

‘FLOATING POPULATIONS’ OF SEABIRDS: THE BANE OF DEMOGRAPHIC MODELERS AND MANAGERS

DAVID G. AINLEY^{1*}, GEORGE J. DIVOKY², PAT BAIRD³ & GREGORY C. SPENCER¹

¹HT Harvey & Associates, 720 University Avenue, Los Gatos, California, 95032, USA *(dainley@harveyecology.com)

²Cooper Island Arctic Research, 652 32nd Avenue East, Seattle, Washington, 98112, USA

³Department of Biological Sciences, Centre for Wildlife Ecology, Simon Fraser University, Burnaby, British Columbia, V5A 1S6, Canada

Received 31 March 2023, accepted 27 March 2024

ABSTRACT

AINLEY, D.G., DIVOKY, G.J., BAIRD, P. & SPENCER, G.C. 2024. ‘Floating populations’ of seabirds: The bane of demographic modelers and managers. *Marine Ornithology* 52: 379–386. <http://doi.org/10.5038/2074-1235.52.2.1589>

‘Floating’ portions of seabird populations (mature but non-breeding individuals) are generally ignored in seabird research and management despite frequent evidence of their existence, especially in cavity-nesting species for whom nest habitat is often limiting. Here we demonstrate, using a few among an appreciable number of cases, that often more adults contribute to regional populations than colony-based censuses reveal, and that these birds are able to breed but do not. Once given the chance through the creation of nesting habitat, either by natural or human-caused processes, these populations reveal themselves by occupying the newly created habitats to become breeders. We include a brief discussion of the degree to which natal philopatry contributes to relatively sudden colony establishment. Not recognizing the existence of floating populations due to exclusively colony-based management, which is often politically necessary (e.g., Wildlife Refuge management), hinders conservation because it ignores the source and role of potential immigrants. Instead, management tends to emphasize supposed natal philopatry. Floaters will exploit mortality-caused vacancies in a breeding population, masking temporal variation in adult mortality, falsely indicating colony-size stability as a measure of the ‘health’ or resilience of a colony/habitat. In addition, the most successful efforts at establishing new colonies or restoring others by ‘social attraction’ are those in which a floating population is present, although unrecognized until it is revealed by the social attraction ‘experiment.’ Success comes when the artificially established breeding aggregation becomes an attractant to ‘floaters.’ Thus, recruitment of these floaters (especially on a predator-free colony or island) accelerates the limited growth provided by the return of hand-raised translocated nestlings. A lack of appreciation for the presence of floaters also limits the validity of assessments of the impact of bird wrecks and the ability of populations to recover from them.

Key words: dispersion, floaters, colony founding, colony growth, colony restoration, natal philopatry

For a given species, the dynamic interaction between philopatry and dispersal (as behaviors and demographic traits) is the product of temporal and spatial variation in the availability of resources needed for successful breeding. In the case of seabirds, these resources are nesting habitat and/or prey, long the subject of discussion beginning with Lack (1954) and Wynne-Edwards (1962). While natal philopatry (i.e., the return to the natal location to breed) helps maintain populations where successful recruitment and breeding have recently occurred (e.g., Bouludier *et al.* 1996), dispersal to non-natal locations allows for prospecting and the discovery of nesting opportunities that are spatially removed from and independent of factors affecting the natal colony. The selective advantage for a species to maintain both recruitment strategies is clear.

The concept of seabirds nesting in non-natal areas, however, has received little attention, in part due to the daunting logistics of maintaining a long-term marking program and searching for marked/banded birds away from their natal location. This is especially so for those individuals that remain at sea or visit colonies in which no recruitment opportunities are available. Thus, their presence at these colonies is brief. Even if there is band-searching effort, unbanded birds are usually not noticed unless some event, such as addition of new habitat, results in a rapid increase in the numbers of breeders.

Relevant to this phenomenon is the award-winning 1989 film *Field of Dreams*, which was centered around a sports enthusiast’s dream that all of his sporting heroes, past and present, would show up and play if he built a baseball stadium in his farm field. He did build it, and they did come; all that was needed was an appropriate venue. This theme got us thinking about some scenarios (described below) involving undetected individuals in seabird populations. These scenarios followed a similar path to that in the film: when an opportunity was created, either naturally or by ‘experiment,’ seabirds arrived relatively quickly in large numbers, seemingly from nowhere, to form a breeding colony. While the concept of natal philopatry has been and still remains the basis for numerous seabird conservation actions to create colonies (e.g., translocation efforts; VanderWerf *et al.* 2022, Spatz *et al.* 2023), we agree with others that although varying portions of seabird populations demonstrate some natal philopatric tendency, much evidence (e.g., genetic analyses) shows that it is not universal (e.g., Warham 1996, Gaston 2004, Bowler & Benton 2005). Here, we demonstrate the existence and importance of ‘floating’ portions of seabird populations, which need to be included when interpreting seabird colony trends and developing management actions, rather than embracing the concept of only natal philopatry.

What is a floater?

The term ‘floater’ has been used in several ways in the ornithological literature (e.g., Brown 1969, Winker 1998). Floaters are individuals in a population that are physiologically mature and able to breed but do not because they lack suitable breeding habitat, lack mates, or are dissuaded by the presence of predators. In the case of the Cassin’s Auklet *Ptychoramphus aleuticus* on the Farallon Islands, California, USA (also known as the Farallones), an experiment that took place in a time before permits—during which all the auklet burrows in a large plot were destroyed by trampling episodes during the non-breeding season—revealed many adults not breeding for lack of a nest cavity. Tellingly, in the following breeding season, the density of nesting burrows became far higher than it had in the previous year (Speich & Manuwal 1974)! Thus, it was territoriality as well as habitat availability that limited the population. Since then and in support, Johns *et al.* (2022) examined decades of banding data for auklet chicks and adults on the Farallones and found that recruitment of first-time breeders buffered the population when years of poor food availability led to high mortality in breeding adults. These would be the floaters. Note, we use the term ‘population’ to refer to a colony or meta-colony, which is an aggregation of nesting birds occupying a locality or cluster of localities apart from another aggregation. The critical degree of spacing is usually defined arbitrarily, though it should be defined demographically. Nesting space is often limited, especially for cavity-nesting species on rocky islands where burrow excavation is not possible (e.g., most parts of the Farallon Islands) or in areas where birds have degraded their own nesting habitat (Hornung 1982, Renner *et al.* 2017).

A number of birds categorized as non-breeders would not be floaters. First, floaters are not the individuals who might vacillate between breeding and non-breeding states during their lifetimes, responding to interannual conditions such as food availability. An exception would be if a nesting area was destroyed, leading the occupants to become non-breeding birds. Whether this is temporary or long-term change depends on when breeding opportunities arise (e.g., Manuwal 1974, Suryan *et al.* 2004, Peery *et al.* 2010). Second, floaters are not the young birds who show up at the colony sometime during the season, usually late, to investigate the colony area for an eventual nest. For example, non-burrow-occupying Sooty Shearwaters *Ardenna grisea* are referred to as ‘unemployed’ (Richdale 1963); young Adelie Penguins *Pygoscelis adeliae* show up late in the nesting season, at which time they search for a future nest site (Ainley *et al.* 1983). Finally, floaters are not the vagrants that establish a presence in a new location outside the normal breeding range and slowly attract other somewhat-out-of-range individuals to form a self-sustaining colony, as in Elegant Terns *Thalasseus elegans* (e.g., Veit 2000, Veit *et al.* 2021).

Apart from floating populations, a number of avian species have evolved life histories to adapt to the issue of excess breeders, for example, by having past offspring helping parents with the current brood as they await their chance, or by brood/nest parasitism (Kruger 2008). These strategies, however, appear to not be options for most seabirds, though there is the occasional interesting possibility of an alternate strategy. For instance, Baird (2010) reported low but consistent numbers of adult trios at nests of Least Terns *Sternula antillarum* in California. It could well be that the third bird was accepted as a ‘helper,’ which is a phenomenon well known in landbirds (Skutch 1935 and subsequent studies) and at least one seabird species (Le Corre *et al.* 2020).

Most seabird research is centered at colonies, given the much easier logistics compared to at-sea work and because of the need to monitor them because they occur in designated and adequately funded reserves and refuges. This has led to a colony mentality, in which researchers ignore the greater regional meta-population that includes floaters. One result is that most views of (apparent) survival or dispersal lead to discussions about emigrants, immigrants, prospectors, etc. relative to the study colony (e.g., Coulson 2001, Kralj *et al.* 2023). Members of the population not holding a territory at a colony, e.g., birds that have not yet recruited to their natal or to any other colony, are typically unobservable without special effort and are not considered; the same assumptions are made for land birds (Weatherhead & Forbes 1994). These individuals, even if recognized as existing, are often viewed as outliers because they often fail to exhibit the philopatry that has incorrectly come to be expected and considered a central characteristic of the generalized, normal seabird. The concept of seabirds nesting in areas other than where they hatched has received little attention, in part due to the daunting logistics of searching for banded birds elsewhere, especially for those that simply remain at sea (where humans rarely venture; Ainley & Johns 2023).

The existence of a floating portion of a seabird population is not evident until a natural or planned ‘experiment’ occurs or, far more rarely, researchers conduct surveys of at-sea populations and compare them to at-colony estimates of the population size. By ‘experiment,’ we refer to the provision of nesting habitat, natural or not, or the use of social attraction to attract far more individuals than would result from mere breeding productivity and survival, i.e., those processes except immigration. Although they cannot be easily quantified, floaters play a major role in seabird ecology and demographics, as seen in the following additional examples of natural, planned, and unforeseen experiments.

Experiment 1

In the early 1970s, the European Hares *Lepus europaeus* that had been present since the mid-1800s were removed from the Farallon Islands, California. To researchers’ surprise, Rhinoceros Auklets *Cerorhinca monocerata* colonized the island within a year, their first appearance in > 100 years (Ainley & Lewis 1974). They used the cavities vacated by the hares to breed. The closest Rhinoceros Auklet colonies at the time were several hundred kilometers to the north, in the state of Washington, USA. Thus, natal philopatry appears not to have been a significant factor, contributing very little, if at all, to the observed recruitment. The species was (and still is) common in waters of the continental slope of the California Current where the Farallones are located (e.g., Leirness *et al.* 2021). Though very difficult to census, given the Farallones’ treacherous terrain and likelihood of disturbing other species in the process of a survey, the number of nesting Rhinoceros Auklets reached at least several dozen within a few years of removing the hares (e.g., Warzybok *et al.* 2017).

Likewise, when Brush Rabbits *Sylvilagus bachmani* were extirpated in 1982 from Año Nuevo Island, California, which is also in the Gulf of the Farallones, Rhinoceros Auklets colonized the island almost immediately for the first time ever (Carle *et al.* 2019, Thayer *et al.* 2020). The island is relatively new, having separated from the mainland < 200 years ago, and for the longest time, it was accessible by predators from the mainland at low tide. Subsequently, when sea lions were controlled in 2011 by erecting barriers to exclude them

from part of island, Rhinoceros Auklet numbers more than doubled within 10 years; that increase, from 260 to 600, was much quicker than could be attributed to breeding productivity and survival (Beck *et al.* 2017). The continental slope, i.e., prime Rhinoceros Auklet marine habitat, is close to Año Nuevo Island (within 20 km), and deep canyons in the vicinity bring shelf-break waters across the continental shelf.

Experiment 2

On Cooper Island, a sand-and-gravel barrier island in the western Beaufort Sea, researchers found a handful of Mandt's Black Guillemots *Cephus grylle mandtii* nesting beneath boxes and other wooden, wave-cast debris in the early 1970s (Divoky *et al.* 1974). The closest neighboring nesting colonies (Herald Island and Wrangel Island in Siberia) were several hundred kilometers to the west. However, the species was common during summer in the marginal ice zone that spread across the Alaskan Chukchi and Beaufort seas (Divoky 1987). When 200 artificial nest boxes were provided in the late 1970s and early 1980s, the colony grew to ~400 breeding birds with ~200 non-breeders within 10 years. In subsequent years, during which every fledgling was banded, about two-thirds of the breeding birds proved to not have originated at Cooper Island (Divoky *et al.* 2015). The large number of non-breeders, the vast majority not being local birds, actually decreased natal philopatry at Cooper Island, as returning fledglings had to compete with floaters for nest sites. Some non-natal floaters were more successful at recruiting than individuals that fledged from Cooper Island (Divoky 1998).

Similarly, in a large colony of Pigeon Guillemots *Cephus columbo* at the Farallon Islands, breeding pairs occupied nest boxes almost immediately after presentation. The box openings were too small for Rhinoceros Auklets and too large for Cassin's Auklets, which were ejected by the guillemots (Ainley *et al.* 1990). The guillemots on the Farallones have been very successful, fledging 0.8 chicks per pair over a 46-year period; in 18 of those years, pairs averaged more than one fledgling. The overall average was reduced mainly by the anomalous food web that comes with El Niño (Warzybok *et al.* 2017).

Experiment 3

By the early 2000s, the Newell's Shearwater *Puffinus newelli* was thought to be nearly extinct on the island of Maui in Hawai'i, USA, with the closest known large colony 300 km away on the Hawaiian island of Kaua'i (Ainley *et al.* 2020). Radar and visual surveys conducted in 2001 failed to detect any shearwaters on Maui, although many individuals of the more common Hawaiian Petrel *Pterodroma sandwichensis* were detected (Cooper & Day 2003). Biologists, however, had reported hearing Newell's Shearwater calls infrequently in a few remote forested locations. Thus, when a private company applied for an endangered species permit to develop wind energy generation on West Maui, wildlife agencies asked them to find the then-unknown colonies of the shearwater and petrel, fence them off, and extract and control mammalian predators. In that way, increased reproductive output would be achieved to mitigate expected mortality of adults from collision with turbines. Finding candidate shearwater colonies proved impossible, so social attraction (call playbacks, decoys, fabricated nest boxes) and predator-exclusion fencing were instead employed to establish new breeding colonies for both species in

2014 (Spencer *et al.* 2024). Both species responded immediately by swooping low over the speakers, and birds began to visit nest boxes the following year. Eggs were laid by shearwaters in the next few years; though many were lost by the inexperienced new breeders (as expected), chicks were fledged within five years. The shearwater colonies have been monitored continuously and slow growth has continued. The shearwater response was surprising, given their supposed near extirpation on the island, but the petrel response has been perplexing. After a few years of investigating nest sites, petrels lost interest (see Spencer *et al.* 2024 for discussion). The petrel is very abundant elsewhere on Maui (Haleakalā Crater) and the equally close Hawaiian island of Lāna'i (totaling ~70% of the world population or 4100 pairs; Pyle & Pyle 2017). Thus, these existing populations may have acted as an 'attractive nuisance.' In other words, the natural social attraction of petrels to these large nearby colonies may have overcome any interest in the output of a few speakers a long way from known viable colonies (this phenomenon is discussed further below).

Experiment 4

Somewhat similarly, the breeding population of Guadalupe Murrelet *Synthliboramphus hypoleuca* on Guadalupe Island, Mexico, was thought to have been extirpated by the 1890s due to predation by introduced cats *Felis catus* and habitat alteration by feral goats *Capra hircus*. The murrelets nest in rock crevices and sometimes under bushes. In 2007, however, seven nests and 68 cat-depredated carcasses were found on the island (Whitworth *et al.* 2021). On the small, cat-free Zapato and Morro Prieto islets, which are 1–3 km away, the breeding population was estimated by varying methods to be 1750 pairs in 1968 (DeLong & Crossin 1968), 2418 pairs in 2007, and in the most intensive survey effort, ~4000 pairs in 2019 (Méndez Sánchez *et al.* 2022). In their independent 2007 survey, Whitworth *et al.* (2021) reported 'scores' of broken eggs in nest cavities on the two islets and found as many as three eggs in some cavities; the normal clutch size is two. They concluded that competition for sites must have been fierce. Among the 50 birds captured by dipnet at night during the egg-laying season in waters around the islets, only eight had incubation patches to indicate breeding.

That was the case until 2015, when two murrelet pairs were discovered nesting in a 60-ha (0.6 km²) enclosure erected in late 2014 by the Grupo de Ecología y Conservación de Islas and the Comisión Nacional de Áreas Naturales Protegidas to protect the Laysan Albatross *Phoebastria immutabilis* colony from cats. By 2020, that number had grown from two to 275 pairs, 252 in natural burrows and 23 in artificial burrows, an astounding 10 044% increase (Méndez Sánchez *et al.* 2022)! By 2023, that number had grown further to 788 pairs, 718 in natural burrows and 70 in artificial burrows (J. Hernández Montoya pers. comm.). Clearly, a floating population had been biding its time for when nesting habitat would become available! The species may also nest, in extremely low numbers (i.e., just a few pairs), 260 km to the southeast at the San Benito Islands (Méndez Sánchez *et al.* 2022).

Experiment 5

On the southern Kerguelen Plateau, Indian Ocean, surveys were conducted at MacDonald and Heard islands in the early 1990s to quantify the seabird nesting fauna (Woehler & Green 1992). On Heard Island, ~3800 King Penguins *Aptenodytes patagonicus* were found, but none occurred on MacDonald Island, 60 km away,

where steep shores apparently prevented access by this lumbering species. In 1997, the MacDonald Island volcano erupted, and the resulting ash doubled the size of the island and established gradually sloping beaches in the process. Within five years, ~7000 King Penguins were breeding on the island (Stephenson *et al.* 2005), their origin unknown. If non-breeders at Heard Island were insufficient, the closest potential source colony was the 250 000 pairs at Kerguelen Island, several hundred km away on the northern edge of the subsea plateau.

Experiment 6

A breakwater, 800 m long, 12 m high, and constructed of concrete blocks and rocks was completed in 2011 to protect a liquid natural gas (LNG) port located south of Lima, Peru. The endangered cavity-nesting Humboldt Penguin *Spheniscus humboldti*, with its largest colonies 100 km to the north and south, began to show up at the breakwater within a year. Each year thereafter, more came to nest. By 2014 there were ~200 birds nesting and by 2021 there were more than 2000 (Zavalaga *et al.* 2023; see also Smithsonian Institution 2016, 2017). The world population is confined to Chile and Peru, and it consists of only 23 000 to 24 000 breeding pairs (de la Puente *et al.* 2013). It had been previously reduced severely by the mining of guano from coastal islands, the penguins having for millennia used the guano for a burrowing substrate (Murphy 1981). Those measures that restricted nesting habitat apparently created a sizeable floating population that went unrecognized until creation of the breakwater.

Experiment 7

In an uncommon opportunity, the total world population of the cavity-nesting Ashy Storm Petrel *Hydrobates homochroa* was estimated from demographic analysis of very extensive at-sea surveys of its entire year-round range in the California Current (Ford *et al.* 2021). The study found that the total population was double that of estimated colony populations (i.e., including breeders and non-breeders). The latter had been determined by extensive surveys counting nests and/or mist-netting birds at the major colonies (25 of ~50 sites, including all but the small coastal rocks). At the South Farallon Islands colony that accounted for about half of the colony-based population, Nur *et al.* (1999, 2019) conducted mist-netting annually over a 14-year period to estimate change in population size. They found that about half of the storm petrels caught were what they considered to be transients, having been caught only once (including a few storm petrels banded elsewhere). That resultant high rate of transient visitation is consistent with the lack of any genetic structure in the species' range-wide population (Nur *et al.* 1999). Clearly, the Ashy Storm Petrel, a non-burrow-digging species, possesses a sizeable floating population that includes many individuals denied breeding for lack of a nest cavity. A similar disparity between at-sea and colony populations has been reported for New Zealand Storm Petrel *Fregetta maoriana*, a population expanding after the eradication of predators at breeding colonies (Rayner *et al.* 2020).

What's going on?

What possibly could be going on in these seabird examples of "build it and they will come"? Clearly, natal philopatry was not driving the observed recruitment, nor was vagrancy (Veit 2000, Veit *et al.* 2021), nor were individual prospectors deciding whether a

colony suited their needs (Boulinier *et al.* 1996). What was revealed was the presence of an excess of adult birds, a floating population, within the species' breeding-season range; in other words, 'breeding range philopatry.' The surplus adults were capable of breeding and prospected for recruitment opportunities within their normal breeding range—that is, possibly but not necessarily at their natal colony. Most of these examples are of either cavity-nesting species whose populations are frequently limited by nest-site or territory availability, or populations where nesting habitat is available but they cannot access it, like the King Penguins at MacDonald Island. Clearly, in these examples, there were many adult birds in the region waiting for the opportunity to nest who then quickly availed themselves when the opportunity arose.

It is important to note that the presence of floaters is most obvious when nesting habitat is provided to species whose populations are limited by nest-site availability. Floaters also play a major but typically undetected role in the growth and maintenance of existing colonies (see Cassin's Auklet example above). That is not to say that floaters occur only in species having these specialized nesting requirements. Nest-site availability, however, can be especially limiting on islands with rocky substrate that does not lend itself to digging burrows. As it is, cavity-nesters dominate seabird species (see Howell & Zuffelt 2019): almost half of penguins (seven of 19 species), all storm petrels (45 species), all diving petrels (six species), most petrels and shearwaters (~90 of 107 species, except for *Procellaria* spp. and most fulmarine petrels), and 85% of alcid (21 of 25 species). Among other families, some species do occupy nesting cavities, e.g., tropicbirds (Brinkley & Sutherland 2020). However, nesting habitat can be limited in the case of surface-nesters as well. For instance, Western Gulls *Larus occidentalis* on the Farallon Islands, the species' largest colony by far, maintain their territories almost year-round, despite a nesting season that lasts for just six months. In that way, as Penniman *et al.* (1990) surmised, they can guard against a large contingent of prospectors looking for nesting space. These prospectors would be floaters until they found a spot.

What is philopatry?

The above examples of detecting floaters, which are uncommon but by no means rare, beg the question of why the term 'philopatry' is still used in reference to seabird life-history characteristics. Philopatry is often invoked: e.g., "The main barrier to translocation of seabirds is their extreme philopatry [and high dispersal ability]...." (Miskelly 2022: p.286), which certainly applies to adults and fledglings in different ways: breeding philopatry among adults, greater dispersal among fledglings. Unless researchers intensively band birds in a colony and then search for them in all the colonies of a region (a very rare accomplishment but see, e.g., Spendlow 1991, Baird 1992, Spendlow *et al.* 1995, Baird 2023), they are left registering some unknown portion of the respective annual recruits that do return to nest in the vicinity of where they were raised and banded. In these cases, demographers must estimate 'apparent survival,' a combination of mortality and dispersal to an unknown/unsurveyed location.

The degree to which birds should be considered philopatric, as opposed to individuals responding to recruitment availability irrespective of natal location, has been discussed for a long time. The term 'dispersal' is "the permanent movement an individual makes from its birth site to the place where it reproduces or would have

reproduced if it ... found a mate" (Greenwood & Harvey 1982; see also Greenwood 1980). The concept of natal philopatry as an innate and dominant aspect of seabird demography has been questioned previously (e.g., Warham 1996, Gaston 2004), as it defies the results of population genetic analysis (e.g., Genovart *et al.* 2007, Graham *et al.* 2023). In their review of the subject of philopatry, Klomp & Furness (1992) concluded that seabirds show a range of natal site fidelity, from the non-colonial Great Skuas *Stercorarius skua* of Foula, Scotland, to regular inter-colony movements among Atlantic Puffins *Fratercula arctica* to the extreme wandering behavior among colonies by storm petrels (noted above).

Floaters relaxing any philopatric tendencies?

The concept of natal philopatry is so deeply ingrained in seabird research and management that numerous efforts have been and are being made to translocate nestlings and artificially raise chicks extracted from viable or decreasing colonies. The goal is to have them fledge and return to establish 'new' colonies (e.g., summarized in Jones & Kress 2012, VanderWerf *et al.* 2022, Spatz *et al.* 2023; also Zhou *et al.* 2017, though translation of only the abstract was available). Spatz *et al.* (2023) summarized results of 851 such projects, ~60% of which involved larids. The fact that larids (mostly tern species) dominated the projects in which social attraction was involved (and often succeeded) is not surprising, since terns often nest in ephemeral habitat prone to flooding or disturbance. Thus, they are flexible and willing to move when an alternate nesting area becomes more attractive (e.g., Baird 2023). That is clearly not the case for cavity-nesting species, which made up just 15% of the species included in the Spatz *et al.* (2023) review. If forces physically remove their nesting habitat, rarely does similar habitat appear elsewhere.

The Jones & Kress (2012) review indicated that little subsequent long-term monitoring is done to document anything more than initial breeding by a few returning birds, which is termed 'translocation success.' The supposition is that a self-sustaining colony would follow. Beyond that initial level of success, establishing a 'core colony' should become a management goal, specifically the attraction of large numbers of recruits (i.e., floaters) from elsewhere to this new colony, which is often one that is protected from predation (Miskelly *et al.* 2004, Sawyer & Fogle 2010). In that regard, chick translocations of eight procellariids in New Zealand resulted in a successful return to breed by some portion of the fledglings produced (Miskelly *et al.* 2009). However, follow-up 17–25 years after the initial translocations found that, in each case, only small self-sustaining colonies had resulted. That outcome was due to there being no natural source or floating population nearby, and there was little evidence of immigration from elsewhere. An exception occurred at Mana Island, New Zealand, where possibly floating Common Diving Petrels *Pelecanoides urinatrix* began to show interest in response to social attraction (recorded calls). Later, with chick translocations also occurring, the colony began to grow much more rapidly (Miskelly 2023).

Referring to seabirds in general, Buxton *et al.* (2014) concluded that having a large source population of floaters within ~25 km greatly facilitates the growth of colonies established by social attraction (see also Oro *et al.* 2011). That raises several questions, the answers to which certainly would vary by species and population. How far and wide do floaters wander looking for nest sites within their breeding range? How much time do floaters spend adjacent to active

colonies in the absence of nesting habitat versus wandering further to look elsewhere? How can the prevalence of floaters at the meta-population and sub-population levels be determined, other than by conducting an experiment or intensive colony and at-sea surveys? Further, what portion of the adult population do floaters represent, and what affects annual variation in that proportion?

Management consequences of not acknowledging floaters

If population ecologists and their client seabird managers want to quantify the abundance and distribution of seabirds, monitor their trends, or create colonies on predator-free islands, then they need to recognize and accept the role of excess breeders: the floaters. The issue cannot be ignored if effective management of seabird populations is to be accomplished. At the same time, we urge researchers to question their views and the views of the seabird research community about the strength of natal philopatry in the colonies they are considering. We contend that it needs to be assessed on a species- and site-specific basis, not just assumed. Many studies demonstrate that avian floating populations are not tangential but can be important components; these must be considered and not labeled as 'renegades' or individuals of low quality (e.g., Smith 1984, Peer *et al.* 2000).

When considering the health of a colony or population (i.e., its temporal stability, growth, or resilience), dismissing floaters has consequences. When there is a die-off, as when large numbers of dead birds are found on beaches, why is there not necessarily an equal reduction in the size of breeding colonies within the corresponding region (e.g., Robles & Ciudad 2017, Johns *et al.* 2021)? It's quite possible that there will be none, depending on the species and regional population. Or, if social attraction does not seem to be working or if such measures are proceeding too slowly relative to management goals (e.g., to restore or establish a colony in a predator-free location to assist in the recovery of an endangered population/species), then utility of the effort should be assessed. It might be necessary to shift locations or pivot to projects more likely to yield desirable outcomes.

From a conservation perspective, the floating portion of seabird populations should be considered very important for their ability to provide population resilience, a function in which natal philopatry alone falls short. Better understanding the relative abundance of floaters, both at colonies and at sea, should help conservation biologists and managers adjust expectations and interpret trends as efforts expand to restore seabird populations worldwide (Spatz *et al.* 2023).

In conclusion, ample evidence indicates that a substantial part of the population of non-breeding but sexually mature seabirds (i.e., pre-breeders regardless of age, but not immature juveniles) is regularly prospecting for potential recruitment opportunities at both established colonies and currently unoccupied locations that might provide suitable habitat. Individuals recruiting to their natal colony may not be demonstrating a species-specific genetic trait for colony philopatry as much as happening upon the existence of opportunity.

ACKNOWLEDGEMENTS

We are indebted to Ryan Carle, Katie Dugger, Michelle Kissling, Federico Méndez Sánchez, Colin Miskelly, and Richard Veit for

their detailed comments and identification of efforts relevant to our paper. J. Hernández Montoya provided unpublished data for Guadalupe Island. We also appreciate the comments by Morten Frederiksen and an anonymous reviewer for forcing us to adjust our paper to make it much clearer and more to the point! We wish also to thank *Marine Ornithology*'s Managing Editor Natasha Gillies for overseeing the review process and Technical Editor Kyra Nabeta for a great job at copy editing.

REFERENCES

- AINLEY, D.G., BOEKELHEIDE, R.J., MORRELL, S.H. & STRONG, C.S. 1990. Pigeon Guillemot. In: AINLEY, D.G. & BOEKELHEIDE, R.J. (Eds.) *Seabird of the Farallon Islands: Ecology, Dynamics and Structure of an Upwelling-System Community*. Stanford, USA: Stanford University Press.
- AINLEY, D.G. & JOHNS, M. 2023. A modest proposal—Seabirds are marine creatures first, land-based marine predators second. *Marine Ornithology* 51: 257–260.
- AINLEY, D.G., LERESCHE, R.E. & SLADEN, W.J.L. 1983. *Breeding Biology of the Adelie Penguin*. Berkeley, USA: University of California Press.
- AINLEY, D.G. & LEWIS, T.J. 1974. The history of Farallon Island marine bird populations, 1854–1972. *The Condor* 76: 432–446. doi:10.2307/1365816
- AINLEY, D.G., TELFER, T.C., REYNOLDS, M.H. & RAINE, A.F. 2020. Newell's Shearwater (*Puffinus newelli*), version 1.0. In: RODEWALD, P.G. (Ed.) *Birds of the World*. Ithaca, USA: Cornell Lab of Ornithology. doi:10.2173/bow.towshe2.01
- BAIRD, P. 1992. *Banding of adult California Least Terns at Camp Pendleton Marine Base 1987–1992*. Final report prepared for the Natural Resources Management Branch. San Diego & San Bruno, USA: Naval Facilities Engineering Systems Command, Southwestern and Western Divisions.
- BAIRD, P. 2010. *Group adherence, age structure, pair bonds, and changes in prey in a Least Tern colony*. Poster presented at the 1st World Seabird Group meeting, 07–11 September, Victoria, Canada.
- BAIRD, P. 2023. Group adherence in endangered California Least Terns (*Sternula antillarum browni*). *Waterbirds* 45: 461–466. doi:10.1675/063.045.0410
- BECK, J., COLETTA, E., CARLE, R. & HESTER, M. 2017. *Año Nuevo State Park Seabird Conservation and Habitat Restoration: Report 2017*. Unpublished Report to California Department of Parks and Recreation, Año Nuevo State Park. Santa Cruz, USA: Oikonos.
- BOULINIER, T., DANCHIN, E., MONNAT, J.-Y., DOUTRELANT, C. & CADIOU, B. 1996. Timing of prospecting and the value of information in a colonial breeding bird. *Journal of Avian Biology* 27: 252–256.
- BOWLER, D.E. & BENTON, T.G. 2005. Causes and consequences of animal dispersal strategies: Relating individual behaviour to spatial dynamics. *Biological Reviews of the Cambridge Philosophical Society* 80: 205–225. doi:10.1017/S1464793104006645
- BRINKLEY, E.S. & SUTHERLAND, K.E. 2020. Bermuda Petrel (*Pterodroma cahow*), version 1.0. In: SCHULENBERG, T.S. (Ed.) *Birds of the World*. Ithaca, USA: Cornell Lab of Ornithology.
- BROWN, J.L. 1969. Territorial behavior and population regulation in birds: A review and re-evaluation. *The Wilson Bulletin* 81: 293–329.
- BUXTON, R.T., JONES, C., MOLLER, H. & TOWNS, D.R. 2014. Drivers of seabird population recovery on New Zealand islands after predator eradication. *Conservation Biology* 28: 333–344.
- CARLE, R.D., HESTER, M.M., COLETTA, E. & BECK, J.N. 2019. Cassin's Auklet (*Ptychoramphus aleuticus*) population size, reproduction, and habitat management on a recently colonized island in California, USA. *Waterbirds* 42: 366–379.
- COOPER, B.A. & DAY, R.H. 2003. Movement of the Hawaiian Petrel to inland breeding sites on Maui Island, Hawai'i. *Waterbirds* 26: 62–71.
- COULSON, J.C. 2001. Colonial breeding in seabirds. In: SCHREIBER, E.A. & BURGER, J. (Eds.). *Biology of Marine Birds*. Boca Raton, USA: CRC Press.
- DE LA PUENTE, S., BUSSALLEU, A., CARDEÑA, M., VALDÉS-VELÁSQUEZ, A., MAJLUF, P. & SIMEONE, A. 2013. Humboldt Penguin (*Spheniscus humboldti*). In: BORBOROGLU, P.G. & BOERSMA, P.D. (Eds.) *Penguins: Natural History and Conservation*. Seattle, USA: University of Washington Press.
- DELONG, R.L. & CROSSIN, R.S. 1968. *Status of Seabirds on Islas de Guadalupe, Natividad, Cedros, San Benitos, and Los Coronados*. Unpublished report of the Pacific Ocean Biological Survey Program. Washington, USA: Smithsonian Institution.
- DIVOKY, G.J. 1987. *The Distribution and Abundance of Birds in the Eastern Chukchi Sea in Late Summer and Fall*. Final Report to the Outer Continental Shelf Environmental Assessment Program. Anchorage, USA: National Oceanic & Atmospheric Administration and Minerals Management Service.
- DIVOKY, G.J. 1998. *Factors Affecting the Growth of a Black Guillemot colony in Northern Alaska*. PhD dissertation. Fairbanks, USA: University of Alaska.
- DIVOKY, G.J., LUKACS, P.M. & DRUCKENMILLER, M.L. 2015. Effects of recent decreases in arctic sea ice on an ice-associated marine bird. *Progress in Oceanography* 136: 151–161.
- DIVOKY, G.J., WATSON, G.E. & BARTONEK, J.C. 1974. Breeding of the Black Guillemot in northern Alaska. *The Condor* 76: 339–343.
- FORD, R.G., TERRILL, S., CASEY, J., ET AL. 2021. Distribution patterns and population size of the Ashy Storm Petrel *Oceanodroma homochroa*. *Marine Ornithology* 49: 193–204.
- GASTON, A.J. 2004. *Seabirds: A Natural History*. New Haven, USA: Yale University Press.
- GENOVART, M., ORO, D., JUSTE, J. & BERTORELLE, G. 2007. What genetics tell us about the conservation of the critically endangered Balearic Shearwater? *Biological Conservation* 137: 283–293.
- GRAHAM, B.A., HIPFNER, J.M., ROJEK, N.A., STEPHENSEN, S.W. & BURG, T.M. 2023. Tufted Puffins exhibit low levels of genetic differentiation among breeding colonies in North America. *Ornithological Applications* 125: duad023. doi:10.1093/ornithapp/duad023
- 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.
- HORNUNG, M.N. 1982 *Burrows and burrowing of the puffin (Fratrula arctica)*. Bangor Occasional Paper No.10. Bangor, USA: Institute of Terrestrial Ecology.
- HOWELL, S.N.G. & ZUFELT, K. 2019. *Oceanic Birds of the World: A Photo Guide*. Princeton, USA: Princeton University Press.

- JOHNS, M.E., WARZYBOK, P., JAHNCKE, J., DOAK, P., LINDBERG, M. & BREED, G.A. 2022. Episodes of high recruitment buffer against climate-driven mass mortality events in a North Pacific seabird population. *Journal of Animal Ecology* 91: 345–355. doi:10.1111/1365-2656.13630
- JONES, H.P. & KRESS, S.W. 2012. A review of the world's active seabird restoration projects. *Journal of Wildlife Management* 76: 2–9. doi:10.1002/jwmg.240
- KLOMP, N.I. & FURNESS, R.W. 1992. The dispersal and philopatry of Great Skuas from Foula, Shetland. *Ringed & Migration* 13: 73–82.
- KRALJ, J., PONCHON, A., ORO, D., ET AL. 2023. Active breeding seabirds prospect alternative breeding colonies. *Oecologia* 201: 341–354.
- KRÜGER, O. 2008. Alternative reproductive tactics in birds. In: OLIVEIRA, R.F., TABORSKY, M. & BROCKMANN, H.J. (Eds.) *Alternative Reproductive Tactics: An Integrative Approach*. Cambridge UK: Cambridge University Press. Chapter 13, pp 343–354.
- LACK, D. 1954. *The Natural Regulation of Animal Numbers*. Oxford UK: Clarendon Press.
- LE CORRE, M., MANOURY, M., ORLOWSKI, S., BIGNON, F. & DICQUE, G. 2020. Camera trapping reveals cooperative breeding in the Red-footed Booby *Sula sula*. *Marine Ornithology* 48: 175–178.
- LEIRNESS, J.B., ADAMS, J., BALLANCE, L.T., ET AL. 2021. *Modeling At-Sea Density of Marine Birds to Support Renewable Energy Planning on the Pacific Outer Continental Shelf of the Contiguous United States*. OCS Study, BOEM 2021-014. Camarillo, USA: US Department of the Interior, Bureau of Ocean Energy Management.
- MANUWAL, D.A. 1974. Effects of territoriality on breeding in a population of Cassin's Auklet. *Ecology* 55: 1399–1406.
- MÉNDEZ SÁNCHEZ, F., BEDOLLA GUZMÁN, Y., ROJAS MAYORAL, E., ET AL. 2022. Population trends of seabirds in Mexican Islands at the California Current System. *PLoS One* 17: e0258632. doi:10.1371/journal.pone.0258632
- MISKELLY, C.M. 2022. Introduction and historical approaches to seabird conservation. In: YOUNG, L. & VANDERWERF, E. (Eds.) *Conservation of Marine Birds, 1st Edition*. London, UK: Academic Press.
- MISKELLY, C.M. 2023. From farm to forest – 50 years of ecological transformation on Mana Island, New Zealand. *Tuhinga* 34: 1–46.
- MISKELLY, C.M., TAYLOR, G.A., GUMMER, H. & WILLIAMS, R. 2009. Translocations of eight species of burrow-nesting seabirds (genera *Pterodroma*, *Pelecanoides*, *Pachyptila* and *Puffinus*: Family Procellariidae). *Biological Conservation* 142: 1965–1980.
- MISKELLY, C.M., TINLIN, G. & COTTER, R. 2004. Common diving petrels (*Pelecanoides urinatrix*) recolonise Mana Island. *Notornis* 51: 245–246.
- MURPHY, R.C. 1981. The guano and the anchovetta fishery. In: GLANTZ, M.H. & THOMPSON, J.D. (Eds.) *Resource Management and Environmental Uncertainty: Lessons from Coastal Upwelling Fisheries*. New York, USA: John Wiley & Sons, pp 81–106.
- NUR, N., BRADLEY, R.W., SALAS, L., WARZYBOK, P. & JAHNCKE, J. 2019. Evaluating population impacts of predation by owls on storm petrels in relation to proposed island mouse eradication. *Ecosphere* 10: e02878. doi:10.1002/ecs2.2878
- NUR, N., SYDEMAN, W.J., GIRMANI, D., SMITH, T.B. & GILMER, D. 1999. *Population status, prospects, and risks faced by two seabirds of the California Current: The Ashy Storm-petrel, Oceanodroma homochroa, and Xantus' Murrelet Synthliboramphus hypoleucus*. Final Report to the United States Geological Survey, Biological Resources Division. Dixon, USA: USGS.
- 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.
- PEER, K., ROBERTSON, R.J. & KEMPENAEERS, B. 2000. Reproductive anatomy and indices of quality in male Tree Swallows: The potential reproductive role of floaters. *The Auk* 117: 74–81.
- PEERY, M.Z., HALL, L.A., SELLAS, A., ET AL. 2010. Genetic analyses of historic and modern Marbled Murrelets suggest decoupling of migration and gene flow after habitat fragmentation. *Proceedings of the Royal Society B* 277: 697–706. doi:10.1098/rspb.2009.1666
- PENNIMAN, T.M., COULTER, M.C., SPEAR, L.B. & BOEKELHEIDE, R.J. 1990. Western Gull. In: AINLEY, D.G. & BOEKELHEIDE, R.J. (Eds.) *Seabirds of the Farallon Islands: Ecology, Dynamics, and Structure of an Upwelling-System Community*. Stanford, USA: Stanford University Press.
- PYLE, R.L. & PYLE, P. 2017. *The Birds of the Hawaiian Islands: Occurrence, History, Distribution, and Status*. Version 2. Honolulu, USA: BP Bishop Museum. [Accessed at <http://hbs.bishopmuseum.org/birds/rlp-monograph/> in April 2021.]
- RAYNER, M.J., GASKIN, C.P., TAYLOR, G.A., ET AL. 2020. Population estimation of the New Zealand Storm Petrel (*Fregetta maoriana*) from mark-recapture techniques at Hauturu/Little Barrier Island and from at-sea resightings of banded birds. *Notornis* 67: 503–510.
- RENNER, H.M., WALKER, L.R. WAYTHOMAS, C.F. WILLIAMS, J.C. & ARTUKHIN, Y.B. 2017. Crevice-nesting auklets are early-successional species requiring disturbance to persist. *Arctic, Antarctic, and Alpine Research* 49: 585–599.
- RICHDALE, L.E. 1963. Biology of the Sooty Shearwater *Puffinus griseus*. *Proceedings of the Zoological Society of London* 141: 1–117. doi:10.1111/j.1469-7998.1963.tb01603.x
- ROBLES, H. & CIUDAD, C. 2017. Floaters may buffer the extinction of small populations: An empirical assessment. *Proceedings of the Royal Society B* 284: 20170074. doi:10.1098/rspb.2017.0074
- SAWYER, S.L. & FOGLE, S.R. 2010. Acoustic attraction of Grey-faced Petrels (*Pterodroma macroptera gouldi*) and Fluttering Shearwaters (*Puffinus gavia*) to Young Nick's Head, New Zealand. *Notornis* 57: 166–168.
- SKUTCH, A.F. 1935. Helpers at the nest. *The Auk* 52: 257–273. doi:10.2307/4077738
- SMITH, S.M. 1984. Flock switching in chickadees: Why be a winter floater? *The American Naturalist* 123: 81–98.
- SMITHSONIAN INSTITUTION. 2016. *The Curious Colonization of the Humboldt Penguin*. Washington, USA: Smithsonian's National Zoo and Conservation Biology Institute. [Accessed at <https://nationalzoo.si.edu/ccs/news/curious-colonization-humboldt-penguin> on 11 September 2023.]
- SMITHSONIAN INSTITUTION. 2017. *Home, Sweet (Artificial) Home*. Washington, USA: Smithsonian's National Zoo and Conservation Biology Institute. [Accessed at <https://nationalzoo.si.edu/ccs/news/home-sweet-artificial-home> on 11 September 2023.]

- SPATZ, D.R., YOUNG, L.C., HOLMES, N.D., ET AL. 2023. Tracking the global application of conservation translocation and social attraction to reverse seabird declines. *Proceedings of the National Academy of Science* 120: e2214574120. doi:10.1073/pnas.2214574120
- SPEICH, S.M. & MANUWAL, D.A. 1974. Gular pouch development and population structure of Cassin's Auklet. *The Auk* 91: 291–306.
- SPENCER, G., CRAIG, M., YUEN, B. & AINLEY, D. 2024. Establishment of an incipient Newell's Shearwater *Puffinus newelli* colony on Maui. *Marine Ornithology* 52: 157–164.
- SPENDELOW, J.A. 1991. Postfledging survival and recruitment of known-origin Roseate Terns (*Sterna dougallii*) at Falkner Island, Connecticut. *Colonial Waterbirds* 14: 108–115.
- SPENDELOW, J.A., NICHOLS, J.D., NISBET, I.C.T., ET AL. 1995. Estimating annual survival and movement rates of adults within a metapopulation of Roseate Terns. *Ecology* 76: 2415–2428.
- STEPHENSON, J., BUDD, G.M., MANNING, J. & HANSBRO, P. 2005. Major eruption-induced changes to the McDonald Islands, southern Indian Ocean. *Antarctic Science* 17: 259–266.
- SURYAN, R.M., CRAIG, D.P., ROBY, D.D., ET AL. 2004. Redistribution and growth of the Caspian Tern population in the Pacific Coast region of North America, 1981–2000. *The Condor* 106: 777–790.
- THAYER, J.A., HESTER, M.M. & SYDEMAN, W.J. 2020. Conservation biology of Rhinoceros Auklets, *Cerorhinca monocerata*, on Ano Nuevo Island, California, 1993–1999. *Endangered Species Update* 17: 63–67.
- VANDERWERF, E.A., KRESS, S., GUZMÁN, Y.B., SPATZ, D., TAYLOR, G. & GUMMER, H. 2022. Restoration: Social attraction and translocation. In: YOUNG, L. & VANDERWERF, E. (Eds.) *Conservation of Marine Birds*. London, UK: Academic Press.
- VEIT, R.R. 2000. Vagrants as the expanding fringe of a growing population. *The Auk* 117: 242–246.
- VEIT, R.R., VELARDE, E., HORN, M.H. & MANNE, L.L. 2021. Population growth and long-distance vagrancy leads to colonization of Europe by Elegant Terns *Thalasseus elegans*. *Frontiers in Ecology and Evolution* 9: 725614. doi:10.3389/fevo.2021.725614
- WARHAM, J. 1996. *The Behaviour, Population Biology and Physiology of the Petrels*. London, UK: Academic Press.
- WARZYBOK, P.M., JOHNS, M. & BRADLEY, R.W. 2017. *Population Size and Reproductive Performance of Seabirds on Southeast Farallon Island, 2017*. Unpublished report to the US Fish and Wildlife Service. Petaluma, USA: Point Blue Conservation Science.
- WEATHERHEAD, P.J. & FORBES, M.R.L. 1994. Natal philopatry in passerine birds: Genetic or ecological influences? *Behavioral Ecology* 5: 426–433.
- WHITWORTH, D.L., CARTER, H.R., PALACIOS, E., ET AL. 2021. The rarest alcid: Status and history of the Guadalupe Murrelet *Synthliboramphus hypoleucus* at Isla Guadalupe, Mexico (1892–2007). *Marine Ornithology* 49: 133–143.
- WINKER, K. 1998. The concept of floater. *Ornitologia Neotropical* 9: 111–119.
- WOEHLER, E.J. & GREEN, K. 1992. Consumption of marine resources by seabirds and seals at Heard Island and the McDonald Islands. *Polar Biology* 12: 659–665.
- WYNNE-EDWARDS, V.C. 1962. *Animal Dispersion in Relation to Social Behaviour*. Edinburgh, Scotland: Oliver & Boyd.
- ZAVALAGA, C., LOZANO-SANELLEHI, S., VELEZ-ZUAZO, X. & VILDOSO, B. 2023. *Successful colonization of Humboldt penguins in breakwaters: The case of the Peru-LNG port terminal*. Poster presented at the 11th International Penguin Congress, 04–09 September, Vina del Mar, Chile. Abstract available at <https://www.penguin-conference.com/abstract-booklet>.
- ZHOU, X., CHEN, D., KRESS, S.W. & CHEN, S. 2017. A review of the use of active seabird restoration techniques. *Biodiversity Science* 25: 364–371. doi:10.17520/biods.2016378