DISPERSAL UNDER THE SEABIRD PARADOX: PROBABILITY, LIFE HISTORY, OR SPATIAL ATTRIBUTES?

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ABSTRACT

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Management of avian species threatened by land use and climate change requires a thorough understanding of their site fidelity and dispersive behaviors. Among long-lived colonial seabird species, the behavior of returning to the natal colony to breed, i.e., natal philopatry, may increase the likelihood that adequate resources and mates are available, but it may also increase the potential for inbreeding, competition, and ecological traps. Successful management of seabird populations—using chick translocation to encourage colony establishment to locations having minimal threats—must also be informed by the likelihood that birds will return to the new sites. However, the extent of philopatry, and the traits that dictate variation across seabirds, have yet to be fully summarized. We evaluated whether seabirds returned to their natal colony at rates greater than those predicted by colony size and various dispersal variables, based on data gathered for 36 seabird species nesting in the British Isles and the Hawaiian Archipelago. We compiled long-term banding and census data across 663 colonies. A linear mixed-effects model was employed to determine the relationship between philopatry and colony demographics, wingspan (mobility), and spatial variables. Our results indicate that philopatric rates are higher in the Hawaiian Archipelago than in the British Isles. Additionally, our research suggests that seabird management using chick translocation will have the greatest success with Procellariiformes species.

Key words: British Isles, dispersal, Hawaiʻi, philopatry, colony demographics, seabirds

INTRODUCTION

Many seabirds exhibit high rates of philopatry despite the often large differences between their breeding and wintering/non-breeding areas, a phenomenon coined 'the seabird paradox' (Milot *et al*. 2008). Within colonial species, there are competing pressures for young seabirds to either disperse to a different colony to breed, thereby reducing intraspecific competition for resources (territories, mates, food; Furness & Birkhead 1984), or to return to their natal colony where the nesting habitat and resources are suitable, or at least at the level at which they departed (Schreiber & Burger 2002). The major advantage of dispersal, or recruitment to a new site, comes with finding a location where resources are more available, but dispersal may also bring additional risks, such as a higher potential to encounter unforeseen threats or the possibility that the novel area will provide habitat that is unsuitable for nesting. Philopatry, on the other hand, can increase the potential for inbreeding, competition, and ecological traps under climate and land-use change (Reynolds *et al*. 2015). Based on evolutionary theory (Van Valen 1971), philopatric tendencies evolved due to higher reproductive success and survival in individuals that returned to the natal site compared with those individuals that attempted to find new breeding grounds and experienced higher mortality and/or lower reproductive success. Philopatry varies among seabird taxa, but some seabird species exhibit highly philopatric tendencies (> 90%; Coulson 2016). This high degree of philopatry among certain seabird species is remarkable given their large foraging ranges and ability to fly long distances (Fisher 1976, Weimerskirch *et al*. 1984, Frederiksen & Peterson 1999, Huyvaert & Anderson 2004, Milot *et al*. 2008).

In the past, the term philopatry was used to describe birds returning to the place individuals fledged (Greenwood 1980), but its use was subsequently widened by some, making it synonymous with returning to the breeding colony at any life stage (Lawrence 1989). More recently, philopatry was used to define breeding site fidelity by adults (Frederick & Ogden 1997). Since then, the term natal philopatry was introduced to differentiate the terms in scientific publications (Thibault 1993, Weatherhead & Forbes 1994). In this paper, the term philopatry is used in its original sense to describe the tendency of individuals to recruit to their natal colony to breed.

A recent review (Coulson 2016) indicated that previous estimates of philopatry among seabirds may be inflated due to a failure to consider factors that may influence coloniality. Colonial breeding is a complex behavior exhibited by the vast majority of seabirds with a few exceptions (e.g., Marbled Murrelet *Brachyramphus marmoratus*, Kittlitz's Murrelet *B. brevirostris*). Defense against predation has long been suggested as important in shaping the evolution of coloniality in birds (Lack 1968). Other hypotheses of coloniality include the information center hypothesis (Ward & Zahavi 1973) and the group foraging hypothesis (Richner & Heeb 1995). More recently, the commodity selection theory (Danchin & Wagner 1997) posits that colonial animals assess environmental conditions—including predator avoidance, as well as nesting habitat, shelter, food, and mates—to choose where to breed. Hence, when assessing philopatric tendencies, one should consider the quality and condition of a potential breeding site.

In the context of 'commodity selection', variation in philopatric rates across seabird taxa may also be due to multiple dispersal-associated

variables (Coulson 2016). For example, wing morphology may influence bird migration by shaping the capacity for long-distance flight (Lo Valvo 1988, Berthold 1996, Rolshausen *et al.* 2009). Taxonomy, linked to life history and classified by morphometrics and genetics (Sites & Marshall 2003), may help predict philopatric variation. The highest rate of success in seabird restoration programs, which rely on recruitment to the restoration site, was found in the Procellariidae family (Jones & Kress 2012).

The degree of relaxation of philopatry can be affected by colony size, the number of colonies, and the space between breeding colonies (Lebreton *et al.* 1992). Social attraction studies and mark-recapture modeling have shown that the colony size of the recipient colony can be a driver of recruitment (Serrano *et al.* 2005, Gauthier *et al.* 2010, Fernández-Chacón *et al.* 2013). In this study, we determined whether fledglings return to their natal colony at rates greater than expected based on colony size and other potential explanatory factors (distance to the nearest colony, number of colonies as related to geographic scale, wingspan (i.e., mobility), taxonomy by order, and region). If the rates of observed philopatry within a given seabird species were proportional to relative colony size independent of other factors, we expected a linear relationship of philopatry to relative colony size, i.e., a higher philopatric tendency among larger colonies (Fig. 1A). If philopatry was consistent with 'the seabird paradox' theory, we expected consistently high philopatry regardless of relative colony size (Fig. 1B). In contrast, if natal dispersal was random, we expected there to be an equal chance of returning to the natal colony compared to nesting at a new colony with respect to relative colony size (Fig. 1C).

METHODS

Species data

Species were selected based on the availability of data, obtained from comprehensive nesting and long-term banding databases. Nesting databases indicating breeding colony size and location included the Bishop Museum Hawai'i Biological Survey (Pyle & Pyle 2017) and the British Isles Seabird 2000 colony census (Mitchell *et al.* 2004). Banding data were provided by the United States Geological Survey (USGS) Bird Banding Laboratory (BBL) for Hawaiian species and by the British Trust for Ornithology (BTO) for British Isles species. Data from BBL were retrieved on 25 May 2017 (USGS Bird Banding Laboratory 2017) and those from BTO on 25 July 2017 (British Trust for Ornithology 2017). Banding recapture data spanned over a century representing 36 seabird species within the orders Phaethontiformes, Procellariiformes, Suliformes, and Charadriiformes, including 19 Hawaiian species and 17 British species (Appendix, Table A1, Fig. A1, available on the website). Phaethontiformes were removed from the final analyses because only a single species was represented.

The BBL and BTO data were filtered to include only recaptured adults that were banded as nestlings/fledglings, including dead or live recaptures. We assumed that any adult individual that was observed at the natal site during the nesting season had returned to breed. For the BBL data, at-sea captures and those found outside of the Hawai'i colonies were excluded. The BTO data did not contain any at-sea captures. For both datasets, philopatry for each species was determined by dividing the number of recaptures at the natal site by the total number of recaptures for the species. Philopatry for a given colony was calculated by dividing the number of recaptures

that returned to the natal colony by the total number of recaptures at the given colony. For this study, individuals returning to sites under 20 km from their natal banding location were considered to have returned to the natal site, similar to previous studies (Coulson 2016).

For this study, the term 'colony' varied by study system due to geographic differences and the inherent nature of the size of the colonies. For the Hawai'i seabird dataset, each major island in the Hawaiian Archipelago was treated as a single colony
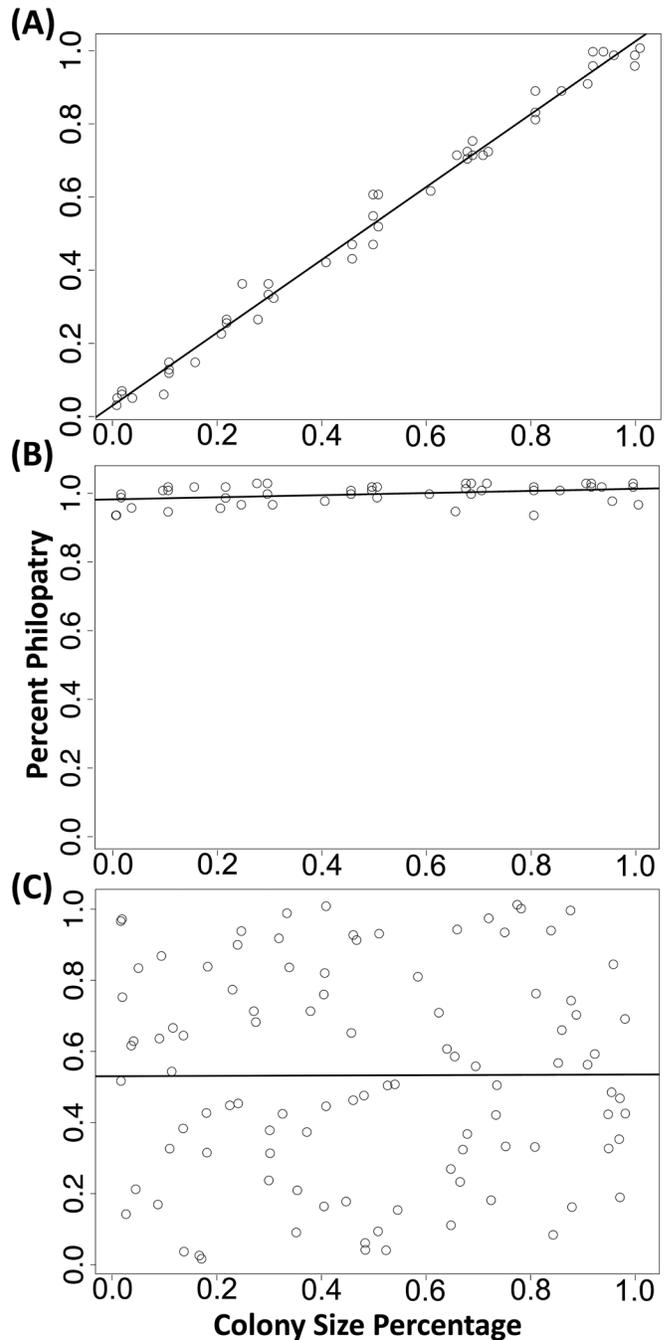
Fig. 1. Potential relationships between colony size percentage and philopatric rate, where (A) depicts philopatric rate in proportion to relative colony size, (B) is consistent with the seabird paradox, where philopatric rate is consistently high when compared to relative colony size, and (C) shows a philopatric rate that is random with respect to relative colony size.

(median = 4.14 km^2). For the British Isles seabird dataset, each county was defined as a single colony (median = 236.75 km^2). The difference between medians is largely due to the geographic differences between the two datasets. The Hawaiian Archipelago Islands are composed of small coral atolls, whereas the British Isles are made up of large continental islands, with some small offshore islets. Distances between colonies were determined by calculating the Euclidean distance between center GPS points of the focal colonies (i.e., island or county). The distances in the Hawai'i dataset ranged 15–608 km (mean 184.88 km ± 10.36 SE), whereas the British Isles dataset ranged 10–302 km (mean 61.33 km ± 1.76 SE). The fact that the colonies in both datasets had similar distance ranges suggested that our analyses were comparable, which lowered our concerns about colony bias between the two datasets.

Wingspan (cm) for each species was collected from online databases: *Birds of North America* (Poole, 2005); *All About Birds* (The Cornell Lab, 2017); *United States Fish and Wildlife Service (USFWS) Hawaiian Island National Wildlife Refuge–Seabirds* (US Fish & Wildlife Service 2017); *Birds of the World* (Billerman *et al.* 2020); and *Wildscreen Arkive Species* (Arkive 2017). Species' metadata are provided in Appendix, Table A4.

Statistical analysis

All statistical analyses were conducted in the statistical environment of R version 3.3.3 (R Core Team 2013). The relationships of variables to rates of philopatry were measured using linear mixed-effects models with R package "lme4". Linear mixed-effects models allowed us to explicitly model and compare inherent groupings in our data using fixed and random effects. We designated species as a random effect to account for among-species variation when determining significance between philopatry and explanatory variables. The fixed effects were independent variables, which included distance to the nearest colony, number of colonies, colony size, wingspan, taxonomy by order, and region. First, we transformed all quantitative variables to meet the assumption of normality under linear regression (Appendix, Table A2) using the skewness test for normality (Shapiro et al. 1968). Then, we performed a sensitivity analysis, excluding from our analysis colonies with fewer than five, 10, and 15 recaptures that resulted in linear mixed-effects models with the same trends in slope and *P*-value for each predictor variable (Appendix, Table A3). Hence, a cutoff of fewer than five recaptures for a given species was applied to the final analysis. Next, we employed a stepwise term deletion

TABLE 1
Akaike Information Criterion (AIC) and R^2 values for the linear mixed-effects models
using random[a] and fixed[b] variables from all seabird species (*n* = 35)

Variables[c] used in the Linear Mixed-Effects Model	AIC	R^2
Null (intercept only)	61.12	0.53
Percent Philopatry ~ Colony Size + Region + (1 | Species)	53.57	0.50
Percent Philopatry ~ Colony Size + Region + Distance to Nearest Colony + (1 | Species)	54.22	0.50
Percent Philopatry ~ Colony Size + Region + Distance to Nearest Colony + Wingspan + (1 | Species)	56.77	0.50
Percent Philopatry ~ Colony Size + Region + Distance to Nearest Colony + Wingspan + Taxonomy + (1 | Species)	63.75	0.50
Percent Philopatry ~ Colony Size + Region + Distance to Nearest Colony + Wingspan + Taxonomy + Number of Colonies + (1 | Species)	86.07	0.51

[a] Species was a random effect variable in all models.
[b] The fixed effects variables included the colony size, region, distance to the nearest colony, wingspan, taxonomy by order, and number of colonies.
[c] Number of colonies, wingspan, distance to the nearest colony, and colony size percentage were transformed to meet assumptions of normality.

TABLE 2
Dispersal variables among all seabird species in Hawai'i and the British Isles (*n* = 35),
with comparison to the rate of philopatry using a linear mixed-effects model

Dispersal variable	x̄ ± SE	*t* value	*P* value
Number of colonies[a]	4 715.00 ± 176.78	$t_{35/459}=0.12$	0.908
Colony size[a]	0.187 ± 0.092	$t_{35/459}=1.68$	0.094
Distance to the nearest colony[a]	-0.535 ± 0.003	$t_{35/459}=1.47$	0.142
Wingspan[a]	4.60 ± 0.024	$t_{35/459}=-1.18$	0.249
Taxonomy (Suliformes)	87 (18.9%)	$t_{35/459}=-0.44$	0.665
Taxonomy (Procellariiformes)	60 (13.0%)	$t_{35/459}=1.23$	0.226
Region (Hawai'i)	98 (21.3%)	$t_{35/459}=3.07$	0.005[*]

[a] Number of colonies, colony size, distance to the nearest colony, and wingspan were transformed to meet assumptions of normality
[*] indicates statistical significance (*P* < 0.05)

process, keeping colony size as the first variable and reordering and removing non-significant terms to produce the model of best fit as determined by Akaike Information Criterion (AIC), using the R "stats" package. The conditional R^2, which gives a measure of the proportion of variance explained by both fixed and random effects, was determined using the R "MuMIn" package. Finally, we split the data by region (Hawai'i and the British Isles) and repeated the stepwise term deletion process to determine the linear mixed-effects model of best fit, as well as the subsequent analyses.

RESULTS

The model with the best fit produced a 53.57 AIC and explained 50% of the variance ($R^2 = 0.50$) within philopatry rates (Table 1). Procellariiformes and seabirds in the Hawaiian Islands exhibited higher than expected philopatry based on relative colony size (Table 2, Fig. 2). Overall, philopatry increased with relative colony size (Fig. 2A). Philopatry was higher in the Procellariiformes order than in the other seabird taxonomic orders (Fig. 2C). Additionally, seabird philopatry was higher in Hawaiian Islands than in the British Isles (Fig. 2B). When split by region, philopatry significantly increased with colony size in the Hawai'i colonies ($t_{18/97} = 2.01$, $P = 0.050$; Table 3). For seabird colonies in the British Isles, philopatry was more prevalent as the distance to the nearest colony increased ($t_{17/361} = 2.20$, $P = 0.030$; Table 4).

DISCUSSION

We investigated whether philopatry in seabirds is proportional to colony size, is consistently high regardless of colony size, or if it is random with respect to relative colony size. Although not directly proportional, colony size was positively correlated with philopatry rates. This suggests that relative colony size is an important consideration when making inferences about philopatric rates from single study locations, especially in large colonies (Deguchi *et al.* 2017). This ties into the theories of coloniality, as large colonies may infer quality and play a role in recruitment (see Ward & Zahavi 1973, Richner & Heeb 1995, Danchin & Wagner 1997).

The higher philopatric rate observed in the Hawaiian Archipelago compared to colonies in the British Isles is likely due to the higher sampling of Procellariiformes in the Hawaiian Archipelago. Overall, Procellariiformes returned to their natal colony at higher rates than those of Charadriiformes or Suliformes (Fig. 2). Our study validated previously published trends in philopatry within the Procellariiformes (Fisher 1976, Weimerskirch *et al.* 1984, Milot *et al.* 2008). Extensive banding records of albatrosses have exemplified 'the seabird paradox', showing over 99% return rates to some colonies (Fisher 1976, Weimerskirch *et al.* 1984). Additionally, seabird chick translocation programs have the highest success within the Procellariidae family (Jones & Kress 2012).

A relationship between philopatry and taxonomic order was not found in colonies in the British Isles, likely due to the low sample size of Procellariiformes within the British Isles ($n = 2$). Furthermore, the Northern Fulmar *Fulmarus glacialis*, one of the two species of Procellariiformes in our study surveyed in the British Isles, had a much lower average philopatric rate (43%; Appendix, Table A1) than other species of Procellariiformes in the study. Research studying dispersive behavior of the Northern Fulmar in the British Isles indicates that this may be due to a genotype that favors range expansion and colonization (Lloyd *et al.* 2010).

Overall, Procellariiformes had high philopatric tendencies, but there were exceptions within the order.

Within the British Isles, philopatry was positively correlated with the distance to the nearest colony (Table 4). This suggests that seabirds are more likely to disperse if they have neighboring colonies. The behavior of dispersing to a neighboring colony may be beneficial because it increases access to new mates while avoiding the energy costs associated with long-distance dispersal, and it allows birds continue to benefit from the foraging grounds surrounding the
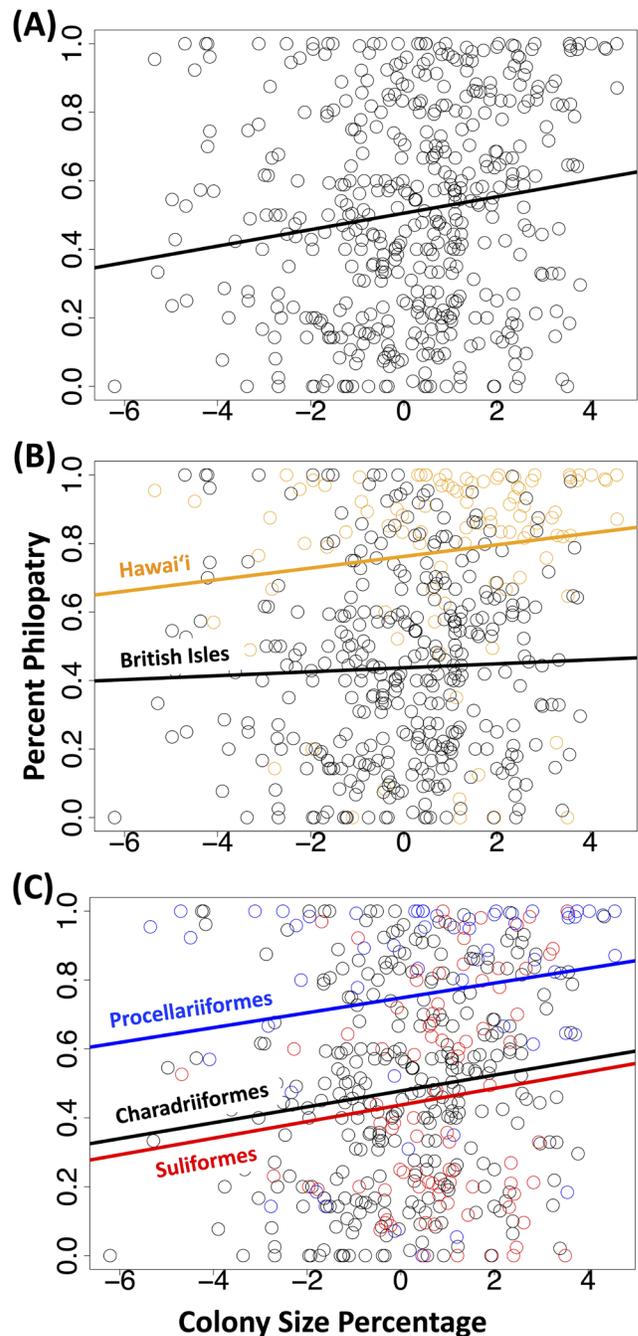
Fig. 2. Log colony size as a percentage of total population size (x-axis) compared to percent philopatry (y-axis) to (A) all seabird colonies ($t_{35/459} = 1.68$, $P = 0.094$), (B) region ($t_{35/459} = 3.07$, $P = 0.005$), and (C) taxonomic seabird order.

natal colony (Greenwood 1980, Hénaux *et al*. 2007). Other studies have concluded that a significant driver of seabird dispersal is the distance from the source colony, indicating that distance may be an important factor for some (Greenwood & Harvey 1982, Serrano *et al*. 2001, Hénaux *et al*. 2007; Oro *et al*. 2011; Buxton 2014) but not all (Jones & Kress 2012; VanderWerf *et al*. 2019) seabird species.

Other environmental factors may account for the difference in regional philopatry. Many of the seabirds observed in Great Britain and Ireland are coastal, inland, and roof nesters that breed in many locations within a county, allowing more options for dispersal in this region. Compared to inland colonies, some coastal seabird colonies tend to be more stable in occupancy, most likely because coastal colonies benefit from more predictable access to food (Schreiber & Burger 2002). In England and Wales, gulls readily moved between inland sites in response to factors such as disturbance and water levels, which may be responsible for the fluctuation in numbers observed at many colonies (Gribble 1976). The British Isles dataset contained a high number of inland colonies, whereas the Hawai'i dataset had no such colonies, and it is this difference that accounted, to a large extent, for the perceived differences in philopatry. When contributing to global seabird colony data sets (e.g., USGS Seabird Colony Atlas, Global Seabird Data Portal), we highly recommend that, in addition to specifying the region, the geographic extent of colonies should be clearly delineated and there should be a clearly-defined use of the term colony.

We addressed some potential dispersal variables across seabird species that explained over 50% of the variation in philopatric rates, but other confounding variables that we did not include were likely at play. For example, the presence of other species of seabirds may influence philopatry. Congeneric species may act as a social attraction, as observed within the Short-tailed Albatross *Phoebastria albatrus* (Deguchi *et al*. 2012), Black-legged Kittiwake *Rissa tridactyla* (Danchin *et al*. 1998), and Great Cormorant *Phalacrocorax carbo sinensis* (Schjørring *et al*. 1999). In contrast, other seabird species may serve as competitors, reducing philopatry. For example, Wedge-tailed Shearwaters *Ardenna pacifica* outcompete Newell's Shearwater *Puffinus newelli*, Bonin Petrel *Pterodroma hypoleuca*, and Tristram's Storm Petrel *Oceanodroma tristrami* for preferred burrowing space (Raine & Vynne 2016). Additionally, sex may influence dispersal, as seen in other long-lived species (Bowen *et al*. 2005, Chang *et al*. 2014). Studies have shown no sex difference (Milot *et al*. 2008, Munilla *et al*. 2016), as well as male-mediated dispersal (Greenwood 1980, Young 2010) and female-mediated dispersal (Steeves *et al*. 2005, González-Jaramillo & Rocha-Olivares 2011) within seabirds, suggesting interspecies-level variation. Furthermore, foraging behavior and changes in food availability highly influence dispersal of some seabirds (Becker & Ludwigs 2004, Barraquand *et al*. 2014). Foraging strategy, correlated with life history traits in seabirds, may influence dispersal (Weimerskirch 2007). Seabirds with small foraging ranges (e.g., some Phalacrocoracidae, Sterncorariidae, and Laridae) may have lower rates of philopatry because they rely on prey

TABLE 3
Dispersal variables from seabird species in the Hawaiian Archipelago (*n* = 18),
with comparison to the rate of philopatry using a linear mixed-effects model

Dispersal variable	x̄ ± SE	*t* value	*P* value
Number of colonies[a]	153.70 ± 9.08	$t_{18/97} = -0.61$	0.550
Colony size[a]	1.011 ± 0.218	$t_{18/97} = 2.01$	0.050*
Distance to the nearest colony[a]	-0.473 ± 0.005	$t_{18/97} = -1.27$	0.210
Wingspan[a]	4.668 ± 0.075	$t_{18/97} = -1.03$	0.322
Taxonomy (Suliformes)	27 (24.5%)	$t_{18/97} = 0.15$	0.887
Taxonomy (Procellariiformes)	44 (44.9%)	$t_{18/97} = 1.17$	0.263

[a] Number of colonies, colony size, distance to the nearest colony, and wingspan were transformed to meet assumptions of normality
* indicates statistical significance (*P* < 0.05)

TABLE 4
Dispersal variables from seabird species in the British Isles (*n* = 17),
with comparison to the rate of philopatry using a linear mixed-effects model

Dispersal variable	x̄ ± SE	*t* value	*P* value
Number of colonies[a]	5 950.00 ± 175.10	$t_{17/361} = 0.24$	0.812
Colony size[a]	-0.036 ± 0.097	$t_{17/361} = 0.85$	0.396
Distance to the nearest colony[a]	-0.551 ± 0.003	$t_{17/361} = 2.20$	0.030*
Wingspan[a]	4.59 ± 0.024	$t_{17/361} = -1.04$	0.321
Taxonomy (Suliformes)	60 (16.6%)	$t_{17/361} = -0.47$	0.645
Taxonomy (Procellariiformes)	16 (4.4%)	$t_{17/361} = 0.59$	0.565

[a] Number of colonies, colony size, distance to the nearest colony, and wingspan were transformed to meet assumptions of normality
* indicates statistical significance (*P* < 0.05)

close to their nesting sites and are thus more likely to change nesting locations due to geographic shifts in food availability (Andersson & Götmark 1980, Weimerskirch 2007, Elliott *et al.* 2009, Isaksson *et al.* 2016, Jovani *et al.* 2016, Wakefield *et al.* 2017). Future studies that address these variables (congeneric species, sex, foraging behavior, food availability, etc.) may help to explain the complex philopatric variation found among seabird species.

Multiple researchers contribute data to long-term databases, inevitably creating sampling biases within the datasets. Individual observer efforts to recapture birds likely varied widely between colonies and species, potentially influencing rates of resighting. Because it is not possible to standardize search efforts across colonies in globally-scaled studies from pooled data sources, we have instead addressed this issue by omitting search efforts of fewer than five individuals at a colony, and we note that overall trends across higher taxa did not change (Appendix, Table A3). Secondly, due to the lack of continuous census data, we assumed a stationary population size as determined from the latest population censuses (Mitchell *et al.* 2004, Pyle & Pyle 2017). To minimize bias, we utilized relative colony size in the analysis. Additionally, following past studies and the format of the data set provided, we defined each major island or county as a single colony, although multiple smaller colonies were likely present. We assumed that seabirds returning to sites under 20 km from their natal area were philopatric, which works best for isolated oceanic islands, but there were some geographic exceptions, as some nesting islands fell within 20 km of each other (Smith *et al.* 2002). Furthermore, any seabird banded as a fledgling that was resighted at their natal colony during the breeding season was considered philopatric, but it is possible that some of those seabirds were not nesting and only visiting, as this behavior has been observed in some seabird species (Young 2010).

Seabirds occur in all seas and oceans worldwide, but due to the limited availability of census data, this study only focused on two distinctly different geographic regions. While our dataset is a large compilation of seabird recapture data, variation between regions not covered by our dataset may mean that conclusions drawn about higher taxa are not generalizable outside of our sample area. Results comparing the two geographic regions should be interpreted with caution due to some variation in colony size and isolation between the two datasets. Unlike the British Isles, the Hawaiian Archipelago consists of isolated oceanic islands, which could be a main contributing factor to the difference in philopatry between the two regions. Despite these inherent and unavoidable biases associated with data from long-term databases, our study compiled a large number of replicates with strong statistical trends within the datasets, and hence identified several important lines of future inquiry for seabird conservation.

Seabird populations are decreasing globally, with many colonies vulnerable to climate change, fishery depletion, and land-use change, leading to potential ecological traps under continued philopatric behavior (Mitchell et al. 2004). Although philopatry in seabirds is complex, this study suggests that taxonomic group, region, distance to nearest colony, and colony size affect some of the underlying mechanisms. Continued research on philopatry across multiple spatial scales within more seabird species, particularly through the use of GPS tracking on fledglings, is needed to support these findings. Non-philopatry is also an extremely important behavior in the formation and growth of new colonies (Coulson & Coulson 2008, Coulson 2011, Jones & Kress 2012). Seabirds with variable philopatric rates, such as certain Suliformes and Charadriiformes (Fig. 2), may be more likely to naturally relocate their colonies in the face of sea-level rise or changes in food supply location. Seabirds with high philopatric rates, such as certain Procellariiformes (Fig. 2), may require translocation to sites that are protected from sea-level rise or invasive predators if they are globally threatened (Jones & Kress 2012). In the Main Hawaiian Islands, management goals include the establishment of safe seabird habitat through the use of translocation and predator control, due to habitat being lost to sea-level rise on the low-lying Northwestern Hawaiian Islands (US Fish & Wildlife Service 2005, VanderWerf 2013, VanderWerf *et al.* 2019). This study suggests that Procellariiformes are good candidates for translocation actions within the Hawaiian Archipelago.

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REFERENCES

ANDERSSON, M. & GÖTMARK, F. 1980. Social organization and foraging ecology in the arctic skua *Stercorarius parasiticus*: a test of the food defendability hypothesis. *Oikos* 35: 63–71.

ARKIVE 2017. *Wildscreen Arkive Species.* Bristol, UK: Wildscreen Network. [Accessed online at http://www.arkive.org/species/ on 01 July 2017.]

BARRAQUAND, F., HØYE, T.T., HENDEN, J.A. ET AL. 2014. Demographic responses of a site-faithful and territorial predator to its fluctuating prey: long-tailed skuas and arctic lemmings. *Journal of Animal Ecology* 83: 375–387.

BECKER, P.H. & J.D. LUDWIGS. 2004. *Sterna hirundo* Common Tern. *BWP Update* 6: 91–137.

BERTHOLD, P. 1996. *Control of bird migration.* Heidelberg, Germany: Springer Science & Business Media, Springer Netherlands.

BILLERMAN, S.M., KEENEY, B.K., RODEWALD, P.G., & SCHULENBERG, T.S. 2020. *Birds of the World*. Ithaca, USA: Cornell Laboratory of Ornithology. [Accessed online at https://birdsoftheworld.org/bow/home on 01 July 2017.]

BOWEN, B.W., BASS, A.L., SOARES, L. & TOONEN, R.J. 2005. Conservation implications of complex population structure: lessons from the loggerhead turtle (*Caretta caretta*). *Molecular Ecology* 14: 2389–2402.

BRITISH TRUST FOR ORNITHOLOGY. 2017. "Online Ringing Data Request". [Received 25 July 2017 at https://app.bto.org/data-request/new-data-request.jsp].

BUXTON, R. 2014. *Ecological drivers of seabird recovery after the eradication of introduced predators*. PhD thesis. Otago, NZ: University of Otago.

CHANG, Z., YANG, B., VIGILANT, L. ET AL. 2014. Evidence of male-biased dispersal in the endangered Sichuan snub-nosed monkey (*Rhinopithexus roxellana*). *American Journal of Primatology* 76: 72–83.

COULSON, J.C. 2016. A review of philopatry in seabirds and comparisons with other waterbird species. *Waterbirds* 39: 229–240.

COULSON, J.C. 2011. *The Kittiwake*. London, UK: T. & A. D. Poyser.

COULSON, J.C. & COULSON, B.A. 2008. Measuring immigration and philopatry in seabirds; recruitment to Black-legged Kittiwake colonies. *Ibis* 150: 288–299.

DANCHIN, E., BOULINIER, T. AND MASSOT, M. 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. *Ecology* 79: 2415–2428.

DANCHIN, E. & WAGNER, R.H. 1997. The evolution of coloniality: the emergence of new perspectives. *Trends in Ecology & Evolution* 12: 342–347.

DEGUCHI, T., JACOBS, J., HARADA, T. ET AL. 2012. Translocation and hand-rearing techniques for establishing a colony of threatened albatross. *Bird Conservation International* 22: 66–81.

DEGUCHI, T., SATO, F., EDA, M. ET AL. 2017. Translocation and hand-rearing result in short-tailed albatrosses returning to breed in the Ogasawara Islands 80 years after extirpation. *Animal Conservation* 20: 341–349.

ELLIOTT, K.H., WOO, K.J., GASTON, A.J., BENVENUTI, S., DALL'ANTONIA, L. & DAVOREN, G.K. 2009. Central-place foraging in an Arctic seabird provides evidence for Storer-Ashmole's halo. *The Auk* 126: 613–625.

FERNÁNDEZ-CHACÓN, A., GENOVART, M., PRADEL, R. ET AL. 2013. When to stay, when to disperse and where to go: survival and dispersal patterns in a spatially structured seabird population. *Ecography* 36: 1117–1126.

FISHER, H.I. 1976. Some dynamics of a breeding colony of Laysan Albatrosses. *The Wilson Bulletin* 88: 121–142.

FREDERICK, P.C. & OGDEN, J.C. 1997. Philopatry and nomadism: contrasting long-term movement behavior and population dynamics of White Ibises and Wood Storks. *Colonial Waterbirds* 20: 316–323.

FREDERIKSEN, M. & PETERSEN, A. 1999. Philopatry and dispersal within a Black guillemot colony. *Waterbirds* 22: 274–281.

FURNESS, R.W. & BIRKHEAD, T.R. 1984. Seabird colony distributions suggest competition for food supplies during the breeding season. *Nature* 311: 655–656.

GAUTHIER, G., MILOT, E. & WEIMERSKIRCH, H. 2010. Small-scale dispersal and survival in a long-lived seabird, the wandering albatross. *Journal of Animal Ecology* 79: 879–887.

GONZÁLEZ-JARAMILLO, M. & ROCHA-OLIVARES, A. 2011. Barriers acting on the genetic structure of a highly aerial seabird: The magnificent frigatebird. *Biochemical Systematics and Ecology* 39: 392–396.

GREENWOOD, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28: 1140–1162.

GREENWOOD, P.J. & HARVEY, P.H. 1982. The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics* 13: 1–21.

GRIBBLE, F.C. 1976. Census of Black-headed gull colonies in England and Wales, 1973. *Bird Study* 23: 139–149.

HÉNAUX, V., BREGNBALLE, T. & LEBRETON, J.D. 2007. Dispersal and recruitment during population growth in a colonial bird, the great cormorant *Phalacrocorax carbo sinensis*. *Journal of Avian Biology* 38: 44–57.

HUYVAERT, K. & ANDERSON, D. 2004. Limited dispersal by Nazca boobies *Sula granti*. *Journal of Avian Biology* 35: 46–53.

ISAKSSON, N., EVANS, T.J., SHAMOUN-BARANES, J. & ÅKESSON, S. 2016. Land or sea? Foraging area choice during breeding by an omnivorous gull. *Movement Ecology* 4: 11.

JONES, H. P. & KRESS, S. W. 2012. A review of the world's active seabird restoration projects. *The Journal of Wildlife Management* 76: 2–9.

JOVANI, R., LASCELLES, B., GARAMSZEGI, L. Z., MAVOR, R., THAXTER, C. B. & ORO, D. 2016. Colony size and foraging range in seabirds. *Oikos* 125: 968–974. doi:10.1111/oik.02781

LACK, D.L. 1968. *Ecological adaptations for breeding in birds*. London, UK: Methuen.

LAWRENCE, E. 1989. *Henderson's dictionary of biological terms 10th Edition*. Harlow, UK: Longman Scientific & Technical.

LEBRETON, J.D., BURNHAM, K.P., CLOBERT, J. & ANDERSON, D.R. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62: 67–118.

LLOYD, C., TASKER, M.L. & PARTRIDGE, K. 2010. *The status of seabirds in Britain and Ireland*. London, UK: A & C Black.

LO VALVO, F., LO VERDE, G. & LO VALVO, M. 1988. Relationships among wing length, wing shape and migration in Blackcap *Sylvia atricapilla* populations. *Ringing & Migration* 9: 51–54.

MILOT, E., WEIMERSKIRCH, H. & BERNATCHEZ, L. 2008. The seabird paradox: dispersal, genetic structure and population dynamics in a highly mobile, but philopatric albatross species. *Molecular Ecology* 17: 1658–1673.

MITCHELL, P.I., NEWTON, S.F., RATCLIFFE, N. & DUNN, T.E. 2004. *Seabird Populations of Britain and Ireland*. London, UK: T & A. D. Poyser.

MUNILLA, I., GENOVART, M., PAIVA, V. H. & VELANDO, A. 2016. Colony foundation in an oceanic seabird. *PLoS One* 11: e0147222.

ORO, D., MARTÍNEZ-ABRAÍN, A., VILLUENDAS, E. ET AL. 2011. Lessons from a failed translocation program with a seabird species: Determinants of success and conservation value. *Biological Conservation* 144: 851–858.

POOLE, A. 2005. *The Birds of North America Online*. Ithaca, USA: Cornell Lab of Ornithology.

PYLE, R.L. & PYLE, P. 2017. *The Birds of the Hawaiian Islands: Occurrence, History, Distribution, and Status, Version 2 (01 January 2017)*. Honolulu, USA: B.P. Bishop Museum. [Accessed online at http://hbs.bishopmuseum.org/birds/rlp-monograph on 01 May 2017.]

RAINE, A.F. & VYNNE, M. 2016. *Annual Report on Monitoring of Newell's Shearwaters at Kilauea Point National Wildlife Refuge*. Pacific Cooperative Studies Unit 27.

R CORE TEAM. 2013. *R: A language and environment for statistical computing*. Vienna, Austria: The R Foundation for Statistical Computing.

REYNOLDS, M.H., COURTOT, K.N., BERKOWITZ, P., STORLAZZI, C.D., MOORE J. & FLINT, E. 2015. Will the effects of sea-level rise create ecological traps for Pacific island seabirds? *PLoS One* 10: e0136773.

RICHNER, H. & HEEB, P. 1995. Is the information center hypothesis a flop? *Advances in the Study of Behaviour* 24: 1–46.

ROLSHAUSEN, G., SEGELBACHER, G., HOBSON, K.A. & SCHAEFER, H.M. 2009. Contemporary evolution of reproductive isolation and phenotypic divergence in sympatry along a migratory divide. *Current Biology* 19: 2907–2101.

SCHJØRRING, S., GREGERSEN, J. & BREGNBALLE, T. 1999. Prospecting enhances breeding success of first-time breeders in the great cormorant, *Phalacrocorax carbo sinensis*. *Animal Behaviour* 57: 647–654.

SCHREIBER, E.A. & BURGER, J. 2002. *Biology of Marine Birds*. Boca Raton, USA: CRC Press.

SERRANO, D., ORO, D., URSUA, E. & TELLA, J.L. 2005. Colony size selection determines adult survival and dispersal preferences: Allee effects in a colonial bird. *The American Naturalist* 166: e22–e31.

SERRANO, D., TELLA, J.L., FORERO, M.G. & DONÁZAR, J.A. 2001. Factors affecting breeding dispersal in the facultatively colonial lesser kestrel: individual experience vs. conspecific cues. *Journal of Animal Ecology* 70: 568–578.

SHAPIRO, S.S., WILK, M.B. & CHEN, H.J. 1968. A comparative study of various tests for normality. *Journal of the American Statistical Association* 63: 1343–1372.

SITES JR, J.W. & MARSHALL, J.C. 2003. Delimiting species: a Renaissance issue in systematic biology. *Trends in Ecology & Evolution* 18: 462–470.

SMITH, D.G., POLHEMUS, J.T. & VANDERWERF, E.A. 2002. Comparison of managed and unmanaged Wedge-tailed Shearwater colonies on O'ahu: Effects of predation. *Pacific Science* 56: 451–457.

STEEVES, T.E., ANDERSON, D.J., & FRIESEN, V.L. 2005. A role for nonphysical barriers to gene flow in the diversification of a highly vagile seabird, the masked booby (*Sula dactylatra*). *Molecular Ecology* 14: 3877–3887.

THIBAULT, J.C. 1993. Natal philopatry in the Cory's Shearwater (*Calonectris d. diomedea*) on Lavezzi Island, Corsica. *Colonial Waterbirds* 16: 77–82.

THE CORNELL LAB. 2017. *All About Birds*. Ithaca, USA: Cornell Lab of Ornithology.

USGS BIRD BANDING LABORATORY. 2017. *North American bird banding and band encounter data set*. Laurel, USA: Patuxent Wildlife Research Center [Received 25 May 2017].

US FISH & WILDLIFE SERVICE. 2005. *Regional Seabird Conservation Plan, Pacific Region*. Portland, USA: US Fish and Wildlife Service, Migratory Birds and Habitat Programs, Pacific Region.

US FISH & WILDLIFE SERVICE. 2017. *"Seabirds" Hawaiian Islands National Wildlife Refuge, Department of the Interior.* [Accessed online at https://www.fws.gov/refuge/hawaiian_islands/wildlife_and_habitat/seabirds.html on 01 July 2017.]

VANDERWERF, E.A. 2013. *Hawaiian Bird Conservation Action Plan*. Honolulu, USA: Pacific Rim Conservation and Portland, USA: US Fish and Wildlife Service.

VANDERWERF, E.A., YOUNG, L.C., KOHLEY, C.R. ET AL. 2019. Establishing Laysan and black-footed albatross breeding colonies using translocation and social attraction. *Global Ecology and Conservation* 19: 00667.

VAN VALEN, L. 1971. Group selection and the evolution of dispersal. *Evolution* 25: 591–598.

WAKEFIELD, E.D., OWEN, E., BAER, J. ET AL. 2017. Breeding density, fine-scale tracking, and large-scale modeling reveal the regional distribution of four seabird species. *Ecological Applications* 27: 2074–2091.

WARD, P. & ZAHAVI, A. 1973. The importance of certain assemblages of birds as "information-centres" for food-finding. *Ibis* 115: 517–534.

WEATHERHEAD, P.J. & FORBES, M.R. 1994. Natal philopatry in passerine birds: genetic or ecological influences? *Behavioral Ecology* 5: 426–433.

WEIMERSKIRCH, H. 2007. Are seabirds foraging for unpredictable resources? *Deep Sea Research Part II: Topical Studies in Oceanography* 54: 211–223.

WEIMERSKIRCH, H., JOUVENTIN, P., MOUGIN, J.L., STAHL, J.C. & BEVEREN, M.V. 1984. Banding recoveries and the dispersal of seabirds breeding in French Austral and Antarctic Territories. *Emu-Austral Ornithology* 85: 22–33.

YOUNG, L.C. 2010. Inferring colonization history and dispersal patterns of a long-lived seabird by combining genetic and empirical data. *Journal of Zoology* 281: 232–240.