollissima*	99%	Swennen 1991
Manx Shearwater	*Puffinus puffinus*	~50% females	Brooke 1978
Northern Fulmar	*Fulmarus glacialis*	6-11%	Dunnet *et al.* 1979
Great Skua	*Stercorarius skua*	94-98%	Klomp and Furness 1992
Arctic Skua	*Stercorarius parasiticus*	43%	O'Donald 1983
Common Guillemot	*Uria aalge*	42% to > 58%	Lyngs 1993; Harris *et al.* 1996
Razorbill	*Alca torda*	83%	Lavers *et al.* 2007
Atlantic Puffin	*Fratecula arctica*	50%	Harris 1984; Harris and Wanless 1991
Black-legged Kittiwake	*Rissa tridactyla*	33%	Coulson and Coulson 2008
Black-headed Gull	*Chroicocephalus ridibundus*	65%	Flegg and Cox 1972
Herring Gull	*Larus argentatus*	~30%	Scotland: J. Coulson (unpubl. data)
		60%	Belgium: Vercruijsse 1999
Least Tern	*Sternula antillarum*	5%	Renken and Smith 1995
Common Tern	*Sterna hirundo*	~10%	Tims *et al.* 2004; Becker *et al.* 2008

Table 2. Estimated levels of philopatry in U.K. seabirds extracted from data in Wernham *et al.* (2002). Estimates of nest-site fidelity are included for comparison.

Common Name	Scientific Name	Total Recoveries of Potential Breeding Birds	Percentage Philopatry (< 20 km)	Percentage Nest-site Fidelity (< 20 km)	Comments
Common Eider	*Somateria mollissima*		> 95%	99% (female)	Abmigration
Northern Fulmar	*Fulmarus glacialis*	118	31%	> 95%	
Manx Shearwater	*Puffinus puffinus*	238	61%	> 95%	
Northern Gannet	*Morus bassanus*		95%?	> 95%	
Great Cormorant	*Phalacrocorax carbo*		~95%	> 95%	
European Shag	*Phalacrocorax aristotelis*		95%	99%	
Razorbill	*Alca torda*	105	29%	> 95%	
Atlantic Puffin	*Fratecula arctica*		50%	High	But see Sandvik *et al.* 2008
Black-legged Kittiwake	*Rissa tridactyla*	277	60%	> 99%	
Black-headed Gull	*Chroicocephalus ridibundus*	962	62%	85%	
Common Gull	*Larus canus*	85	89%	High	
Herring Gull	*Larus argentatus*	4,051	19%	90%	
Lesser Black-backed Gull	*Larus fuscus*	1,780	~25%	90%	
Great Black-backed Gull	*Larus marinus*	233	~20%	High	
Little Tern	*Sternula albifrons*	61	18%	Colony	
Common Tern	*Sterna hirundo*	469	25%	High	
Arctic Tern	*Sterna paradisaea*	458	67%	High	
Sandwich Tern	*Thaslasseus sandvicensis*	666	15%	~75%	Colony movement

show considerable between-species differences. When data from both sources are combined (Table 3), the 32 measures of the intensity of philopatry (two estimates for one species) varied from less than 10% to over 90% and suggest that generalizations about philopatry in seabirds as a whole are inappropriate. In all cases, the estimated levels of philopatry are lower than values for the nest-site fidelity by adults between successive years.

Comparisons Between Seabirds and Other Waterbirds

Tables 3 and 4 show estimates of the levels of philopatry in other waterbird species for comparison with those shown in Tables 1 and 2 for seabirds. The comments made above for seabirds apply equally to other waterbird species, and these also show a wide range of values obtained from different species. The data for a total of 57 estimates are summarized in Table 5, and this emphasizes the wide range of values obtained for the levels of philopatry in waterbirds in general.

Tables 2 and 4 show levels of nest-site fidelity between years for breeding adults and for comparison with the estimated levels of philopatry. In all cases where suitable data exist, nest-site fidelity is higher, and often considerably so, than the level of philopatry recorded for both seabirds and also for other waterbirds.

Abmigration

The distances non-philopatric individuals moved from their natal areas to breed often follows a simple decay curve, with fewer individuals occurring at increasing distances (Fig. 2: White Stork (*Ciconia ciconia*)).

An exception to this pattern is abmigration (Thomson 1936), which usually produces a bimodal distribution of distances moved from the natal area and is well known in ducks. In species exhibiting abmigration, many individuals are philopatric, but a small proportion move long distances to breed in a completely different geographical area. Males usually dominate in these movements (Baldassarre and Bolen 1994; Baillie 2002; Blums *et al.* 2003), although no sex bias was found in the Eurasian Wigeon (*Anas penelope*) (Owen and Mitchell 1988) or Eurasian Teal (*Anas crecca*) (Guillemain *et al.* 2005). Such long distance dispersal reduces the intensity of philopatry and increases gene flow.

It has been assumed, probably correctly, that abmigration arises in ducks when individuals from very different geographical areas winter in the same wintering area, pair there, and then both move to the natal area of one to breed. An alternative possibility is that an individual joins a flock from different areas and migrates with them.

Similar bimodal dispersal has been reported in the Northern Lapwing (*Vanellus vanellus*) (Thompson *et al.* 1994) (Fig. 3), Eurasian Woodcock (*Scolopax rusticola*)

Table 3. Estimated levels of philopatry in other waterbird species from studies that have made efforts to detect the number of individuals that have moved from their natal areas.

Common Name	Scientific Name	Percent Philopatric	Source
Canada Goose (U.K.)	*Branta canadensis*	66%	Lessells 1985
Mute Swan	*Cygnus olor*	93%	Coleman and Minton 1979
Mallard	*Anas playrhynchos*	> 90%	Abmigration: Thomson 1936
White Stork	*Ciconia ciconia*	33%	Based on Itonaga 2009
Whooping Crane	*Grus americana*	76%	Johns *et al.* 2005
Greater Flamingo	*Phoenicopterus roseus*	79%	Johnson and Cèzilly 2007
Northern Lapwing	*Vanellus vanellus*	61%	Thompson *et al.* 1994 (updated)
Ringed Plover	*Charadrius hiaticula*	82%	Jackson 1994
Redshank	*Tringa totanus*	89%	Jackson 1994
Black-tailed Godwit	*Limosa limosa*	< 85%	Kruk *et al.* 1998
Common Sandpiper	*Actitis hypoleucos*	< 5%	Holland and Yalden 1994
Dunlin	*Calidris alpina*	82%	Jackson 1994
White-throated Dipper	*Cinclus cinclus*	> 95%	Tyler *et al.* 1990

Table 4. Estimated levels of philopatry in other waterbird species in the U.K. extracted from data in Wernham *et al.* (2002). Estimates of nest-site fidelity are included for comparison. Values based on small samples are shown in parentheses.

Common Name	Scientific Name	Total Recoveries of Potential Breeding Birds	Percentage Philopatry (< 20 km)	Percentage Nest-site Fidelity (< 20 km)	Comments
Little Grebe	*Tachybaptus ruficollis*	11	(36%)		Small sample
Canada Goose	*Branta canadensis*		~95%	High	
Mute Swan	*Cygnus olor*		~90%	High	
Mallard	*Anas playrhynchos*			57% female	Abmigration
Eurasian Teal	*Anas crecca*		40%		Abmigration
Tufted Duck	*Aythya fuligula*	11	(9%)		Small sample; abmigration
Common Merganser	*Mergus merganser*	25	24%	High	Abmigration?
Eurasian Oystercatcher	*Haematopus ostralegus*	121	71%	> 90%	
Grey Heron	*Ardea cinerea*	279	39%	High	
Northern Lapwing	*Vanellus vanellus*	325	80%	> 95%	Abmigration
Common Redshank	*Tringa totanus*	18	(56%)	> 95%	
Eurasian Woodcock	*Scolopax rusticola*	45	(< 89%)		Small sample; abmigration
Grey Wagtail	*Motacilla cinerea*	31	48%		

Table 5. Distributions of the levels of philopatry in seabirds and other waterbird species based on data in Tables 1-4.

	Percentage Philopatry										
Avian Group	0-9%	10-19%	20-29%	30-39%	40-49%	50-59%	60-69%	70-79%	80- 90%	Over 90%	Total Cases
Seabirds (Table 1)	2	1	0	2	1	3	2	0	1	2	14
Seabirds (Table 2)	0	3	4	1	0	1	4	0	1	4	18
Total seabirds	**2**	**4**	**4**	**3**	**1**	**4**	**6**	**0**	**2**	**6**	**32**
Other waterbirds (Table 1)	1	0	0	0	0	0	2	2	4	3	12
Other waterbirds (Table 2)	1	0	1	3	1	2	0	1	3	1	13
Total other waterbirds	**2**	**0**	**1**	**3**	**1**	**2**	**2**	**3**	**7**	**4**	**25**
Grand total	**4**	**4**	**5**	**6**	**2**	**6**	**8**	**3**	**9**	**10**	**57**

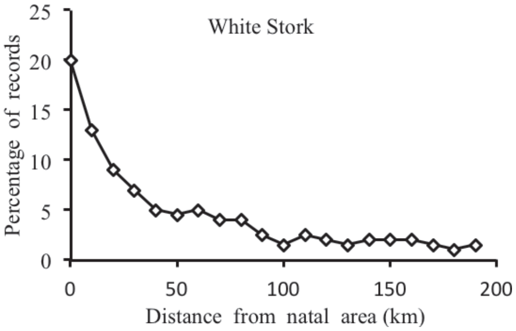

Figure 2. The distance White Storks (*Ciconia ciconia*) nested from their natal areas. Based on Itonaga (2009) and presented in 10-km zones. Note the progressive decrease with distance, approximating a simple decay curve.

(Hoodless and Coulson 1994) and Black-legged Kittiwake (Fig. 1). The explanation of these movements in ducks may apply to the Northern Lapwing, but the Eurasian Woodcock does not form pairs or flock and the Black-legged Kittiwake is not known to pair while birds of mixed origins are in their common oceanic winter distribution, thus other explanations may be needed.

Study of Conspicuous Species

Some waterbird species are conspicuous when breeding, and the Whooping Crane (*Grus americana*) and Sandhill Crane (*G. canadensis*) in North America (Johns *et al.* 2005; Hayes 2015) and the White Stork in Europe (Itonaga 2009) are good examples where records of marked individuals have been reported over large areas by both the public and ornithologists and are likely to produce unbiased values of the intensity of philopatry (e.g., Fig. 2: White Stork).

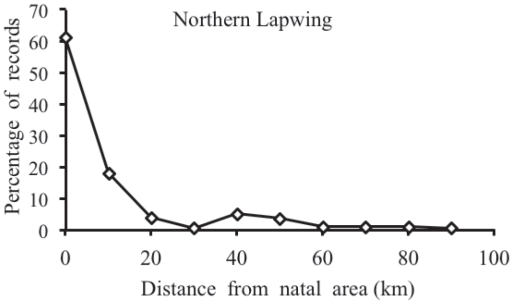

Figure 3. The bimodal distances moved by Northern Lapwings (*Vanellus vanellus*) banded as chicks in northern England to where they were seen or recovered in the breeding season when old enough to breed. The data are based on those in Thompson *et al.* (1994) and more recent records. Two records of birds found in the breeding season in Russia are not shown.

DISCUSSION

The conclusions derived from this review suggest that philopatry in many waterbirds varies markedly between species and that its intensity has sometimes been exaggerated. These conclusions do not diminish the remarkable ability of waterbirds to remember, locate and visit their natal sites when approaching maturity. In recent years, increasing numbers of studies have shown that many seabirds visit their natal areas and, only after doing so, some decide to move elsewhere to breed. A study of Herring Gulls (*Larus argentatus*) uniquely marked as chicks found that all that survived to maturity visited their natal colony and, after doing so, some move elsewhere to breed (Vercruijsse 1999).

Young South Polar Skuas (*Catharacta maccormicki*), Black-legged Kittiwakes, Herring Gulls, Common Terns, Common Murres and Atlantic Puffins *(Fratercula arctica)* often visit several colonies, including their natal one, irrespective of where they eventually breed (Harris 1984; Porter 1987; Ainley *et al.* 1990; Halley and Harris 1993; Harris *et al.* 1996; Vercruijsse 1999; Dittmann *et al.* 2005; Coulson and Coulson 2008; Coulson 2011). The ability to identify their natal area, which is a necessary component of philopatry, is present in more individuals than just those that eventually breed there. These visits offer the visiting individuals the opportunity of appraising and responding to density, competition for nest sites or availability of food, and each individual presumably makes a choice as to where they will breed. To my knowledge, similar examples of waterbirds other than seabirds behaving in this manner have not been reported.

That philopatry is often less intense than has often been assumed has important consequences for conservation. For example, there is no necessity for a relationship between reproductive productivity and a species' numerical status at a local level. It may be possible for an individual colony or local populations to persist and even flourish in spite of low breeding success, because of continuous immigration of non-philopatric individuals. In such cases, it is likely that the reproductive output over a much larger area is of key importance.

In those species where philopatry is low, it is evident that many individuals are making a choice of where to breed, rather than simply returning to the natal locality. The clues used in making the choice are not well understood. Several workers have suggested the presence of many near-fledged young in a colony or area in one year may indicate a safe and favorable location for potential recruits to return and breed in a subsequent year, but experimental proof of this possibility is still lacking. Determining how young seabirds and waterbirds in general select a colony or a group and choose to breed there is an important new aspect of avian research.

There are several factors that influence the intensity of philopatry in a species. The risk of predation is important and is particularly obvious where it causes the mass movement of all individuals in colonies to new sites, and this is well known in Royal Terns (*Thalasseus maxima*), Sandwich Terns (*T. sandvicensis*), Little Terns (*Sternula albifrons*), Least Terns (*S. antillarum*), Black Skimmers (*Rhynchops niger*), and also shorebirds such as the Little Ringed Plover (*Charadrius dubius*) and Snowy Plover (*C. alexandrinus*), and in the Common Eider (*Somateria mollissima*).

Variation of available food is known to affect where Long-tailed Jaegers (*Stercorarius longicaudus*) breed, with young individuals moving to new areas of temporary lemming abundance (Barraquand *et al.* 2014) and, as a result, this decreases the intensity of philopatry. Changes in food availability are believed to reduce the persistence of colonies of White Ibis (*Eudocimus albus*) (Frederick and Ogden 1997) and, indirectly, the extent of philopatry. Human intervention can also influence philopatry, such as the deliberate disturbance resulting in the dispersal and displacement of Double-crested Cormorants (*Phalacrocorax auritus*) (Glahn *et al.* 2000).

The pioneer study of Greenwood (1980) and more recent studies (Jackson 1994; Thompson *et al.* 1994) reported that the males of most bird species show a greater degree of philopatry than females, although there are exceptions. No sex difference was found in the Semipalmated Sandpiper (*Calidris pusilla*) (Grotto *et al.* 1985), Semipalmated Plover (*Charadrius semipalmatus*) (Nol *et al.* 2010), and Upland Sandpiper (*Bartramia longicauda*) (Casey *et al.* 2011).

Excessive numbers of some colonial waterbirds can force movement and reduced philopatry. For example, nesting sites of the Atlantic Puffin were extensively degraded by erosion initiated by over-burrowing as on Grassholm in Wales (Lockley 1953; Harris 1984) and on South Wamses, West Wideopens and Brownsman islands of the Farne Islands in Northumberland (Harris 1984; J. C. Coulson, unpubl. data). Double-crested Cormorants are well known to damage and kill trees, causing colonies to move (Herbert *et al.* 2005).

An effect of intensive philopatry is that individuals in local groups or sub-colonies could show genetic relatedness. Friesen *et al.* (1996) and Ibarguchi (2011), using DNA analyses, claim to have detected kin groups within sub-colonies of Common and Thick-billed murres. Relatedness within groups of breeding female of both Common Eiders have been reported (McKinnon *et al.* 2006; Tiedemann *et al.* 2011), but the levels and frequency of relatedness remain unknown.

At present, there are few studies that compare DNA analyses indicating gene flow with those based on banded or individuals carrying transmitters in the field. DNA analyses detect the gene flow sometime in the past, while studies on the movements of individual birds evaluate the current situation. Further, these studies are probably complimentary because the two types of investigations may not agree as most gene flow could depend on the few extreme individuals that move the greatest distances from where they were reared as suggested by Black-legged

Kittiwakes and Northern Lapwings, and not on the proportion of individuals that did or did not return to or near their natal areas.

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