

# Speciation in seabirds: why are there so many species...and why aren't there more?

Vicki L. Friesen<sup>1</sup>

Received: 5 January 2015 / Revised: 30 April 2015 / Accepted: 6 May 2015 / Published online: 31 May 2015  
© Dt. Ornithologen-Gesellschaft e.V. 2015

**Abstract** Speciation—the multiplication of species through the evolution of barriers to reproduction between populations—plays a central role in evolution since it enables two or more populations to adapt and evolve independently. However, mechanisms of speciation are notoriously difficult to study and poorly understood. Seabirds provide useful models to investigate factors that may promote or inhibit speciation because their ecology and evolutionary genetics are relatively well understood. Here I review population genetic studies of seabirds to test the importance of six factors with the potential to disrupt gene flow enough to result in speciation. Over 200 studies, including over 100 species, have been published to date. Most show evidence of restrictions in gene flow. Physical (geographic) barriers to dispersal are clearly important: conspecific populations that are separated by large expanses of land or ice show evidence of restricted gene flow, and sister species often are separated by physical barriers to gene flow. However, many species of seabirds show evidence of restrictions in gene flow in the absence of physical barriers to dispersal. Study results indicate that differences in ocean regimes, nonbreeding distributions, foraging distributions during the breeding season, and breeding phenology also can disrupt gene flow enough to lead to

speciation. Of these, physical isolation and differences in ocean regime appear to be the most important. Philopatry alone may be sufficient to result in reproductive isolation, but usually it acts in combination with other barriers to gene flow. The effects of many other potential influences on gene flow need to be investigated more thoroughly, including colony distribution/location, wind, interspecific interactions, environmental stability/variability, variation in phenotypic traits associated with mate choice (morphology, behaviour, vocalisations) and intrinsic (genomic) incompatibilities. Recent advances in genome sequencing, especially if used in combination with ecological tools such as geolocators and new methods for data interpretation, are opening exciting new avenues to test the importance of various behavioural, ecological, demographic and genomic factors in reducing or promoting gene flow and so affecting speciation.

**Keywords** Allochrony · Foraging distribution · Gene flow · Meta-analysis · Nonbreeding distribution · Ocean regime

## Introduction

Speciation—the evolution of reproductive isolation between populations—allows populations to evolve and adapt independently and so plays a key role in evolution (Coyne and Orr 2004; Price 2008; Seehausen et al. 2014). Mayr stated (1963, p. 621) that “Without speciation there would be no diversification of the organic world, no adaptive radiation, and very little evolutionary progress”. Furthermore, many aspects of ecology and behaviour relate to species recognition. Thus, understanding speciation is fundamental to many aspects of biology. Understanding

---

Communicated by E. Matthysen.

**Electronic supplementary material** The online version of this article (doi:10.1007/s10336-015-1235-0) contains supplementary material, which is available to authorized users.

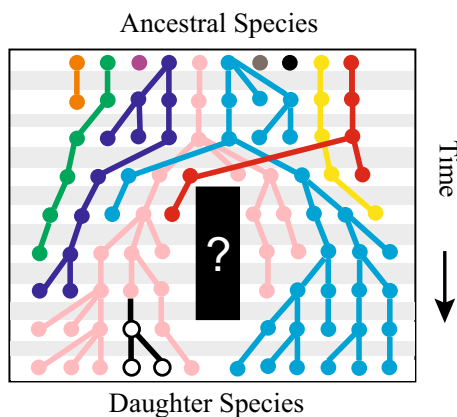
---

✉ Vicki L. Friesen  
vlf@queensu.ca

<sup>1</sup> Department of Biology, Queen's University, Kingston, ON K7L 3N6, Canada

speciation also is critical for conserving biodiversity, to protect not only the existing diversity but also the diversification process (Rosenzweig 2001; Butlin et al. 2012). As Soule and Wilcox (1980, p. 8) stated, “Death is one thing, an end to birth is something else”. To protect the diversification process we need to know how anthropogenic changes are affecting speciation. For example, can habitat fragmentation potentially promote speciation? And to what extent does hybridisation inhibit or promote population differentiation and speciation?

Despite its importance, speciation is poorly understood (Coyne and Orr 2004; Price 2008; Butlin et al. 2012). According to the classical, allopatric model of speciation (‘speciation without gene flow’), a physical barrier to gene flow is required to initiate genetic divergence of populations (Fig. 1). With sufficient time, pre- or post-mating barriers to reproduction evolve through either genetic drift or selection. This model is well supported by both theory and empirical evidence. However, the identity and importance of non-physical barriers to gene flow are less clear. For example, birds encounter few physical barriers to dispersal, yet there are more species of birds than of any other class of vertebrates except actinopterygian fishes. Determining the factors that disrupt gene flow sufficiently to initiate speciation requires inferring historical processes from contemporary patterns, which is notoriously difficult. There are at least two general approaches to study barriers to gene flow (Nosil 2012), but both have shortcomings:



**Fig. 1** Schematic diagram of the evolution of reproductive isolation (speciation). Coloured dots represent alleles in the gene pool of a species, and lines represent ancestor/descendent relationships; a change in colour represents a mutation. The black box represents a barrier to gene flow that eventually results in reproductive isolation even if the barrier disappears. The question mark indicates that the nature of the barrier that initiates speciation. Investigations into these barriers can involve (1) comparisons of conspecific populations, but these populations may not form new species if the barrier does not last sufficiently long for reproductive isolation to evolve, or (2) comparisons of sister species, but differences between sister species may not represent the barriers that initiated speciation is often unknown

comparisons of ecological and phenotypic differences among conspecific populations; and comparisons of ecological and phenotypic differences between sister species. However, conspecific populations may not ultimately form new species, and differences between sister species do not necessarily reflect the barriers that initiated speciation. Thus, use of these two approaches together may help determine the relative importance of different potential barriers to gene flow.

Seabirds provide good models for studying speciation because they encounter very few physical barriers to dispersal, so non-physical barriers that can promote diversification across a range of organisms may be more evident in seabirds than in less mobile organisms. Seabirds also are generally well studied, and so these barriers should be relatively easy to identify. Friesen et al. (2007a) and other researchers (e.g., Gomez-Diaz et al. 2009) identified several factors that may inhibit gene flow sufficiently to initiate speciation in seabirds. In the present review I update and extend the previous study of Friesen et al. (2007a) to explore the importance to speciation in seabirds of six potential barriers to gene flow: physical (geographic) isolation; philopatry; and differences in ocean regime, non-breeding distribution, foraging distribution and breeding phenology. For each factor I present the rationale, an example, support from population genetic studies and support from comparisons of sister species. Several of these factors may be inter-related: for example, species that forage close to colonies also tend to stay near colonies when not breeding; the timing of breeding may differ between colonies that occur in different ocean regimes, even if the colonies are geographically proximate; and wintering areas often occur in different ocean regimes. Analyses also are partially confounded by phylogeny; e.g., albatrosses tend to range widely both seasonally and while foraging. Disentangling these factors will ultimately require more studies and a multivariate meta-analysis.

## Methods

Population genetic studies of seabirds were collated from the primary literature, including any study that incorporated at least one molecular marker and that compared two or more colonies (Supplementary Table 1). The existence of restrictions to gene flow was inferred either from evidence of strong population genetic or phylogeographic differences (Wright 1969) or from direct estimates of gene flow [e.g., from programmes such as IMA (Hey and Nielsen 2007)]. The potential factor(s) restricting gene flow were inferred from either the original studies or other literature sources. Studies that covered only a small portion of the species’ range were not included, and not all information

could be collated for all species. Populations or species for which population genetic structure and gene flow appear to have been strongly affected by human activities (e.g., overexploitation or translocation; e.g., Short-tailed Albatross *Phoebastria albatrus*, Eda et al. 2012) or that breed primarily inland (i.e., not in association with marine waters; e.g., White Pelican *Pelecanus erythrorhynchos*) also were not included. Interpretations were sometimes complicated by taxonomy, especially as subspecies are sometimes elevated to full species based on molecular data.

## Results and discussion

Over 200 population genetic studies of seabirds, covering over 100 species, have been published since the initial allozyme studies in the 1990s (Supplementary Table 1). Of 86 species included in the present analyses, 64 showed evidence of restrictions in gene flow. Support was found from the literature for potential roles in speciation for each of the six factors investigated.

### Physical isolation

#### *Rationale*

Although most seabirds are strong fliers, most pelagic and coastal species will not fly over large stretches of either land or ice. Thus, Atlantic and Pacific populations of holarctic and north temperate species may be isolated by arctic ice in the north and continental landmasses in the south. Similarly, Atlantic and Indopacific populations of tropical and subtropical species may be isolated by Africa and the Isthmus of Panama; and populations of species that breed and feed along coastlines may be isolated by open ocean. For example, Brown Boobies (*Sula leucogaster*) breed on islands throughout the tropical Atlantic, Pacific and Indian oceans. Variation in both mitochondrial and nuclear DNA among Brown Boobies sampled throughout their range indicate that Atlantic and Indo-Pacific populations are strongly differentiated and have been genetically isolated for approximately 350,000 years (Morris-Pocock et al. 2011).

#### *Support from the literature*

All of the 16 species whose distributions are fragmented by large expanses of land or ice show evidence of restrictions in gene flow between oceans, and in most cases the populations are highly differentiated (Supplementary Table 1a). Even the Isthmus of Panama, which is only 35 km wide at its narrowest, appears to present a

significant barrier to gene flow in most seabirds; this is probably due to its elevation (Steeves et al. 2005), which ranges up to 3500 m. Population genetic structure in at least nine additional species appears to represent secondary contact between two or more populations that differentiated in Pleistocene refugia (Supplementary Table 1b). Sister species also are often separated by large expanses of land or ice. For example, speciation in the white-headed gulls (*Larus* spp.) appears to be due partially to fragmentation of an ancestral species into multiple refugia by Pleistocene glaciers (Liebers et al. 2004; Sonsthagen et al. 2012; Sternkopf et al. 2014).

However, 56 species of seabirds show evidence of restrictions in gene flow that are not associated with any obvious contemporary or historical physical barrier to dispersal (Supplementary Table 1c, d). For example, gene flow appears to be restricted between Cassin's Auklets (*Ptychoramphus aleuticus*) breeding in Baja California/Guadalupe Island and those farther north (Wallace et al. 2015). Furthermore, sister species often are not separated by any obvious physical barrier to dispersal. For example, Scripps's and Guadalupe Murrelets (*Synthliboramphus scrippsi* and *S. hypoleucus* respectively) diverged very recently and have small breeding ranges that overlap off Baja California (Birt et al. 2012). Thus, factors additional to physical isolation must restrict gene flow in seabirds, potentially sufficiently to lead to reproductive isolation. To help identify these factors, the analyses below are based on populations within ocean basins only (Supplementary Table 1c, d).

### Philopatry

#### *Rationale*

In theory, philopatry (defined here as the tendency to return to the natal site to breed) may restrict gene flow sufficiently to lead to reproductive isolation given sufficient time. Seabirds are well known for their philopatric behaviour (Coulson 2002), and although strong philopatry is not universal, it is probably the second most obvious potential barrier to gene flow in seabirds. For example, no ecological differences or physical barriers to dispersal occur among breeding colonies of Shy Albatrosses (*Thalassarche cauta*), which are noted for strong philopatry (e.g., Sagar et al. 1998), yet Shy Albatrosses from three Tasmanian colonies differ at mitochondrial and nuclear markers (Abbott and Double 2003a, b).

#### *Support from the literature*

Of 36 species for which there is independent evidence of strong philopatry (usually from ring returns), 27 (75 %)

have restrictions in gene flow in at least part of their breeding range, sometimes even within archipelagoes (Fig. 2). In addition, there are many examples of sister species that are not separated by any obvious physical or ecological barrier to dispersal, arguing against a role for physical isolation or ecological segregation in these cases. For example, New Zealand has very high endemism, with closely related but reproductively isolated species sometimes breeding on neighbouring islands [Fig. 3; e.g., shags (Phalacrocoracidae), del Hoyo et al. 1996; Rawlence et al. 2004]. Similarly, islands off the west coast of Baja California have several endemic species and subspecies of seabirds, especially storm-petrels (del Hoyo et al. 1992, 1996).

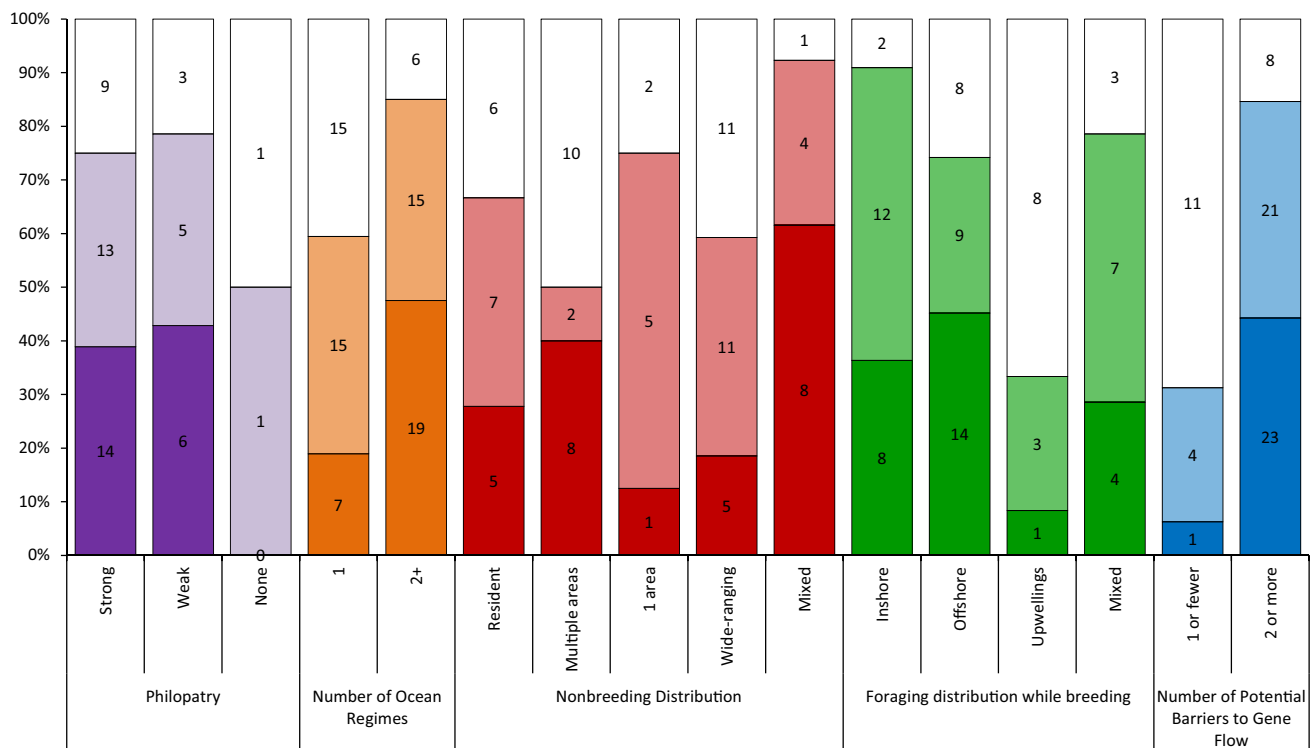
However, 12 (75 %) of 16 species that are not strongly philopatric also show evidence of disruptions to gene flow (e.g., Magnificent Frigatebirds *Fregata magnificens* in the Galapagos compared to the rest of the range, Hailer et al. 2011). Furthermore, in most cases where

gene flow is restricted in philopatric species, populations differ in one or more ecological features. And nine strongly philopatric species show no evidence of restrictions in gene flow (e.g., Grey-headed Albatross *Thalasarche chrysostoma*, Burg and Croxall 2001). Thus, additional barriers to gene flow must be involved in speciation in seabirds.

## Differences in ocean regime

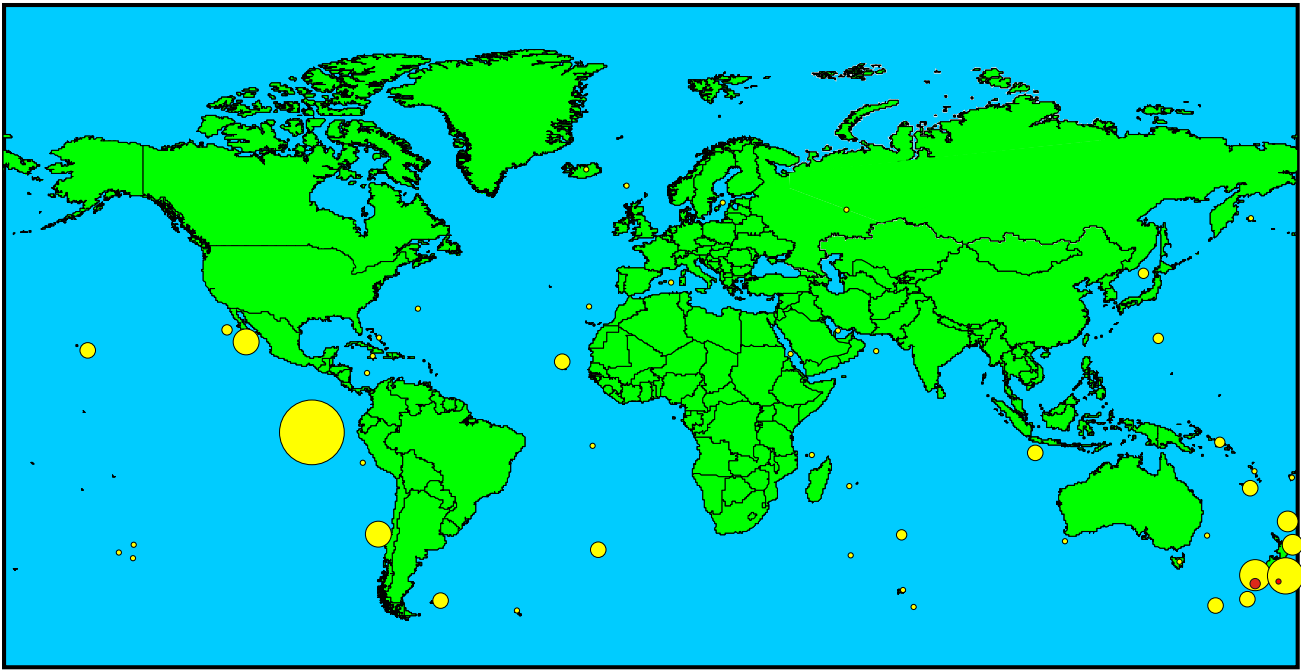
### Rationale

Local differences in selection pressures can disrupt gene flow and potentially lead to reproductive isolation (“ecological speciation”; Coyne and Orr 2004; Hendry et al. 2007; Nosil 2012). Such differences could result from any of a myriad of environmental variables, including (but not limited to) climate, prey species, predators, competitors, parasites and disease (reviewed in Karvonen and



**Fig. 2** Proportions of studies showing evidence of strong, weak or no interruptions in gene flow given various potential barriers to gene flow. Collated from Supplementary Table 1c, d (populations with no evidence of historical or contemporary physical barriers to gene flow). *Dark shades* Species showing strong population genetic or phylogeographic structure; *intermediate shades* species with populations that differ in allele or haplotype frequencies only; *white* species with little or no geographic variation in allele or haplotype frequencies. *Numbers* numbers of studies. ‘Strong philopatry’ = few records of adults or juveniles changing breeding colonies despite extensive banding records; ‘weak philopatry’ = generally philopatric but

evidence of individuals changing breeding colonies or of metapopulation dynamics; ‘none’ = extensive records of individuals changing breeding colonies or of colonies changing locations. ‘Resident’ = little or no dispersal of adults from colonies during nonbreeding season; ‘multiple areas’ = seasonal connectivity between colonies and two or more discrete nonbreeding areas; ‘1 area’ = birds from all breeding colonies migrate to a common nonbreeding area; ‘wide-ranging’ = wide-ranging dispersal during the nonbreeding season; ‘mixed’ = a combination of nonbreeding distributions (e.g., some colonies resident; others migratory)



**Fig. 3** Numbers of species and subspecies of seabirds endemic to single islands or archipelagos. Volumes of circles are proportional to numbers of species or subspecies. Collated from del Hoyo et al. (1992, 1996)

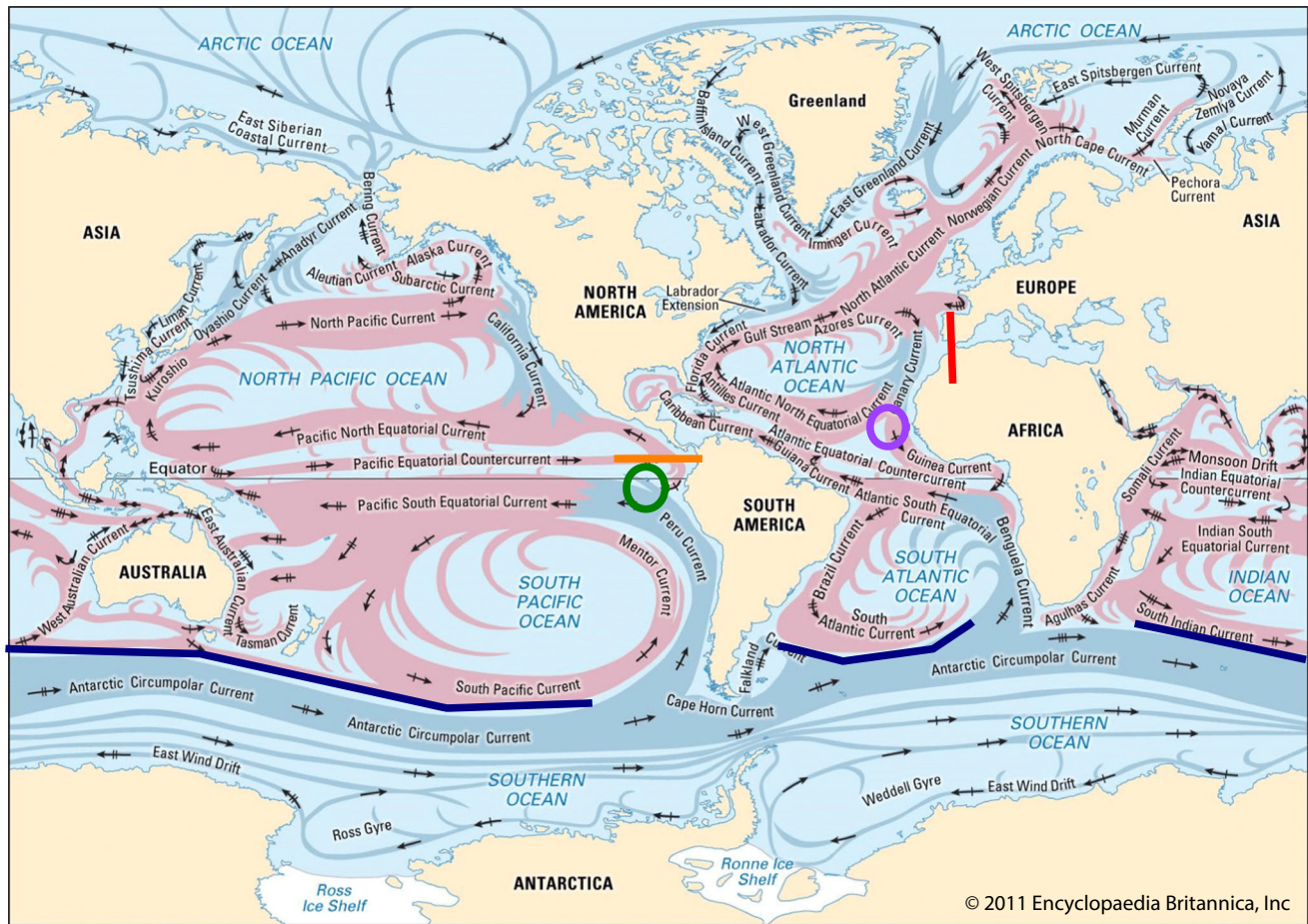
Seehausen 2012). Ocean regimes can exert very different selective pressures (Fig. 4). For example, they can differ in sea surface temperature, productivity, seasonality, upwelling, prey, competitors and food web complexity. These differences could inhibit gene flow either by reducing the fitness (survival or reproductive success) of migrant individuals or simply by deterring dispersal. For example, Gomez-Diaz et al. (2009) provided evidence that the Almeria-Oran Oceanographic Front is a barrier to gene flow in Cory's Shearwaters (*Calonectris diomedea*). Similarly, ocean surface temperature north and south of the Subtropical Convergence differs by 10 °C, and Rockhopper Penguins (*Eudyptes chrysocome*) breeding in these two areas have distinct mitochondrial DNA (mtDNA; Jouventin et al. 2006). They also differ in vocalisations and facial ornaments, and are now classified as separate species (*E. chrysocome* and *E. moseleyi*).

#### Support from the literature

Of 39 population genetic studies that include populations that breed in two or more ocean regimes within an ocean basin, 34 (85 %) found evidence of restricted gene flow (Fig. 2). Furthermore, sister species often occur in different ocean regimes (e.g., Blue-footed and Peruvian boobies *Sula nebouxii* and *S. variegata*). Ocean differences in five areas in particular appear to restrict gene flow enough for speciation in seabirds (Supplementary Table 1c, d): ocean

currents around the Galapagos (five species with genetically distinct populations; several endemic species such as the Nazca Booby *Sula granti* with sister species in the eastern tropical Pacific; four species with restrictions in gene flow among islands within the Galapagos); the Almeria-Oran Oceanographic Front (three species with genetically differentiated populations in the Mediterranean versus the Atlantic; several endemic Mediterranean species such as the Yelkouan Shearwater *Puffinus yelkouan* with sister species in the eastern Atlantic); the Subtropical Convergence [three species with genetically differentiated populations north versus south of the Convergence; several pairs of species such as White-chinned and Spectacled Petrels *Pterodroma conspicillata* and *P. aequinoctialis* (Techow et al. 2009) distributed north versus south of the Convergence]; the Equatorial Counter-current (e.g., one pair of boobies *Sula* spp. and two pairs of storm-petrels *Oceanodroma* spp. distributed north versus south of the Counter-current; S. Wallace et al., unpubl. data); and ocean currents around Cape Verde (several endemic procellariiform species; e.g., Cape Verde Petrel *Pterodroma feae*, Gangloff et al. 2013).

Despite these results, evidence for restrictions in gene flow also exists in 22 (59 %) of 37 species that breed (or were sampled) within a single ocean regime (Supplementary Tables 1c, d). Furthermore, sister species often co-exist within the same ocean regime. For example, four species of auklets (*Aethia* spp.), which appear to have



**Fig. 4** World ocean currents. *Thick lines* represent ocean fronts that appear to present significant barriers to dispersal in seabirds: *red* Almeria-Oran Oceanographic Front; *yellow* Equatorial Counter-current; *green* currents around the Galapagos; *blue* Subtropical

Convergence; *purple* currents around Cape Verde. Modified from map provided by courtesy of Encyclopaedia Britannica, Inc., © 2011; used with permission

arisen from a common ancestor within a very short time interval (Humphries and Winker 2010; Smith and Clark 2014), coexist within the North Pacific Ocean and Bering Sea areas, often breeding in the same colonies. Thus, ocean regime alone does not explain speciation in seabirds.

## Nonbreeding distribution

### Rationale

Species that are resident at colonies year-round, or that migrate to population-specific nonbreeding areas (i.e. that have high seasonal connectivity), may have less opportunity for gene flow than those that have a single common nonbreeding area or that simply disperse in the nonbreeding season. For example, Brünnich's Guillemots (*Uria lomvia*) from throughout the North Atlantic tend to congregate in the northwest Atlantic during winter and are genetically panmictic (Birt-Friesen et al. 1992; Tigano et al. 2015); in contrast, Black Guillemots (*Cepphus grylle*)

tend to winter near colonies and have a marked population genetic structure (Kidd and Friesen 1998). Correspondingly, Friesen et al. (2007a) found that nonbreeding distribution correlated with the extent of geographic variation in mtDNA in seabirds. Similar associations have been found in landbirds (Kelly and Hutto 2005) and waterbirds (Kraaijeveld 2008). For example, a recent migratory divide in European Blackcaps (*Sylvia atricapilla*) in Germany correlates with rapid morphological divergence and assortative mating between individuals wintering in different areas (Bearhop et al. 2005; Rolshausen et al. 2009).

### Support from the literature

In population genetic studies for which data on nonbreeding distributions are available, restrictions in gene flow occur in 34 (67 %) of 51 species that are resident at colonies year-round, that migrate to population-specific nonbreeding areas or that have mixed nonbreeding strategies (Fig. 2). Furthermore, sister species often differ in

nonbreeding distributions [e.g., Cape vs. Australasian Gannets (*Sula capensis* vs. *S. serrator*); Ismar et al. 2011; Patterson et al. 2011].

However, nonbreeding distribution alone does not explain restrictions in gene flow in seabirds. Of 35 species whose breeding populations mix in the nonbreeding area, 22 (63 %) show evidence of restrictions in gene flow. Additionally, sister species often overlap in the nonbreeding area (e.g., Common *U. aalge* and Brünnich's Guillemots; McFarlane Tranquilla et al. 2014).

### Foraging distribution during the breeding season

#### Rationale

Burg and Croxall (2001) argued that species with population-specific feeding areas have less opportunity for gene flow among colonies than if foraging ranges overlap among colonies. For example, stable isotopes indicate that Hawaiian petrels (*Pterodroma sandwichensis*) breeding on Hawaii versus Kauai forage in different areas, and analyses of molecular genetic variation using coalescent theory indicated that fewer than 1 migrant is exchanged per 1000 generations between these breeding sites (Welch et al. 2011; Wiley et al. 2012). Similarly, Friesen et al. (2007a) argued that inshore-feeding species should have less potential for gene flow among colonies and found that all of seven inshore-feeding species had population genetic or phylogeographic structure in their mtDNA. As a corollary, Taylor et al. (2011a) proposed that species that feed at upwellings have to change distributions periodically to track foraging areas, and so have more opportunity for gene flow. Accordingly, gene flow appears to be higher within Blue-footed and Peruvian Boobies and Peruvian Pelicans (*Pelicanus thagus*), all upwelling specialists, than within any other tropical seabird species (Taylor et al. 2011a, b; Jeyasingham et al. 2013)

#### Support from the literature

The possibility that foraging distribution affects gene flow and potentially leads to speciation is supported by the observation that, of 22 species that have been studied that either feed inshore or have population-specific foraging areas, 20 (91 %) show evidence of restrictions in gene flow (Fig. 2). Also, many sister species differ in foraging distributions (e.g., Black-browed vs. Campbell Island Albatrosses *Thalassarche impavida*; Burg and Croxall 2001). Furthermore, strong population genetic structure has been found in only 1 (8 %) of 12 upwelling specialists that have been studied (Fig. 2).

However, the relationship between foraging distribution and gene flow is not strong: 23 (74 %) of 31 species that feed offshore also show restrictions in gene flow. And sister species

often have similar foraging distributions (e.g., Common and Brünnich's Guillemots; Gaston and Jones 1998).

### Breeding phenology

#### Rationale

According to theory, differences in breeding phenology (allochryony) can reduce or eliminate gene flow between populations, even in the absence of selection, provided that breeding time is heritable (Hendry and Day 2005). Many convincing examples of speciation by allochryony exist in plants, insects and fishes (Hendry and Day 2005; e.g., Ordning et al. 2010). The possibility that allochryony alone can restrict gene flow is supported by examples of sympatric seasonal populations that differ genetically, since restrictions in gene flow for ecological reasons are unlikely in these cases. Geographic variation in breeding phenology is common in birds including seabirds (del Hoyo et al. 1992, 1996), and seasonal populations have been reported within archipelagos and even within breeding colonies of seabirds (e.g., Galapagos Petrels *Pterodroma phaeopygia*, Tomkins and Milne 1991; Herald Petrels, *Pterodroma heraldica*, Brooke and Rowe 1996). Furthermore, evidence for restrictions in gene flow between sympatric seasonal populations has been found in storm-petrels (*Oceanodroma* spp.): seasonal races appear to have arisen independently and sympatrically at least five times in the Madeiran (Band-rumped) Storm-petrel species complex (*O. castro/ Monteiroi/jabejabe*) and Leach's Storm-petrel (*O. leucorhoa*, Friesen et al. 2007b, unpubl.), leading to reproductive isolation at least once (Bolton et al. 2008).

#### Support from the literature

All but one of at least nine species of seabirds that have geographic variation in breeding phenology also show evidence of restricted gene flow (Supplementary Table 1c), and three species also show evidence of restrictions in gene flow among allochryonic populations within archipelagos (Supplementary Table 1d). Furthermore, sister species often differ in breeding chronology (e.g., Spectacled and White-chinned Petrels, Techow et al. 2009; Scripps's and Guadalupe Murrelets, reviewed in Birt et al. 2012).

Although results for storm-petrels suggest that speciation by allochryony is possible in seabirds, it is probably not common. Few other possible cases of population differentiation due to allochryony have been reported, and most populations that differ in breeding phenology also differ in other features such as ocean regime (e.g., South American Tern *Sterna hirundinacea*; Faria et al. 2010). Furthermore, many colonies show strong breeding synchrony, and allochryony cannot occur in strongly seasonal ocean regimes.

## Synthesis and future studies

Results of this review indicate that all of the six factors investigated have the potential to restrict gene flow in seabirds, potentially enough for speciation (Fig. 2). Physical isolation clearly can lead to speciation. Of the remaining factors, ocean regime has the strongest relationship to gene flow: 85 % of 39 conspecific populations that breed in different regimes show evidence of restricted gene flow (and those that do not are primarily upwelling specialists), and 15 (39 %) of 38 species that occur in only one regime appear to be genetically panmictic. Nonbreeding distribution also appears to be important, and the effect of wintering in different ocean regimes merits further investigation. However, none of these factors provides a complete model of speciation in seabirds. Generally, disruptions in gene flow appear to be associated with two or more factors, one of which is usually strong philopatry (Fig. 2): only 5 (31 %) of 16 species that are influenced by only one feature (aside from physical isolation) show interruptions in gene flow, and only one of these has strong population genetic differentiation. In contrast, 44 (85 %) of 52 species that are affected by two or more factors show evidence of restricted gene flow. Of the eight exceptions, four involve upwelling specialists, one has a very restricted range (two islands off New Zealand), three are not strongly philopatric, and one was only studied with allozymes.

Other factors that may contribute to, or inhibit, the evolution of reproductive isolation need to be tested broadly. These can be classified generally into environmental features (additional to those outlined above), factors affecting mate choice, and intrinsic (genomic) isolating mechanisms (Table 1).

### Other environmental features

#### *Peripheral isolation*

Mayr (1963) and subsequent researchers argued that peripheral isolation is an important mechanism of speciation. Populations on the edge of a species' range may be genetically isolated from central populations because of lower immigration rates and/or because of selection associated with suboptimal habitat (Eckert et al. 2008). Alternatively or additionally, small population size often associated with peripheral populations could induce sufficient genetic drift to lead to reproductive isolation (see Intrinsic genetic isolation, below). Accordingly, Liebers et al. (2001) argued that the Armenian Gull (*Larus armenicus*) is a relict of an ancient colonisation of Armenia from the Atlantic by Yellow-legged Gulls (*Larus* spp.),

probably associated with a population bottleneck. Similarly, the Shy Albatross (*Thalassarche cauta*) putatively arose following range expansion by the White-capped Albatross (*T. steadi*; Abbott and Double 2003b). The general importance of peripheral isolation in speciation in seabirds remains to be explored.

#### *Pattern of gene flow*

In theory, the pattern of gene flow among colonies can affect the level of genetic divergence and thus the potential for local adaptation and ultimately reproductive isolation. If migrants are exchanged at random among colonies (n-island model of dispersal; Wright 1969), then in theory one migrant per generation can homogenise colonies genetically. However, more gene flow is needed to homogenise populations if migrants are exchanged primarily between neighbouring colonies (stepping-stone model of dispersal), especially if colonies are distributed linearly, e.g., along a coastline. The pattern of gene flow is rarely known for seabirds, but Friesen et al. (2007a) found a weak effect of colony distribution (coastal versus offshore islands) on population genetic structure. In addition, genetic distance correlates with geographic distance between colonies in many species that have been studied (reviewed in Friesen et al. 2007a), as would be expected if dispersal was primarily between neighbouring colonies. Thus, the influence of dispersal pattern on gene flow merits further investigation.

#### *Prevailing winds*

Winds can have a strong influence on foraging patterns and migration routes of seabirds (e.g., Weimerskirch et al. 2000; Felicimo et al. 2008; Gonzalez-Solis et al. 2009) and have the potential to promote gene flow among colonies, either on an on-going basis or sporadically, during storms. Ocean currents are often associated with prevailing winds, and currents may direct gene flow among colonies (e.g., de Dinechin et al. 2009). However, the effect of wind itself on gene flow in seabirds is largely unexplored.

#### *Interspecific interactions*

The presence of competitors or predators may reduce or prevent gene flow among colonies. The potential for competitors or predators to disrupt gene flow and potentially lead to reproductive isolation is unexplored in seabirds. In contrast, ectoparasite infestations can lead to large-scale abandonment of breeding colonies (Duffy 1983) and could promote gene flow if birds relocate to either new or existing colonies. This possibility also is largely unexplored, although it may help explain genetic



**Table 1** Potential for different factors to restrict gene flow, and so promote speciation in seabirds, or to promote gene flow and so inhibit speciation

Factor	Potential effect on gene flow
Environmental factors	
Physical (geographic) barriers to dispersal	Restrict
Philopatry	Restrict
Differences in ocean currents	Restrict
Difference in nonbreeding distributions	Restrict
Difference in foraging areas	Restrict
Specialisation to upwellings	Promote
Difference in breeding time	Restrict
Peripheral colonies	Restrict
Stepping-stone dispersal	Restrict
Strong winds	Promote
Interspecific interactions	Either
Habitat change/disturbance	Promote
Mate choice	
Differences in morphology (plumage, bare part colouration)	Restrict
Differences in vocalisations	Restrict
Sexual selection	Either
Intrinsic (genomic) reproductive isolation	Restrict

panmixia within Peruvian Pelicans and Peruvian Boobies (Taylor et al. 2011a, b).

#### *Environmental variability*

Environmental changes can potentially promote gene flow due to either improved breeding conditions promoting colonisation or deteriorating conditions promoting emigration. Habitat deterioration in turn could result from either extrinsic forces (e.g., climate change) or the activities of the birds themselves (e.g., prey depletion, or destruction of nesting trees by cormorants). Distributions of several seabird species have clearly changed as a result of the climate changes of the Pleistocene. Frequent environmental changes could select against philopatry, potentially leading to higher levels of gene flow and lower rates of speciation. A temporally variable environment also could favour phenotypic plasticity, which can reduce local adaptation. In contrast, a stable environment can provide a species with enough time to adapt genetically to local conditions and/or develop reproductive isolation (e.g., Alderman et al. 2005). The possibility that a temporally variable environment promotes gene flow needs to be explored further.

#### **Mate choice**

Geographic variation in any feature important for species recognition during mate choice may inhibit gene flow and eventually lead to reproductive isolation.

#### *Body colouration*

Following a review of the incidence of hybridisation in sympatric congeneric seabirds, Pierotti (1987) argued that bill and foot colours are primary isolating mechanisms in surface-nesting seabirds. In a comprehensive evaluation of morphology, breeding phenology, breeding success and variation in neutral molecular markers among Herring (*Larus argentatus*) and Caspian Gulls (*L. cachinnans*) in a hybrid zone in Poland, Gay et al. (2007) and Neubauer et al. (2009) inferred that the colour of the orbital ring was an important, although incomplete, premating barrier. Many species of seabirds show geographic variation in plumage and other colouration (e.g., Brown Boobies; Nelson 1978); however few studies have examined the influence of this variation on intraspecific gene flow.

#### *Vocalisations*

Closely related species of birds often differ in vocalisations, and changes in these cues can not only reinforce but also potentially initiate reproductive isolation in landbirds (Edwards et al. 2005). In seabirds, many sister species differ in vocalisations (e.g., Rockhopper Penguins, Jouventin et al. 2006; Madeiran Storm-petrels, Bolton 2007; auklets, Seneviratne et al. 2012), as do some conspecific populations (e.g., Madeiran Storm-petrels; Bolton 2007). These differences may result from either neutral divergence or adaptation to local acoustic conditions (e.g., Thumser et al. 1996; Seneviratne et al. 2012). Whether or

not variation in vocalisations can initiate speciation in seabirds remains largely unexplored.

### Sexual selection

Compelling evidence for sexual selection has been reported in seabirds (e.g., Jones and Hunter 1993; Torres and Velando 2005), and differences between avian species, including seabirds, often involve sexually selected characters (Edwards et al. 2005; e.g., Jones and Hunter 1998; Serrano-Meneses and Szekely 2006). The potential for sexual selection to drive speciation is an area of active research and controversy (Ritchie 2007; Kraaijeveld et al. 2011; Seddon et al. 2013). Although sexually selected characters can show extensive intraspecific variation (e.g., Jones et al. 2000), only a few examples of geographic variation or divergent selection on sexually selected characters exist in seabirds (e.g., Snow Petrels *Pagodroma nivea*, Barbraud and Jouventin 1998; Brown Boobies, Tershy and Croll 2000), and few studies have analysed the effect of sexual selection on gene flow or population genetic structure (but see Pons et al. 2014).

### Intrinsic reproductive isolation

Genomic differences between individuals from different populations have the potential to restrict gene flow and lead to reproductive isolation (Butlin 2010; Nosil and Feder 2012; Seehausen et al. 2014). Such differences include (but are not limited to) chromosomal rearrangements and intra-genomic conflicts such as Dobzansky-Mueller incompatibilities. Although little karyotopic or other genomic information is available for seabirds, and karyotypes tend to be conserved across birds (Ellegren 2013), genome sequencing is revealing that chromosomal rearrangements are common (Ellegren et al. 2012; Ellegren 2013). Next-generation sequencing provides exciting new avenues for exploring the role of intrinsic barriers to reproduction in seabirds (Ellegren et al. 2012). Genomic differences could be promoted through population bottlenecks or founder events, as rearrangements are more likely to become fixed in small populations (Carson and Templeton 1984). The origins of at least two species of seabirds have been linked to population bottlenecks (the Armenian Gull and Shy Albatross, above), although whether the bottlenecks were associated with intrinsic genomic changes is unreported.

### Synergisms

Studies that combine neutral molecular markers with other analyses will be especially useful for improving our understanding of the factors promoting—and reducing—speciation in seabirds. There are many examples of

research synergisms that result from combining analyses of neutral markers with data from functional genes, band returns, tracking, quantitative traits, ecology, behaviour, immunology or endocrinology. The study of Cook's Petrels (*Pterodroma cookii*) by Rayner et al. (2011) provides a notable example. Cook's Petrels are philopatric seabirds that breed on Little Barrier and Codfish Islands, New Zealand. Rayner et al. combined data from mtDNA, light-based data loggers, satellite sensing of the environment, stable isotopes and breeding surveys. They proposed that differences in nonbreeding distribution are associated with differences in breeding phenology, which, in combination with philopatry, reduces gene flow between colonies. New methods for data analysis (e.g., approximate Bayesian computation, ecological niche modeling) also promise to provide useful insights into speciation by enabling rigorous tests of multiple explicit hypotheses. Application of these new methods to multi-factorial studies, as well as mate choice experiments, next-generation sequencing, and meta-analyses of studies of seabirds and other taxa, should have many benefits. They should help us to disentangle cause and effect, to estimate population genetic structure in unstudied species (especially those of conservation concern), to predict the potential existence of cryptic species and ultimately to protect the diversification process.

**Acknowledgments** Tim Birt and present and past graduate and undergraduate students in the Friesen/Birt conducted many of the studies described in this review. Eric Saulnier and Vanessa Hrvatin (funded through the Queen's University Summer Work Experience Program) helped with literature searches. Elisa Dierickx, Lisa Nupen, Anna Lashko Cheryl Baduini, Sarah Wallace Ken Warheit and colleagues shared unpublished data. Tim Birt, David Anderson, Anna Tigano, Rebecca Taylor, Nathaniel Clark, Catherine Dale and Raphael Lavoie provided insightful discussions. Anna Tigano provided help with figure design. Dorit Liebers-Helbig and Franz Bairlein invited me to present this study at the 26th International Ornithological Congress.

### References

- Abbott CL, Double MC (2003a) Phylogeography of shy and white-capped albatrosses inferred from mitochondrial DNA sequences: implications for population history and taxonomy. *Mol Ecol* 12:2747–2758
- Abbott CL, Double MC (2003b) Genetic structure, conservation genetics and evidence of speciation by range expansion in shy and white-capped albatrosses. *Mol Ecol* 12:2953–2962
- Alderman R, Double MC, Valencia J, Gales RP (2005) Genetic affinities of newly sampled populations of wandering and black-browed Albatross. *Emu* 105:169–179
- Barbraud C, Jouventin P (1998) What causes body size variation in the Snow Petrel *Pagodroma nivea*? *J Avian Biol* 29:161–171
- Bearhop S, Fiedler W, Furness RW, Votier SC, Waldron S, Newton J, Bowen GJ, Berthold P, Farnsworth K (2005) Assortative mating as a mechanism for rapid evolution of a migratory divide. *Science* 310:502–504

- Birt TP, Carter HR, Whitworth DL, McDonald A, Newman SH, Gress F, Palacios E, Koepke JS, Friesen VL (2012) Range-wide population genetic structure of the Xantus's Murrelet (*Synthliboramphus hypoleucus*). *Auk* 129:44–55
- Birt-Friesen VL, Montevecchi WA, Gaston AJ, Davidson WS (1992) Genetic structure of thick-billed murre (*Uria lomvia*) populations examined using direct sequence analysis of amplified DNA. *Evolution* 46:267–272
- Bolton M (2007) Playback experiments indicate absence of vocal recognition among temporally and geographically separated populations of Madeiran Storm-petrels *Oceanodroma castro*. *Ibis* 149:255–263
- Bolton M, Smith AL, Gomez-Diaz EE, Friesen VL, Medeiros R, Bried J, Roscales JL, Furness RW (2008) Monteiro's Storm-petrel *Oceanodroma monteiroi*: a new species from the Azores. *Ibis* 150:717–727
- Brooke MD, Rowe G (1996) Behavioural and molecular evidence for specific status of light and dark morphs of the Herald Petrel *Pterodroma heraldica*. *Ibis* 138:420–432
- Burg TM, Croxall JP (2001) Global relationships amongst black-browed and grey-headed albatrosses: analysis of population structure using mitochondrial DNA and microsatellites. *Mol Ecol* 10:2647–2660
- Butlin RK (2010) Population genomics and speciation. *Genetica* 138:409–418
- Butlin R et al (2012) What do we need to know about speciation? *Trends Ecol Evol* 27:27–39
- Carson HL, Templeton AR (1984) Genetic revolutions in relation to speciation phenomena: the founding of new populations. *Ann Rev Ecol Syst* 15:97–131
- Coulson JC (2002) Colonial breeding in seabirds. In: Schrieber EA, Burger J (eds) *Biology of marine birds*. CRC Press, Boca Raton
- Coyne AE, Orr HA (2004) *Speciation*. Sinauer Associates, Sunderland
- de Dinechin M, Ottvall R, Quillfeldt P, Jouventin P (2009) Speciation chronology of rockhopper penguins inferred from molecular, geological and palaeoceanographic data. *J Biogeogr* 36:693–702
- del Hoyo J, Elliott A, Sargatal J (1992) *Handbook of the birds of the world*, vol 1. Lynx Edicions, Barcelona
- del Hoyo J, Elliott A, Sargatal J (1996) *Handbook of the birds of the world*, vol 3. Lynx Edicions, Barcelona
- Duffy DC (1983) The ecology of tick parasitism on densely nesting Peruvian seabirds. *Ecology* 64:110–119
- Eckert CG, Samis KE, Loughheed SC (2008) Genetic variation across species' geographical ranges: the central-marginal hypothesis and beyond. *Mol Ecol* 17:1170–1188
- Eda M, Koike H, Kuro-O M, Mihara S, Hasegawa H, Higuchi H (2012) Inferring the ancient population structure of the vulnerable Phoebeastria albatrus, combining ancient DNA, stable isotope, and morphometric analyses of archaeological samples. *Cons Gen* 13:143–151
- Edwards SV, Kingan SB, Calkins JD, Balakrishnan CN, Jennings WB, Swanson WJ, Sorenson MD (2005) Speciation in birds: genes, geography, and sexual selection. *Proc Natl Acad Sci USA* 102:6550–6557
- Ellegren H (2013) The evolutionary genomics of birds. *Ann Rev Ecol Evol Syst* 44:239–259
- Ellegren H, Smeds L, Burri R, Olason PI, Backstrom N, Kawakami T, Kunstner A, Makinen H, Nadachowska-Brzyska K, Qvarnstrom A, Uebbing S, Wolf JBW (2012) The genomic landscape of species divergence in *Ficedula flycatchers*. *Nature* 491:756–760
- Faria PJ, Campos FP, Branco JO, Musso CM, Morgante JS, Bruford MW (2010) Population structure in the South American tern *Sterna hirundinacea* in the South Atlantic: two populations with distinct breeding phenologies. *J Avian Biol* 41:378–387
- Felicimo AM, Munoz J, Gonzalez-Solis J (2008) Ocean surface winds drive dynamics of transoceanic aerial movements. *PLoS One* 3:e2928
- Friesen VL, Burg TM, McCoy K (2007a) Mechanisms of population differentiation in seabirds. *Mol Ecol* 16:1765–1785
- Friesen VL, Smith AL, Gomez-Diaz EE, Bolton M, Furness RW, Gonzalez-Solis J, Monteiro LR (2007b) Sympatric speciation by allochrony in a seabird. *Proc Natl Acad Sci USA* 104:18589–18594
- Gangloff B, Zino F, Shirihai H, Gonzalez-Solis J, Couloux A, Pasquet E, Bretagnolle V (2013) The evolution of north-east Atlantic gadfly petrels using statistical phylogeography. *Mol Ecol* 22:495–507
- Gaston AJ, Jones IL (1998) *The auks: alcidae*. Oxford University Press, Oxford
- Gay L, Neubauer G, Zagalska-Neubauer M, Debain C, Pons J-M, David P, Crochet P-A (2007) Molecular and morphological patterns of introgression between two large white-headed gull species in a zone of recent secondary contact. *Mol Ecol* 16:3215–3227
- Gomez-Diaz E, Gonzalez-Solis J, Peinado MA (2009) Population structure in a highly pelagic seabird, the Cory's shearwater *Calonectris diomedea*: an examination of genetics, morphology and ecology. *Mar Ecol Progr Ser* 382:197–209
- Gonzalez-Solis J, Felicissimo A, Fox JW, Afanasyev V, Kolbeinsson Y, Munoz J (2009) Influence of sea surface winds on shearwater migration detours. *Mar Ecol Progr Ser* 391(221):230
- Hailer F, Schreiber EA, Miller JM, Levin II, Parker PG, Chesser RT, Fleischer RC (2011) Long-term isolation of a highly mobile seabird on the Galapagos. *Proc R Soc B* 278:817–825
- Hendry AP, Day T (2005) Population structure attributable to reproductive time: isolation by time and adaptation by time. *Mol Ecol* 14:901–916
- Hendry AP, Nosil P, Rieseberg LH (2007) The speed of ecological speciation. *Funct Ecol* 21:455–464
- Hey J, Nielsen R (2007) Integration within the Felsenstein equation for improved Markov chain Monte Carlo methods in population genetics. *Proc Natl Acad Sci USA* 104(2785):2790
- Humphries EM, Winker K (2010) Working through polytomies: auklets revisited. *Mol Phylogen Evol* 54:88–96
- Ismar SMH, Phillips RA, Rayner MJ, Hauber ME (2011) Geolocation tracking of the annual migration of adult Australasian gannets (*Morus serrator*) breeding in New Zealand, Wilson. *J Ornithol* 123:121–125
- Jeyasingham W, Taylor SA, Zavalaga CB, Simeone A, Friesen VL (2013) Specialization to cold water upwellings facilitates gene flow in seabirds: additional evidence from the Peruvian pelican, *Pelecanus thagus* (Aves: Pelecanidae). *J Avian Biol* 44:297–304
- Jones IL, Hunter FM (1993) Mutual sexual selection in a monogamous bird. *Nature* 362:238–239
- Jones IL, Hunter FM (1998) Heterospecific mating preferences for a feather ornament in least auklets. *Behav Ecol* 9:187–192
- Jones IL, Hunter FM, Fraser G (2000) Patterns of variation in ornaments of Crested Auklets *Aethia cristatella*. *J Avian Biol* 31:119–127
- Jouventin P, Cuthbert RJ, Ottvall R (2006) Genetic isolation and divergence in sexual traits: evidence for the northern rockhopper penguin *Eudyptes moseleyi* being a sibling species. *Mol Ecol* 15:3413–3423
- Karvonen A, Seehausen O (2012) The role of parasitism in adaptive radiations—when might parasites promote and when might they constrain ecological speciation? *Int J Ecol* 2012:280169
- Kelly JF, Hutto RL (2005) An east-west comparison of migration in North American wood warblers. *Condor* 107:197–211

- Kidd MG, Friesen VL (1998) Analysis of mechanisms of microevolutionary change in *Cephus* guillemots using patterns of control region variation. *Evolution* 52:1158–1168
- Kraaijeveld K (2008) Non-breeding habitat preference affects ecological speciation in migratory waders. *Naturewissenschaften* 95:347–354
- Kraaijeveld K, Kraaijeveld-Smit FJL, Maan ME (2011) Sexual selection and speciation: the comparative evidence revisited. *Biol Rev* 86:367–377
- Liebers D, Helbig AJ, de Knijff P (2001) Genetic differentiation and phylogeography of gulls in the *Larus cachinnans-fuscus* group (Aves: Charadriiformes). *Mol Ecol* 10:2447–2462
- Liebers D, de Knijff P, Helbig AJ (2004) The herring gull complex is not a ring species. *Proc R Soc B* 271:893–901
- Mayr E (1963) *Animal species and evolution*. Harvard University Press, Cambridge
- McFarlane Tranquilla LA, Montevecchi WA, Fifield DA, Hedd A, Gaston AJ, Robertson GJ, Phillips RA (2014) Individual winter movement strategies in two species of murre (*Uria* spp.) in the northwest Atlantic. *PLoS One* 9:e90583
- Morris-Pocock JA, Anderson DJ, Friesen VL (2011) Mechanisms of global diversification in the brown booby (*Sula leucogaster*) revealed by uniting statistical phylogeographic and multilocus phylogenetic methods. *Mol Ecol* 20:2835–2850
- Nelson JB (1978) *The Sulidae: gannets and boobies*. Oxford University Press, Oxford
- Neubauer G, Zagalska-Neubauer MM, Pons J-M, Crochet P-A, Chylarecki P, Przystalski A, Gay L (2009) Assortative mating without complete reproductive isolation in a zone of recent secondary contact between Herring Gulls (*Larus argentatus*) and Caspian Gulls (*L. cachinnans*). *Auk* 126:409–419
- Nosil P (2012) *Ecological speciation*. Oxford University Press, Oxford
- Nosil P, Feder JL (2012) Genomic divergence during speciation: causes and consequences. *Phil Trans R Soc B* 367:332–342
- Ording GJ, Mercader RJ, Aardema ML, Scriber JM (2010) Allochronic isolation and incipient hybrid speciation in tiger swallowtail butterflies. *Oecologia* 162:523–531
- Patterson SA, Morris-Pocock JA, Friesen VL (2011) A multilocus phylogeny of the Sulidae (Aves: Pelecaniformes). *Mol Phylogen Evol* 58:181–191
- Pierotti R (1987) Isolating mechanisms in seabirds. *Evolution* 41:559–570
- Pons J-M, Sonsthagen S, Dove CJ, Crochet PA (2014) Extensive mitochondrial introgression in North American great black-backed gulls (*Larus marinus*) from the American herring gull (*Larus smithsonianus*) with little nuclear DNA impact. *Heredity* 112:226–239
- Price T (2008) *Speciation in birds*. Roberts and Company, Greenwood Village
- Rawlance NJ, Till CE, Scofield RP, Tennyson AJD, Collins CJ, Lalas C, Loh G, Matisoo-Smith E, Waters JM, Spencer HG, Kennedy M (2004) Strong phylogeographic structure in a sedentary seabird, the Stewart Island shag (*Leucocarbo chalconotus*). *PLoS One* 9:e90769
- Rayner MJ, Hauber ME, Steeves TE, Lawrence HA, Thompson DR, Sagar PM, Bury SJ, Landers TJ, Phillips RA, Ranjard L, Shaffer SA (2011) Contemporary and historical separation of transequatorial migration between genetically distinct seabird populations. *Nat Commun* 2:332
- Ritchie MG (2007) Sexual selection and speciation. *Ann Rev Ecol Evol Syst* 38:79–102
- Rolshausen G, Segelbacher G, Hobson KA, Schaefer HM (2009) Contemporary evolution of reproductive isolation and phenotypic divergence in sympatry along a migratory divide. *Curr Biol* 19:2097–2101
- Rosenzweig ML (2001) Loss of speciation rate will impoverish future diversity. *Proc Natl Acad Sci USA* 98:5404–5410
- Sagar PM, Stahl J-C, Molloy J (1998) Sex determination and natal philopatry of southern Buller's mollymawks (*Diomedea bulleri bulleri*). *Notornis* 45:271–278
- Seddon N, Botero CA, Tobias JA, Dunn PO, MacGregor HEA, Rubenstein DR, Uy JAC, Weir JT, Whittingham LA, Safran RJ (2013) Sexual selection accelerates signal evolution during speciation in birds. *Proc R Soc B* 280:1065
- Seehausen O, Butlin RK, Keller I, Wagner CE, Boughman JW, Hohenlohe PA, Peichel CL, Saetre G-P et al (2014) Genomics and the origin of species. *Nat Rev* 15:176–192
- Seneviratne SS, Jones IL, Carr SM (2012) Patterns of vocal divergence in a group of non-oscine birds (auklets; Alcidae, Charadriiformes). *Evol Ecol Res* 14:95–112
- Serrano-Meneses M-A, Szekely T (2006) Sexual size dimorphism in seabirds: sexual selection, fecundity selection and differential niche-utilisation. *Oikos* 113:385–394
- Smith NA, Clark JA (2014) Systematics and evolution of the pan-Alcidae (Aves, Charadriiformes). *J Avian Biol* 45:125–140
- Sonsthagen SA, Chesser RT, Bell DA, Dove CJ (2012) Hybridization among arctic white-headed gulls (*Larus* spp.) obscures the genetic legacy of the Pleistocene. *Ecol Evol* 2:1278–1295
- Soule ME, Wilcox BA (1980) *Conservation biology: an evolutionary-ecological approach*. Sinauer Associates, Sunderland
- Steeves TE, Anderson DJ, Friesen VL (2005) The Isthmus of Panama: a major physical barrier to gene flow in a highly mobile pantropical seabird. *J Evol Biol* 18:1000–1008
- Sternkopf V, Liebers-Helbig D, Ritz MS, Zhang J, Helbig AJ, de Knijff P (2014) Introgressive hybridization and the evolutionary history of the herring gull complex revealed by mitochondrial and nuclear DNA. *BMC Evol Biol* 10:348
- Taylor SA, MacLagan L, Anderson DJ, Friesen VL (2011a) Could specialization to cold water upwelling systems influence gene flow and population differentiation in marine organisms? A case study using the blue-footed booby, *Sula nebouxii*. *J Biogeogr* 38:883–893
- Taylor SA, Zavalaga CB, Luna-Jorquera G, Simeone A, Anderson DJ, Friesen VL (2011b) Panmixia and high genetic diversity in a Humboldt Current endemic, the Peruvian Booby (*Sula variegata*). *J Ornithol* 152:623–630
- Techow NMSM, Ryan PG, O'Ryan C (2009) Phylogeography and taxonomy of white-chinned and spectacled petrels. *Mol Phylogen Evol* 52:25–33
- Tershry BE, Croll DA (2000) Parental investment, adult sex ratios, and sexual selection in a socially monogamous seabird. *Behav Ecol Sociobiol* 48:52–60
- Thumser NN, Karron JD, Ficken MS (1996) Interspecific variation in the calls of *Spheniscus* penguins. *Wilson Bull* 108:72–79
- Tigano A, Damus M, Birt TP, Morris-Pocock JA, Artukhin YB, Friesen VL (2015) The arctic: glacial refugium or area of secondary contact? Inference from population genetic structure of the thick-billed murre (*Uria lomvia*) and implications for management. *J Hered (in press)*
- Tomkins RJ, Milne BJ (1991) Differences among dark-rumped petrel (*Pterodroma phaeopygia*) populations within the Galapagos Archipelago. *Notornis* 38:1–35
- Torres R, Velando A (2005) Male preference for female foot colour in the socially monogamous blue-footed booby. *Sula nebouxii*. *Anim Behav* 69:5965
- Wallace SJ, Wolfe SG, Bradley SW, Harvey AL, Friesen VL (2015) The influence of biogeographically barriers on the population genetic structure and gene flow in a coastal seabird. *J Biogeogr* 42:390–490

- Weimerskirch H, Guionnet T, Martin J, Shaffer SA, Costa DP (2000) Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proc R Soc B* 267:1869–1874
- Welch AJ, Yoshida AA, Fleischer RC (2011) Mitochondrial and nuclear DNA sequences reveal recent divergence in morphologically indistinguishable petrels. *Mol Ecol* 20:1364–1377
- Wiley AE, Welch AJ, Ostrom PH, James HF, Stricker CA, Fleischer RC, Gandhi H, Adams J, Ainley DG, Duvall F, Holmes N, Hu DC, Judge S, Penniman J, Swindle KA (2012) Foraging segregation and genetic divergence between geographically proximate colonies of a highly mobile seabird. *Oecologia* 168:119–130
- Wright S (1969) *Evolution and the genetics of populations, Vol. 2: The theory of gene frequencies*. University of Chicago Press, Chicago