

DISPARATE DECADAL TRENDS IN KAUA‘I SEABIRD POPULATIONS: POSSIBLE EFFECTS OF RESOURCE COMPETITION AND ANTHROPOGENIC IMPACTS

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ABSTRACT

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Population trends of seabirds nesting on Kaua‘i in the Hawaiian Islands, USA, were assessed across four decades using data from the Save Our Shearwaters (SOS) program. Started in 1979, the SOS database was intended to track the incidence of attraction of Kaua‘i’s seabirds to artificial lights, but recovery rate data also became useful to index population trends. These data documented precipitous declines of Newell’s Shearwater *Puffinus newelli* through 2017. Here we expand on those efforts by including four additional species and consider data to 2018. All five species exhibited increasing trends during SOS’s first decade, coincidental with increasing human population, suburban infrastructure, and public awareness. Counts of the once-numerous Newell’s Shearwater decreased sharply beginning in the late 1980s, but stabilized around 2012. Since that approximate time, counts of Wedge-tailed Shearwater *Ardenna pacifica* and White-tailed Tropicbird *Phaethon lepturus* have increased. Conversely, counts of Hawaiian Petrel *Pterodroma sandwichensis* and Band-rumped Storm Petrel *Hydrobates castro* have remained stable since 1990. The implications of sizable decreases in a population are rarely considered from a community ecology perspective, but in this case, such an examination is possible: the decline of Newell’s Shearwater may have led to a competitive release of trophic resources and nesting habitat, benefitting Wedge-tailed Shearwaters and White-tailed Tropicbirds, respectively. We also explore other issues potentially explaining observed trends. Clearly the SOS program is an important contributor to the success of both seabird conservation, by rehabilitating seabirds grounded by artificial lights, and management, by documenting long-term population changes that would have otherwise been unknown.

Key words: Band-rumped Storm Petrel, competitive release, Hawaiian Petrel, nesting habitat competition, Kaua‘i, Newell’s Shearwater, trophic competition, Wedge-tailed Shearwater, White-tailed Tropicbird

INTRODUCTION

In general, seabird populations in many regions of Earth have been decreasing over the past several decades (e.g., Croxall *et al.* 2012, Paleczny *et al.* 2015, Grémillet *et al.* 2018) or longer (e.g., Steadman 1995), alarming seabird biologists and managers alike. Seabirds are deemed to be sensitive indicators of their environment, which has been widely deteriorating, especially as related to fisheries/food webs and climate change (e.g., references above, Piatt *et al.* 2007, Einoder 2009, Piatt *et al.* 2020). In this context, the scientific need for information to better understand and conserve the world around us has overlooked opportunities to take advantage of “natural experiments” involving shifts in the relative abundance of sympatric species (i.e., some populations increase while others decrease).

Understanding competitive relationships between sympatric seabirds is complicated because the vast majority of seabird research is conducted on one species at one colony. Thus, differential responses to change in a given region on the part of all species present has received little attention. However, in the rare instances where multiple species at a single locality or in a limited region can be studied, complementary patterns and drivers of population change can be instructive, especially when “natural experiments” are involved. For example, at sites along the western Antarctic Peninsula (e.g., Anvers Island and nearby areas) where sea ice is disappearing on a decadal time scale owing to the “climate change experiment,” a species of ice-

loving penguin has been declining but, at the same time, a different species that avoids sea ice has been increasing (Schofield *et al.* 2010). While these differences in habitat affinities were previously known, the strength and complementarity of their responses could not have been fully appreciated without the interspecific comparison. As another example, observing fishery manipulation “experiments” by piscine competitors that share prey resources with sympatric seabirds can reveal the competitive relationships among these species through the resulting disparate population shifts or changing trends on the basis of diet (e.g., Springer & van Vliet 2014, Crawford *et al.* 2015, Ainley *et al.* 2018).

Herein, we review simultaneous population trends of five species of seabirds nesting on Kaua‘i, Hawaiian Islands, USA, where human interference has directly and indirectly caused major changes in various species’ populations at a broad range of time scales (e.g., Olson & James 1982a, 1982b; Harrison 1990; Rauzon 1991). Considering the similarities and differences in respective natural histories among Newell’s Shearwater *Puffinus newelli* (NESH), Wedge-tailed Shearwater *Ardenna pacifica* (WTSH), Hawaiian Petrel *Pterodroma sandwichensis* (HAPE), Band-rumped Storm Petrel *Hydrobates castro* (BRSP), and White-tailed Tropicbird *Phaethon lepturus* (WTTR) may reveal some of the factors responsible for what appears to be disparate population trends, especially for the minimally studied WTSH, WTTR, and BRSP. We include observations of changes of individual species previously

documented by others (e.g., Raine *et al.* 2017a, 2020). Considering the collective trends over the past several decades, we speculate about why some species have increased while others have declined.

METHODS

The trends analysis presented here focuses on the five most abundant seabird species nesting on Kaua'i. Only WTSH nests in habitat that is easily accessible by researchers (see direct colony counts below), while the other four species nest in remote, treacherous habitat that is nearly impossible for researchers to access (e.g., Ainley & Holmes 2011). For these inaccessible species, it is not possible to directly measure abundance and trends via surveys of nesting populations and, therefore, trends must be inferred by proxy. Indeed, they all nest in burrows and cavities, thus increasing the difficulty of counting. For some time now, the consensus among Hawai'i seabird researchers and managers has been that the annually augmented prevalence of seabirds in the "Save Our Shearwaters" (SOS) database can be used as an index to gauge trends in the size of source populations (e.g., Ainley *et al.* 2001, Day *et al.* 2003, Raine *et al.* 2017a). Such data have been used elsewhere for similar purposes (e.g., Rodríguez *et al.* 2012a, 2012b, 2017; Chevillon *et al.* 2022). This use of the database is possible for our species of interest because almost all individuals

logged in the SOS database have been fledglings and, as such, they each represented a single breeding pair (each species having a clutch of one egg).

The SOS database is much more extensive than what has been used to support the trends analysis presented here—the SOS program, organized in 1979 by the Hawai'i Division of Forestry and Wildlife and now operated in cooperation with the Hawai'i Wildlife Center, receives all types of seabirds and non-seabirds. These individuals are either already dead, need to be euthanized, or can be successfully rehabilitated and released. Annual tallies of all birds received have been maintained (Rauzon 1991). For purposes of our analysis, the full SOS database was filtered to include only the species of interest and circumstances of interest (e.g., individuals encountered on neighborhood streets, resorts, and facilities, some of which are specifically monitored for downed seabirds each autumn at the time of fledging). With one exception, all relevant fledglings and adults were included in this analysis; most (> 95%) seabirds turned over to SOS, as noted, are fledglings (see also Telfer 1981–1995, Telfer *et al.* 1987, Ainley *et al.* 1995). The exception was the 118 NESH attracted to lights at a US Air Force radar facility high in the Kaua'i mountains in 2015, an anomalous event atypical of any other year in the SOS time series. After filtering, annual counts were re-tallied and plotted to construct relative trends from 1980 to 2018 for each species.

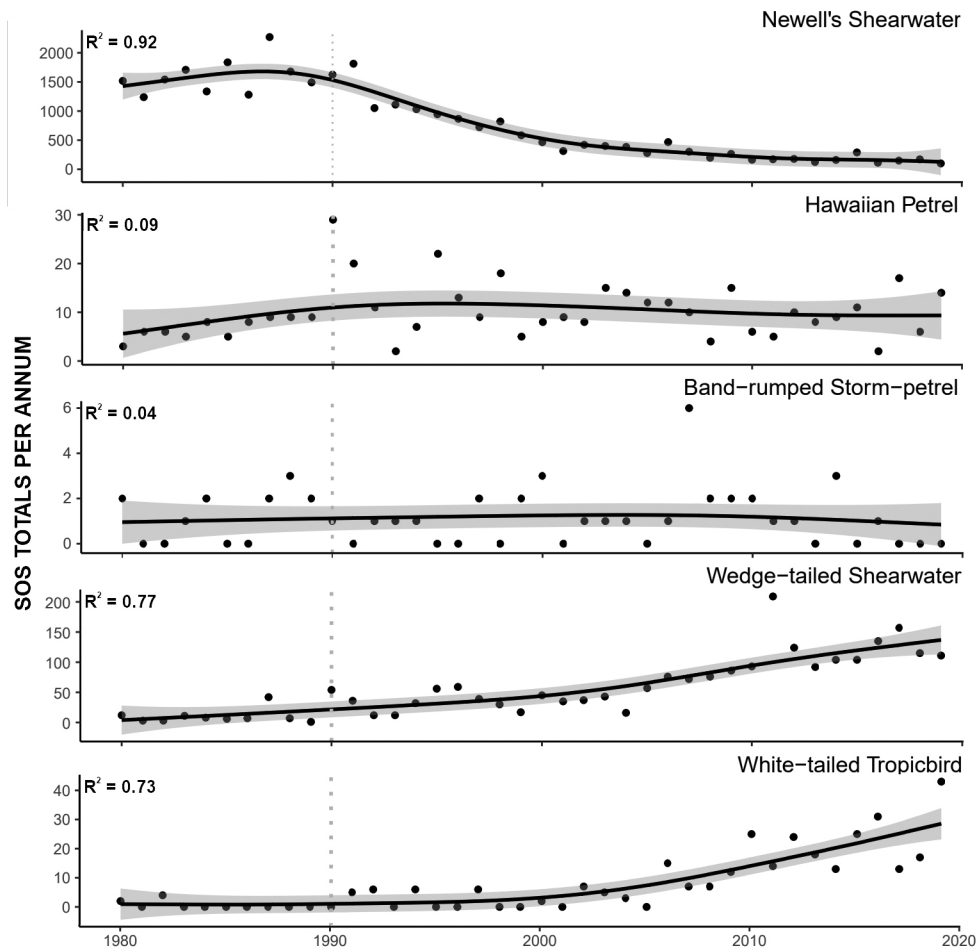


Fig. 1. Temporal variation, indicated by generalized additive model analysis of annual totals of specimens provided to the Save Our Shearwaters (SOS) program on Kaua'i (1980–2018), Hawaiian Islands, USA, as an index to long-term population trends for the five most abundant seabird species nesting on the island. Shading indicates 95% confidence intervals.

Generalized additive models (GAMs) were used to describe non-linear trends for each of the five species and provide a 95% confidence interval (CI) around each trendline. GAMs were generated using R (version 4.0.5; R Core Team 2021) and the *gam* function in the “mgcv” package (Wood 2011). GAMs included a single dependent variable, species-specific SOS tallies, and a single explanatory variable (year). Furthermore, the associated thin-plate penalized regression splines were set to have 10 knots (k), with 10 selected per guidance provided by Wood (2017): “exact choice of k is not generally critical: it should be chosen to be large enough that you are reasonably sure of having enough degrees of freedom to represent the underlying ‘truth’ reasonably well, but small enough to maintain reasonable computational efficiency.” In the Appendix, we provide the first derivative of trends to illustrate where the slope of each trend line differs significantly from zero, indicating periods of certain decrease, stability, and increase for each species.

RESULTS AND DISCUSSION

Long-term trendlines for the five most abundant seabird species on Kaua‘i (Fig. 1) revealed the following: (1) all species increased during the first 8 to 10 years of SOS specimen retrieval, though this increase was most evident in the more abundant species; (2) beginning in the early 1990s and continuing until the mid-2000s, a steady decrease in tallies of the once-abundant NESH occurred, followed by a recent leveling off to the present; (3) increase in numbers of WTSH and the much less abundant WTTR in the SOS database began in the early 2000s, continuing to the present; and (4) despite the initial increase for HAPE and BRSP, the SOS trendline has remained stable across the remainder of the study period. It is clear that changes have occurred, and they raised some questions: why were such disparate patterns manifested? And, what were the chances that an “experiment”—namely, a dramatic decrease in the predominant and once super-abundant NESH—played a role in the population dynamics of other species?

Decreasing populations

Newell's Shearwater

A dramatic decline in the NESH population has been previously documented by others using various land-based methods. Raine *et al.* (2017a) used SOS and radar data, and they estimated a 94% decrease in the NESH population that occurred from the late 1980s to 2015 (Fig. 1). Trends derived from radar and SOS tallies are consistent with each other in terms of direction and magnitude of change. Given this degree of corroboration between radar and SOS methods, it is likely that both methods can serve as a reliable index of population trends over the last few decades. For the SOS data, tallies are linked to population size because the vast majority of NESH (and other species) in the database were fledglings (> 95% of SOS annual totals; see Telfer 1981–1995) and because NESH (and other species in this paper) lay only one egg per nesting attempt; a single fledgling represents a single breeding pair of adults. An added benefit of using SOS tallies relative to radar as a proxy for population trends is that species can be identified with certainty when they are turned into SOS, whereas with radar, assumptions must be made about the species appearing as a target. If multiple species are inadvertently counted as one due to cross-species misidentification of counts (e.g., in cases where species that are indistinguishable via radar are active simultaneously), reliance on such contaminated data could result in erroneous conclusions regarding trends of affected species (see below).

The trend in NESH populations evident in at-sea surveys was consistent with the overall decrease determined using land-based methods. The size of the NESH population on Kaua‘i in 1980 was only roughly estimated, and this was thought to contribute 90% of the world population (Ainley *et al.* 2020). A review of at-sea data revealed that the Kaua‘i population even in modern times was substantial: 84 000 birds (CI 57 000–115 000) were estimated from data collected between 1980 and 1994 (Spear *et al.* 1995), reduced to 29 000 birds (CI 18 000–43 000) estimated from data collected between 1998 and 2017 (Joyce 2016). Otherwise, the initial increase observed for NESH and the other species in the SOS time series likely resulted from the rapidly increasing human population, their infrastructure (lights), and increased attention by citizens to participate in SOS (Telfer *et al.* 1987, Ainley *et al.* 2001). Such public awareness has influenced totals of SOS programs elsewhere (e.g., Rodríguez *et al.* 2012a, 2012b; Gineste *et al.* 2017), and this was the reason why we excluded data from the first year (i.e., 1979) of the Kaua‘i program.

Although introduced mammalian predators (the main cause of decline in NESH; Ainley *et al.* 2020) have been present on Kaua‘i for the previous 800 years due to introduction by Polynesian immigrants (references above), the diversity and abundance of predators have increased in modern times due to numerous factors. These factors include widespread sugarcane plantations that facilitate increased rodent populations (especially rats *Rattus* spp.), reduction in hunting among modern Hawaiians of introduced pigs *Sus scrofa* and other ungulates, the introduction of domestic cats *Felis catus* by Europeans in the 1800s (Hess & Banko 2006), and introductions of other harmful species such as Western Barn Owl *Tyto alba* in the 1950s (Raine *et al.* 2019). There is little doubt that the NESH population was historically many times larger, even larger than what existed in 1980. It was around that year that the human population on Kaua‘i began to notably increase (Ainley *et al.* 2001). By the mid-2010s, the NESH population had decreased dramatically, with Pyle & Pyle (2017) reporting 10 000 pairs on Kaua‘i, in accordance with the at-sea surveys by Joyce (2016). Ainley *et al.* (2020) detailed the contribution of powerline collisions and mortality stemming from light attraction (“fallout”; Telfer *et al.* 1987), as well as how depredation played a role in the downward trend.

The decreasing trend, as seen in the SOS data, slowed or even leveled for the NESH population in the 2010s, and this may have various explanations. It is possible that SOS no longer receives birds from any NESH colonies on eastern and southern slopes of Kaua‘i, as once was the case (surmised also by Troy *et al.* 2013), since those near-to-civilization colonies have disappeared. The species now mostly nests in colonies remaining among very steep terrain on the North Shore/Nāpali Coast, where human habitation and urban expansion have not occurred (Fig. 2). This has minimized the species’ probability of direct interaction with people (Ainley *et al.* 2020). In addition, owing to regulatory protections, various mitigation measures have been implemented, such as turning off or replacing particular bright lights (e.g., such as at hotels) that were considered responsible for a significant amount of fallout (Telfer *et al.* 1987, State of Hawai‘i 2020). For example, compare the changed light imagery over the course of just a few years in Fig. 2; fallout thus has been reduced. Most NESH processed by SOS in the recent years must have originated from the fraction of locations where they have managed to persist (e.g., the North Shore/Nāpali Coast as noted above, but see maps in Ainley & Holmes 2011). In order for fledglings reared on the northern coast to become impacted by

artificial lights on the southern or eastern coasts (Fig. 2), fledglings would need to make a 180-degree reversal in the direction of nest departure (down slope to the nearby ocean), gain several hundred meters altitude, then fly across the island to eventually encounter brightly lit eastern and southern coasts. This scenario is unlikely, given that most nesting areas on the dark northern coast are in direct proximity to the ocean (within a few kilometers), and the energetic cost for fledgling birds to fly up and over the coastal range would be considerable. Rather, we propose that most birds now retrieved by SOS have fledged from nest sites on the northern shore, and upon successfully reaching the sea, fly over water around the island to be attracted by coastal lights on the opposite shore (Troy *et al.* 2013). Based on band recoveries, Telfer (1981–1995) reached the same conclusion, i.e., attraction of some portion of birds from the sea, after realizing that numerous SOS-banded birds that had been released to the sea were found grounded at coastal lights a few days later, at sites typically several kilometers away from the initial grounding site. Further support for the hypothesis that shearwater fledglings fly to sea prior to being attracted back to land by artificial lights comes from the well-studied grounding patterns observed for WTSHs elsewhere in Hawai'i. In most cases, WTSH nest only on offshore islets or along main island beaches seaward of any lights and where artificial lights were not visible to fledglings as they leave their nest for the sea (Urmston *et al.* 2022). Consequently, the vast majority of WTSH found grounded beneath lights on land had to have been attracted from the sea. This same scenario has to be true for WTSH logged by SOS on Kaua'i as well (see below).

Increasing populations

Both WTSH and WTTR exhibited disparate, increasing population trends relative to NESH (Fig. 1).

Wedge-tailed Shearwater

Following the initial increase in WTSH associated with increased citizen participation in the SOS program, annual tallies remained at a low level for several years (< 50 birds recovered per annum)

but increased beginning in the late 1980s, eventually reaching 100–200 per annum (Fig. 1). The increase has leveled off over the last few years (Fig. 1, Appendix). Pyle & Pyle (2017) estimated 40 000 pairs of WTSH on Kaua'i during the mid-2010s, including the islets Lehua and Ka'ula, which are ~10 km away from Kaua'i. More recently in 2019, US Geological Survey personnel (J. Adams & J. Felis pers. comm.) estimated 21 000 pairs at Kilauea Point alone and 51 000 pairs for the whole island and islets (more below). Seemingly the species must still be increasing. It is highly likely that there are now a lot more WTSH, and many fewer NESH, using the waters around Kaua'i than at the time when NESH first began their apparent decline.

White-tailed Tropicbird

Using archived SOS information, Raine *et al.* (2020) described seasonal and interannual trends exhibited by WTTR in several aspects of their natural history, which has been poorly studied on Kaua'i and elsewhere in Hawai'i. They described an 85% increase in WTTR prevalence in the SOS record, with annual numbers of rescued birds increasing from just a few per year to annual tallies in the 30s by 2016. Most of the increase occurred starting in the early 2000s (Fig. 1). The relatively low counts of WTTR are consistent with a small local breeding population in a species that is not colonial. An estimate for the entire Hawaiian Islands is < 3 000 pairs, and only half of these breed in any given year (Lee & Walsh-McGee 2020); an estimated 700–800 pairs possibly breed on Kaua'i (Pyle & Pyle 2017). It is possible that increased public awareness of seabird conservation and SOS was involved in the apparent increase, in accordance with awareness of the plight of endangered species. Thus, citizens may have become even more inclined to bring downed birds of any species to SOS drop-off stations. Therefore, with little historical information on abundance, other than SOS, assessing what factors could be involved in explaining the WTTR trend requires much speculation. The Christmas Bird Count data from the community of Kapa'a on Kaua'i, 1971–2014, do not indicate a trend (Pyle & Pyle 2017). Those counts, after all, are quite limited in geographic scope and thus less useful for our purposes.

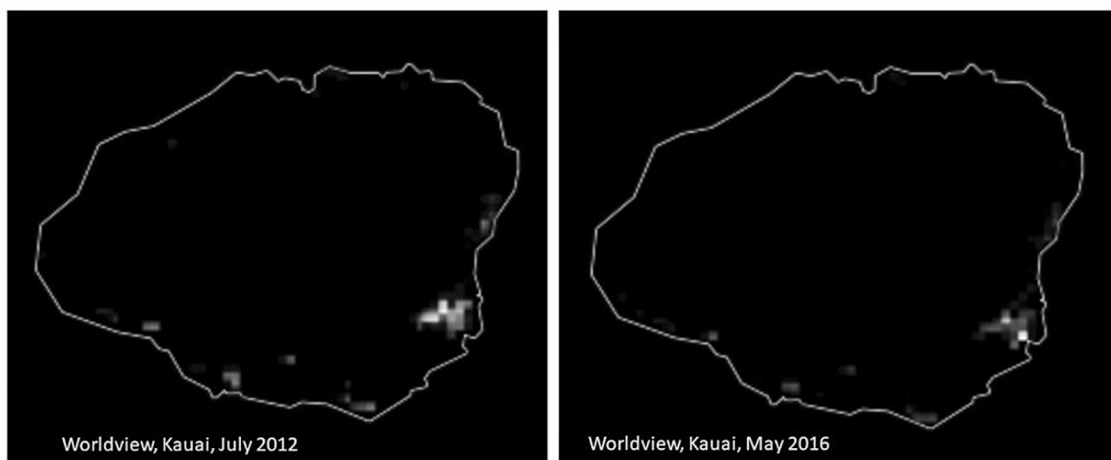


Fig. 2. Satellite views at night of the brightest lighting footprint on Kaua'i, Hawaiian Islands, USA, showing diminution from 2012 to 2016; data was taken from Worldview (<https://worldview.earthdata.nasa.gov/>) in April 2021. These days, Newell's Shearwater *Puffinus newelli* (NESH), Hawaiian Petrel *Pterodroma sandwichensis* (HAPE), and Band-rumped Storm Petrel *Hydrobates castro* (BRSP), nest in the steep mountain terrain of the North Shore, far from the developed portion of the island. At current nesting locations, it is not likely for fledglings, before encountering the sea at the base of their nesting mountains, to fly across the island to south and east coast before being attracted to the city lights. Rather they quickly descend to the sea and then some encounter the lights after flying offshore around the island.

The WTTR increase in actual population size (regardless of public awareness) could also be a result of the efforts by the SOS program itself since 2008. Almost all WTTR turned into SOS, like the shearwaters and petrels, have been recently fledged juveniles, with the majority emaciated; this is possibly the case, too, for retrieved seabirds elsewhere (e.g., Rodríguez *et al.* 2012a, 2017). Rehabilitating these individuals required an extended amount of time (i.e., almost three weeks), a period that greatly exceeds the typical duration of rehabilitation needed for petrels and shearwaters (i.e., a few days; M. Bache of the Hawai'i Wildlife Center pers. comm.). The explanation for why juvenile WTTR tend to be more emaciated than shearwaters is unknown. It could be related to differences in foraging habitat and associated food resources and to the relative difficulties in learning to forage efficiently by young WTTR parents—there would be more young parents in an increasing population and, hence, a greater incidence of underfed chicks. Not participating in foraging flocks, and thereby being limited from outside foraging cues, could add to the seemingly difficult skills that must be learned in order to locate and obtain sub-surface prey by aerial plunge-diving. The process of learning to effectively plunge-dive has been well studied in at least one other aerial plunge-diving species, the Brown Pelican *Pelecanus occidentalis*. In Brown Pelicans, plunge-diving skills improve dramatically with age and are influenced by several environmental and sensory factors that affect age-differentiated foraging success (e.g., Carl 1987).

It is unlikely that other factors have contributed to the increased prevalence of WTTR in the SOS records. While it is possible that the expansion of internet and social media may facilitate wildlife rescue, the SOS program has been effective at promoting public awareness across multiple decades (e.g., SOS has long been advertised via local radio and television; Rauzon 1991). Thus, it is unlikely that this circumstance alone can adequately account for the increased WTTR submitted to the SOS program. It is unknown whether WTTR fledglings are prone to light attraction, but this would be an unlikely explanation for the increased SOS trend because the lighting footprint of Kaua'i has been decreasing in recent years due to measures instituted to reduce seabird fallout (Fig. 2). The WTTR population does appear to have increased.

Speculation regarding WTSH and WTTR trends

As indicated by the increasing trends derived from SOS tallies, greater abundance of WTSH and WTTR on Kaua'i over the study period is interesting to consider in the context of the simultaneous, significant decline of NESH abundance. The WTSH and WTTR began to increase once the population of NESH reached a relatively low level in the early 2000s. It is possible that an ecological connection exists. WTSH typically nest in habitat separate from NESH, with WTSH excluding NESH when the latter attempt to establish neighboring nest sites (Ainley *et al.* 2020). Such competition leading to shifts in on-island distribution among petrels has been observed elsewhere (e.g., Rodríguez *et al.* 2022, O'Dwyer *et al.* 2023). Otherwise, WTSH nesting habitat occurs along the immediate island shores just above the beach, but NESH occurs in the montane interior of the island, where WTSH do not occur (Ainley *et al.* 2020). In accord with these patterns, WTSH are notorious for excluding other procellariid species on Australian islands (N. Carlile of the Department of Planning & Environment, Australia, pers. comm.). In the end, it does not appear that exclusion of NESH from nesting by WTSH is an issue.

In the case of the WTTR, however, it is possible that some sort of competitive release that involves nesting habitat availability has been occurring. WTTR nest in the outer portion of natural cavities (i.e., a shelter from only rain) located in steep valleys and on cliff faces along the coast and in the interior of Kaua'i, e.g., on the near-vertical walls of Waimea Canyon (Harrison 1990, Raine *et al.* 2020). Such habitat could have been used by NESH, when the NESH population was large and likely used both optimal and suboptimal habitat. A small, remnant NESH nesting population still nests on the walls of Waimea Canyon (Ainley *et al.* 2020). In Puna District on the island of Hawai'i, where a small remnant population of NESH also exists, NESH are known to nest in cavities in near-vertical walls of volcanic craters (Reynolds & Ritchotte 1997), relatively safe from alien predators. While comfortable using this habitat, WTTRs would not likely build a nest at a cliff-face opening across which NESH might scamper daily to reach further into the cavity. On the other hand, competition for nesting habitat between WTTR and various petrel species is well known (e.g., Bermuda Petrel *Pterodroma cahow*; Brinkley & Sutherland 2020). Thus, the decrease in prevalence of NESH on Kaua'i, which once would have included more suitable nesting areas for WTTR, could partially explain the recent increase in the WTTR population.

The disappearance of NESH could also have contributed to the increasing trend of the WTSH population due to trophic competitive release. Both species feed in multispecies flocks over schools of tuna and other large predatory fish where competition is intense, especially interference competition based on bird size; prey size is based on bill size, which is related to bird size (Spear *et al.* 2007). These two shearwaters are close enough in size and mode of foraging (Ainley 1977; surface to shallow depths) that competition between them is likely where their occurrence overlaps at sea. In fact, both species feed extensively in waters adjacent to Kaua'i (Harrison 1990, Adams *et al.* 2020, Ainley *et al.* 2020). The latter overlap would be especially true in these nearby waters frequented on the short foraging trips undertaken by NESH parents to provision chicks, where one parent provisions the chick daily for 6–12 days while the other parent, needing to recover condition, is free to forage further afield (B. Zahn & K. Uyehara in Ainley *et al.* 2020). Because of the large initial size of the NESH population (or at least, its size when SOS began) and its subsequent major decrease, we propose that appreciably more trophic resources or at least more foraging habitat space has become available to Kaua'i WTSHs. A corresponding population increase may be the response. Whether the increasingly abundant WTSH is now having a negative influence on NESH population recovery is an interesting question that needs direct evidence to resolve. Interaction between WTSH and NESH regarding nesting habitat would be exploitative competition (even to the point of aggression, e.g. territorial exclusion), but interaction at sea more likely would be interference competition (with NESH being overwhelmed by the sheer abundance of WTSH in foraging flocks, with WTSH taking most available prey). Given that the WTTR does not generally participate in multispecies flocks (Harrison *et al.* 1983, Lee & Walsh-McGee 2020), such competitive trophic release likely would not be a principle factor to explain that species' population increase.

Stable populations

In contrast to WTSH and WTTR, trends were not evident in SOS totals for either HAPE or BRSP following the slight increase during SOS's initial years (Fig. 1).

Hawaiian Petrel

There was a small decrease in SOS totals of HAPE early in the period after the initial peak. Based on at-sea surveys of a large portion of the eastern Pacific, Spear *et al.* (1995) estimated the entire Hawaiian Islands population of HAPE to be 88 000 (CI 54 000–130 000) for 1984–1994, while Joyce (2016) estimated 52 000 (CI 40 000–67 000) for 1998–2011. The HAPE population is divided principally among Lanaʻi, Maui, and Kauaʻi, with Kauaʻi contributing least to the total (Simons & Bailey 2020). However, based on radar data from 1993–2013, Raine *et al.* (2017a) proposed that the HAPE population on Kauaʻi has progressively decreased from possibly low tens of thousands during the 1980s (Joyce 2016) to a current level that is 78% fewer. Pyle & Pyle (2017) estimate 1500 pairs present on Kauaʻi as of the mid-2010s.

Although the SOS data indicate a relatively stable population during our study period after the initial increase, Raine *et al.* (2017a) came to a different conclusion using radar, though they disregarded SOS data. As noted above, radar targets are difficult to assign to species without corroborating data. Further assignment often relies on assumptions based on observed timing of flights in order to infer identification of the reported target (see Day & Cooper 1995, Ainley *et al.* 1997, Day *et al.* 2003). Assumptions to correct for bias made by Raine *et al.* (2017a), which were different from those made by Day *et al.* (2003), may have excluded some of the earlier-in-the-evening times when HAPE were actually flying (and available for detection by radar) and consequently underestimated the number of HAPE. Moreover, tallies of supposed HAPE based on periods of the night when both HAPE and NESH were flying, as defined by Raine *et al.* (2017a), could have been influenced by the certain decrease in NESH—species identification was not possible but the overall numbers of targets declined. This appears to have led to an erroneous conclusion about trends for HAPE. Thus, the decadal decrease in radar target detections might have been more representative of fewer NESH (misidentified as HAPE) during the sampling period, as opposed to an actual decrease in HAPE, whose numbers remained stable in the passage rate data. Therefore, the supposed 78% decrease in the HAPE population, as indexed by radar data, appears not to have happened. The HAPE decrease, although discernable in the radar data, appears to be just a few percent throughout the period from 1990 to 2018, as judged from SOS data.

The current nesting distribution of HAPE on Kauaʻi, like NESH, is almost completely relegated to the steep razor-backed ridges of the North Shore/Nāpali Coast (Ainley & Holmes 2011). This was seemingly established long ago, when the Polynesians arrived and brought dogs *Canis domesticus* and pigs to the island (Olson & James 1982a, 1982b; Steadman 1995). Omnivorous pigs, owing to their habit of seeking food by rooting in the soil, can be particularly detrimental to burrow-nesting species. For example, they have devastated the Townsend's Shearwater *Puffinus auricularis* nesting in the Revillagigedo Islands, Mexico (Everett 1988, Howell & Webb 1989). Pigs are also involved in the Endangered status of the closely-related Hutton's Shearwater *Puffinus huttoni* in New Zealand (Cuthbert 2001) and other seabird species (Bretagnolle *et al.* 2021). Subsequently, the pigs, dogs, rats, and feral cats on Kauaʻi have prevented HAPE from re-occupying the breeding habitat used before arrival of humans, and this is facilitated by other anthropogenic factors (Raine *et al.* 2017a). Past localized extirpations and the presence of predators have confined HAPE

(and NESH) nesting to the steep and mountainous terrain of the northern shore, which is remote from civilization and incredibly difficult to traverse, even for non-humans. This enables colony access with little to no interaction with urbanization or introduced predators, which has resulted in the observed low encounter rate by SOS.

Band-rumped Storm Petrel

Like WTTR, little is known of the population of BRSP on Kauaʻi that is involved in the population trend, independent of SOS data (Fig. 1). The greatest number of BRSP turned into SOS in a single year is six though typically it has been zero to three in any year. The population must be very small and/or not as affected by lights as are the other cavity-dwelling procellariids. Based on auditory surveys indicating prevalence of breeding sites mostly along the North Shore/Nāpali coast (Raine *et al.* 2017b), the BRSP population must number no more than hundreds of pairs. Pyle & Pyle (2017) estimated 250 pairs as of the mid-2010s. BRSP, like HAPE and NESH, apparently have been forced by introduced predators to breed on steep, crumbly cliffs principally in the northern and northwestern part of Kauaʻi (Raine *et al.* 2017b).

CONCLUSIONS

The SOS program has played a key role in seabird conservation on Kauaʻi, not just in rehabilitating downed seabirds but also in helping to monitor trends in difficult-to-assess seabird populations, as demonstrated by the results presented herein and by others; see Rodríguez *et al.* (2012a, 2012b) and Gineste *et al.* (2017) for similar efforts elsewhere. Considering the various disparate trends, ecologists need to understand what factors have contributed to these disparities. In that regard, considering the trends of all species collectively illuminates additional factors that may have contributed to continued decline and/or slow recovery of the once dominant NESH. Specifically, competition for food resources between NESH and WTSH, two species that occupy a similar foraging niche, may substantially limit the ability of NESH populations to attain historical or even recent levels. To confirm the hypothesis that WTSH may be limiting the population recovery of NESH by gaining competitive trophic advantage will require additional research, especially at sea. If this is indeed the case, successful conservation actions would also need to incorporate actions that address this impediment to population recovery for NESH on Kauaʻi.

Especially problematic, too, are the trends evident for WTTR and the recent lack of trends in HAPE. The limited information available on WTTR natural history from which to infer the potential response to trophic factors, the spotty geographic distribution of their SOS fallout records, and the degree to which competitive release (from NESH, in the form of nesting habitat availability) is occurring all add to the complexity of interpreting these trends. This complicates any efforts to develop firm hypotheses concerning the availability or quality of food resources and its effect on regulating the population of the WTTR as discussed in this paper. Finally, due to contradictions with inferences made via radar observations, the lack of or minimal decreasing trend in the HAPE record was not anticipated before we conducted the analysis presented here, and this was indeed very surprising. If confirmed by other research, it could significantly change some of the recovery projections expected to result from conservation actions being considered for this species on Kauaʻi.

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REFERENCES

- ADAMS, J., FELIS, J., PENNIMAN, J., HESTER, M., YOUNG, L. & CZAPANSKIY, M. 2020. At-sea movements and ranging behaviors of breeding Wedge-tailed Shearwaters (*Ardenna pacifica*) in the subtropical Hawaiian metapopulation. In: *Book of Abstracts for the 47th Annual Meeting of the Pacific Seabird Group*, 12–15 February, Portland, Oregon, USA. [Accessed at https://pacificseabirdgroup.org/wp-content/uploads/2020/05/PSG2020_Abstracts.pdf on April 2021.]
- AINLEY, D.G. 1977. Feeding methods in seabirds: a comparison of polar and tropical communities in the eastern Pacific Ocean. In: LLANO, G.A. (Ed.) *Adaptations Within Antarctic Ecosystems: Proceedings of the Third SCAR Symposium on Antarctic Biology*. Washington, USA: Smithsonian Institution Press.
- AINLEY, D.G. & HOLMES, N.D. 2011. *Species accounts for three endemic Hawaiian seabirds on Kaua'i: Hawaiian Petrel, Newell's Shearwater and Band-Rumped Storm Petrel*. Final Report from H.T. Harvey & Associates to USFWS, Pacific Islands Fish and Wildlife Office, Honolulu, Hawai'i. Los Gatos, USA: H.T. Harvey & Associates.
- AINLEY, D.G., PODOLSKY, R., DEFOREST, L. & SPENCER, G. 1997. New insights into the status of the Hawaiian Petrel on Kauai. *Colonial Waterbirds* 20: 24–30.
- AINLEY, D.G., PODOLSKY, R., DEFOREST, L., SPENCER, G. & NUR, N. 1995. *The Ecology of Newell's Shearwater and Dark-Rumped Petrel on the Island of Kaua'i*. Final Report Task 2. Palo Alto, USA: Electric Power Research Institute.
- AINLEY, D. G., PODOLSKY, R.R., NUR, N., DEFOREST, L.N. & SPENCER, G.C. 2001. The status and population trends of the Newell's Shearwater on Kaua'i: Insights from modeling. *Studies in Avian Biology* 22: 108–123.
- AINLEY, D.G., SANTORA, J.A., CAPITOLO, P.J. ET AL. 2018. Ecosystem-based management affecting Brandt's Cormorant resources and populations in the central California Current region. *Biological Conservation* 217: 407–418.
- AINLEY, D.G., TELFER, T.C., REYNOLDS, M.H. & RAINE, A.F. 2020. Newell's Shearwater (*Puffinus newelli*), version 2.0. In: RODEWALD, P.G. (Ed.) *Birds of the World*. Ithaca, USA: Cornell Lab of Ornithology. doi:10.2173/bow.towshe2.01
- BRETAGNOLLE, V., RENAUDET, L., VILLARD, P., SHIRIHAI, H., CARLILE, N. & PRIDDEL, D. 2021. Status of Gould's Petrel *Pterodroma leucoptera caledonica* in New Caledonia: distribution, breeding biology, threats and conservation. *Emu - Austral Ornithology* 121: 303–313. doi:10.1080/01584197.2021.1938611
- BRINKLEY, E.S. & SUTHERLAND, K. 2020. Bermuda Petrel (*Pterodroma cahow*), version 1.0. In: SCHULENBERG, T.S. (Ed.) *Birds of the World*. Ithaca, USA: Cornell Lab of Ornithology. doi:10.2173/bow.berpet.02
- CARL, R.A. 1987. Age-class variation in foraging techniques by Brown Pelicans. *The Condor* 89: 525–533.
- CHEVILLON, L., TOURMETZ, J., DUBOS, J. ET AL. 2022. 25 years of light-induced petrel groundings in Reunion Island: Retrospective analysis and predicted trends. *Global Ecology and Conservation* 38: e02232.
- CRAWFORD, R.J.M., MAKHADO, A.B., WHITTINGTON, P.A., RANDALL, R.M., OOSTHUIZEN, W.H. & WALLER, L.J. 2015. A changing distribution of seabirds in South Africa—the possible effects of climate and its consequences. *Frontiers in Ecology and Evolution* 3: 10. doi:10.3389/fevo.2015.00010
- CROXALL, J.P., BUTCHART, S.H.M., LASCELLES, B. ET AL. 2012. Seabird conservation status, threats and priority actions: a global assessment. *Bird Conservation International* 22: 1–34.
- CUTHBERT, R.J. 2001. *Conservation and ecology of Hutton's Shearwater* (*Puffinus huttoni*). Conservation Advisory Science Notes No. 335. Wellington, New Zealand: Department of Conservation.
- DAY, R.H. & COOPER, B.A. 1995. Patterns of movement of Dark-rumped Petrels and Newell's Shearwaters on Kaua'i. *The Condor* 97: 1011–1027.
- DAY, R.H., COOPER, B.A. & TELFER, T.C. 2003. Decline of Townsend's (Newell's) Shearwaters (*Puffinus auricularis newelli*) on Kauai, Hawaii. *The Auk* 120: 669–679.
- EINODER, L.D. 2009. A review of the use of seabirds as indicators in fisheries and ecosystem management. *Fisheries Research* 95: 6–13.
- EVERETT, W.T. 1988. Notes from Clarion Island. *The Condor* 90: 512–513.
- GINESTE, B., SOUQUET, M., COUZI, F.-X. ET AL. 2017. Tropical Shearwater population stability at Reunion Island, despite light pollution. *Journal of Ornithology* 158: 385–394.
- GRÉMILLET, D., PONCHON, A., PALECZNY, M., PALOMARES, M.-L.D., KARPOUZI, V. & PAULY, D. 2018. Persisting worldwide seabird-fishery competition despite seabird community decline. *Current Biology* 28: 4009–4013.e2.
- HARRISON, C.S. 1990. *Seabirds of Hawai'i: Natural History and Conservation*. Ithaca, USA: Cornell University Press.
- HARRISON, C.S., HIDA, T.H. & SEKI, M.P. 1983. Hawaiian seabird feeding ecology. *Wildlife Monographs* 85: 1–71.
- HESS, S.C. & BANKO, P.C. 2006. *Feral Cats: Too Long a Threat to Hawaiian Wildlife*. Publications of the US Geological Survey, No. 112. Fact Sheet 2006-3006. [Accessed online at <https://digitalcommons.unl.edu/usgspubs/112> in April 2021.]
- HOWELL, S.N.G. & WEBB, S. 1989. Additional notes from Isla Clarion, Mexico. *The Condor* 91: 1007–1008.
- JOYCE, T.W. 2016. Estimates of Hawaiian Petrel (*Pterodroma sandwichensis*) and Newell's Shearwater (*Puffinus newelli*) abundance based on data collected at sea, 1998–2011. In: JOYCE, T.W. *Foraging Ecology, Biogeography, and Population Biology of Seabird and Toothed Whale Predators in the Anthropocene*. PhD dissertation. San Diego, USA: University of California.
- LEE, D.S. & WALSH-MCGEE, M. 2020. White-tailed Tropicbird (*Phaethon lepturus*), version 1.0. In: BILLERMAN, S.M. (Ed.) *Birds of the World*. Ithaca, USA: Cornell Lab of Ornithology. doi:10.2173/bow.whttro.01
- O'DWYER, T., CARLILE, N., O'NEILL, L. & HALPIN, L.R. 2023. Changing fortunes of the Black-winged Petrel *Pterodroma nigripennis* following the Lord Howe Island Rodent Eradication Project - interactions with other recovering species. *Bird Conservation International* 33: E18. doi:10.1017/S0959270922000132
- OLSON, S.L. & JAMES, H.F. 1982a. *Prodromus of the Fossil Avifauna of the Hawaiian Islands*. Smithsonian Contributions to Zoology, No. 365. Washington, USA: Smithsonian Institution Press.

- OLSON, S.L. & JAMES, H.F. 1982b. Fossil birds from the Hawaiian Islands: Evidence for wholesale extinction by man before Western contact. *Science* 217: 633–635.
- PALECZNY, M., HAMMILL, E., KARPOUZI, V. & PAULY, D. 2015. Population trend of the world's monitored seabirds, 1950–2010. *PLoS One* 10: e0129342. doi:10.1371/journal.pone.0129342
- PIATT, J.F., PARRISH, J.K., RENNER, H.M., ET AL. 2020. Extreme mortality and reproductive failure of Common Murres resulting from the northeast Pacific marine heatwave of 2014–2016. *PLoS One* 15: e0226087. doi:10.1371/journal.pone.0226087
- PIATT, J., SYDEMAN, W. & WIESE, F. 2007. Introduction: A modern role for seabirds as indicators. *Marine Ecology Progress Series* 352: 199–204.
- 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/> in April 2021.]
- R CORE TEAM. 2021. *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>
- RAINE, A.F., ANDERSON, T., DRISKILL, S. & TIPPIN, T. 2020. Assessing the breeding phenology of the White-tailed Tropicbird *Phaethon lepturus dorotheae* on the island of Kaua'i, Hawai'i, using fledgling fallout data. *Marine Ornithology* 48: 23–26.
- RAINE, A.F., BOONE, M., MCKOWN, M. & HOLMES, N. 2017b. The breeding phenology and distribution of the Band-rumped Storm petrel *Oceanodroma castro* on Kaua'i and Lehua Islet, Hawaiian Islands. *Marine Ornithology* 45: 73–82.
- RAINE, A.F., HOLMES, N.D., TRAVERS, M., COOPER, B.A. & DAY, R.H. 2017a. Declining population trends of Hawaiian Petrel and Newell's Shearwater on the island of Kaua'i, Hawai'i, USA. *The Condor* 119: 405–415.
- RAINE, A.F., VYNNE, M. & DRISKILL, S. 2019. The impact of an introduced avian predator, the Barn Owl *Tyto alba*, on Hawaiian seabirds. *Marine Ornithology* 47: 33–38.
- RAUZON, M.J. 1991. Save our shearwaters! *Living Bird Quarterly* 10: 28–32.
- REYNOLDS, M.H. & RITCHOTTE, G.I. 1997. Evidence of Newell's Shearwater breeding in Puna District, Hawaii. *Journal of Field Ornithology* 68: 26–32.
- RODRÍGUEZ, A., MOFFETT, J., REVOLTÓS, A. ET AL. 2017. Light pollution and seabird fledglings: Targeting efforts in rescue programs. *Journal of Wildlife Management* 81: 734–741.
- RODRÍGUEZ, A., RODRÍGUEZ, B., CURBELO, Á.J., PÉREZ, A., MARRERO, S. & NEGRO, J.J. 2012a. Factors affecting mortality of shearwaters stranded by light pollution. *Animal Conservation* 15: 519–526.
- RODRÍGUEZ, A., RODRÍGUEZ, B. & LUCAS, M.P. 2012b. Trends in numbers of petrels attracted to artificial lights suggest population declines in Tenerife, Canary Islands. *Ibis* 154: 167–172.
- RODRÍGUEZ, B., RODRÍGUEZ, A., SIVERIO, F., MARTÍNEZ, J.M., SACRAMENTO, E. & ACOSTA, Y. 2022. Introduced predators and nest competitors shape distribution and breeding performance of seabirds: feral pigeons as a new threat. *Biological Invasions* 24: 1561–1573.
- SCHOFIELD, O., DUCKLOW, H.W., MARTINSON, D.G., MEREDITH, M.P., MOLINE, M.A. & FRASER, W.R. 2010. How do polar marine ecosystems respond to rapid climate change? *Science* 328: 1520–1523. doi:10.1126/science.1185779
- SIMONS, T.R. & BAILEY, C.N. 2020. Hawaiian Petrel (*Pterodroma sandwichensis*), version 1.0. In: POOLE, A.F. & GILL, F.B. (Eds). *Birds of the World*. Ithaca, USA: Cornell Lab of Ornithology. doi:10.2173/bow.hawpet1.01
- SPEAR, L.B., AINLEY, D.G., NUR, N. & HOWELL, S.N.G. 1995. Population size and factors affecting at-sea distributions of four endangered procellariids in the tropical Pacific. *The Condor* 97: 613–638.
- SPEAR, L.B., AINLEY, D.G. & WALKER, W.A. 2007. Foraging dynamics of seabirds in the eastern tropical Pacific Ocean. *Studies in Avian Biology* 35: 1–99.
- SPRINGER, A.M. & VAN VLIET, G.B. 2014. Climate change, pink salmon, and the nexus between bottom-up and top-down forcing in the subarctic Pacific Ocean and Bering Sea. *Proceedings of the National Academy of Sciences* 111: E1880–E1888. doi:10.1073/pnas.1319089111
- STATE OF HAWAII'I. 2020. *Kaua'i Seabird Habitat Conservation Plan*. Honolulu, USA: State of Hawai'i Department of Land and Natural Resources, Division of Forestry and Wildlife.
- STEADMAN, D.W. 1995. Prehistoric extinctions of Pacific island birds: Biodiversity meets zooarchaeology. *Science* 267: 1123–1131.
- TELFER, T.C. 1981–1995. *Annual Job Progress Reports: Seabird Investigations, Statewide Non-game and Endangered Species Program, Project W-18-R-19, Job R-VI-A(a)*. Honolulu, USA: Hawai'i Department of Forest and Wildlife.
- TELFER, T.C., SINCOCK, J.L., BYRD, G.V. & REED, J.R. 1987. Attraction of Hawaiian seabirds to lights: Conservation efforts and effects of moon phase. *Wildlife Society Bulletin* 15: 406–413.
- TROY, J.R., HOLMES, N.D., VEECH, J.A. & GREEN, M.C. 2013. Using observed seabird fallout records to infer patterns of attraction to artificial light. *Endangered Species Research* 22: 225–234.
- URMSTON, J., HYRENBACH, K.D. & SWINDLE, K. 2022. Quantifying Wedge-tailed Shearwater (*Ardenna pacifica*) fallout after changes in highway lighting on Southeast O'ahu, Hawai'i. *PLoS One* 17: e0265832. doi:10.1371/journal.pone.0265832
- WOOD, S.N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society* 73: 3–36. doi:10.1111/j.1467-9868.2010.00749.x
- WOOD, S.N. 2017. *Generalized Additive Models: An Introduction with R, 2nd Edition*. New York, USA: CRC Press.