

Declining population trends of Hawaiian Petrel and Newell's Shearwater on the island of Kaua'i, Hawaii, USA

Authors: Raine, André F., Holmes, Nick D., Travers, Marc, Cooper, Brian A., and Day, Robert H.

Source: The Condor, 119(3) : 405-415

Published By: American Ornithological Society

URL: <https://doi.org/10.1650/CONDOR-16-223.1>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.



RESEARCH ARTICLE

Declining population trends of Hawaiian Petrel and Newell's Shearwater on the island of Kaua'i, Hawaii, USA

André F. Raine,^{1*} Nick D. Holmes,² Marc Travers,¹ Brian A. Cooper,^{3a} and Robert H. Day^{4b}

¹ Kaua'i Endangered Seabird Recovery Project, Hanapēpē, Kaua'i, Hawaii, USA

² Island Conservation, Santa Cruz, California, USA

³ ABR—Environmental Research & Services, Forest Grove, Oregon, USA

⁴ ABR—Environmental Research & Services, Fairbanks, Alaska, USA

^a Current address: Forest Grove, Oregon, USA

^b Current address: Fairbanks, Alaska, USA

* Corresponding author: araine6@hawaii.edu

Submitted November 26, 2016; Accepted March 30, 2017; Published June 7, 2017

ABSTRACT

The island of Kaua'i, Hawaii, USA, holds a large breeding populations of the endangered Hawaiian Petrel (*Pterodroma sandwichensis*) and a majority of the world population of the threatened Newell's Shearwater (*Puffinus newelli*). We evaluated island-wide population trends of both species. For Newell's Shearwaters, we considered radar counts at 13 sites between 1993 and 2013 and annual island-wide tallies of fledglings retrieved after being grounded by light attraction in 1979–2015 (Save Our Shearwaters [SOS] program). For Hawaiian Petrels, we considered radar counts alone. Radar data indicated a 78% decline overall in numbers of Hawaiian Petrels (at an average rate of ~6% per year) and a 94% decline overall in numbers of Newell's Shearwaters (at an average rate of ~13% per year) during the survey period. Most (92%) radar sites showed significant declines of Newell's Shearwaters across the entire survey period, as did 62% of sites for Hawaiian Petrels. The SOS recovery effort collected 30,522 Newell's Shearwater fledglings between 1979 and 2015. When we compared this dataset in pre- and post-Hurricane Iniki (September 1992) periods, we found a significant downward trend after Hurricane Iniki, similar to the trend seen in the radar data. The large-scale declines found in this study are not surprising, considering the significant threats facing both species on Kaua'i, which include powerline collisions, light attraction, introduced predators, and habitat modification—threats which were potentially exacerbated after Hurricane Iniki. Improved conservation initiatives and an increased understanding of the various threats facing the 2 species are key to reversing these declines.

Keywords: seabird, Hawaiian Petrel, monitoring, Newell's Shearwater, population trends, radar

Tendencias poblacionales decrecientes para *Pterodroma sandwichensis* y *Puffinus newelli* en la Isla de Kaua'i

RESUMEN

La isla de Kaua'i alberga grandes poblaciones reproductivas de la especie en peligro *Pterodroma sandwichensis* y la mayoría de la población mundial de la especie amenazada *Puffinus newelli*. Evaluamos las tendencias poblacionales de dos maneras para ambas especies en toda la isla. Para *P. newelli*, consideramos los conteos de radar en 13 sitios entre 1993–2013 y recuentos anuales en toda la isla de volantones recuperados después de ser atraídos con luz a tierra entre 1979–2015 (Programa Salve Nuestras Pardelas [SNP]); para *P. sandwichensis*, consideramos solamente los conteos de radar. Los datos de radar indican una disminución global del 78% en el número de individuos de *P. sandwichensis* (a una tasa promedio anual de 6%) y una disminución global del 94% en el número de individuos de *P. newelli* (a una tasa promedio anual de 13%) durante el período de muestreo. La mayoría (92%) de los sitios de radar mostraron disminuciones significativas para *P. newelli* a lo largo de todo el período de muestreo, así como para el 62% de los sitios para *P. sandwichensis*. El esfuerzo de recuperación del programa SNP colectó 30,522 volantones de *P. newelli* entre 1979 y 2015. Cuando comparamos este set de datos entre los períodos previo y posterior al Huracán Iniki (septiembre 1992), encontramos una tendencia decreciente significativa luego del Huracán Iniki, similar a la tendencia vista en los datos de radar. Las disminuciones a gran escala encontradas en este estudio no son sorprendentes, considerando las amenazas significativas que enfrentan las especies en Kaua'i, que incluyen colisiones con líneas eléctricas, atracción de la luz, depredadores introducidos y modificación del hábitat—amenazas que se han visto potencialmente exacerbadas luego del Huracán Iniki. Es fundamental contar con iniciativas de conservación mejoradas y con un mejor entendimiento de las múltiples amenazas que enfrentan las dos especies para revertir esta disminución.

Palabras clave: aves marinas, monitoreo, *Pterodroma sandwichensis*, *Puffinus newelli*, radar, tendencias poblacionales

INTRODUCTION

The Hawaiian island of Kaua'i holds internationally important populations of 2 endangered seabird species—the Hawaiian Petrel (*Pterodroma sandwichensis*; 'Ua'u in Hawaiian) and the Newell's Shearwater (*Puffinus newelli*; 'A'o in Hawaiian). The Newell's Shearwater was thought to be extinct until it was rediscovered in 1947, and was only confirmed to be breeding on Kaua'i 2 decades later, in 1967 (Sincock and Swedberg 1969). Kaua'i holds a significant proportion of the breeding population of the Hawaiian Petrel (Ainley et al. 1997) and the majority of the remaining breeding populations of Newell's Shearwater (Harrison 1990, Day and Cooper 1995, Spear et al. 1995).

Both species share threats common to Hawaiian birds, including collisions with powerlines (Cooper and Day 1998, Podolsky et al. 1998, Ainley et al. 2001, Travers et al. 2014); attraction of fledglings to artificial lights, where they then die after grounding due to predation, collisions with infrastructure, dehydration, and starvation (Reed et al. 1985, Telfer et al. 1987, Ainley et al. 1997, Cooper and Day 1998, Rodríguez et al. 2017); predation by introduced predators, particularly feral cats (*Felis catus*), feral pigs (*Sus scrofa*), Barn Owls (*Tyto alba*), black rats (*Rattus rattus*), and Polynesian rats (*Rattus exulans*; Ainley et al. 2001, Hodges and Nagata 2001, Raine and Banfield 2015a, 2015b); diseases such as avian pox and avian malaria (Warner 1968, Simons 1985, VanderWerf and Young 2016); and habitat modification within breeding colonies due to invasive plants and pigs (Duffy 2010, VanZandt et al. 2014). These seabirds also undoubtedly face threats at sea that, while poorly known, are recognized to be important issues for similar species worldwide and could include marine pollution (Sileo et al. 1990, Derraik 2002), plastic ingestion (Kain et al. 2016), overfishing (Ainley et al. 2014), and the effects of climate change and fisheries bycatch (Gilman et al. 2008). Based on a combination of many of these factors, the Hawaiian Petrel is listed under the U.S. Endangered Species Act as Endangered and the Newell's Shearwater as Threatened (USFWS 1983). On the IUCN Red List, the Hawaiian Petrel is listed as Vulnerable (BirdLife International 2016a) and the Newell's Shearwater as Endangered (BirdLife International 2016b).

Most breeding colonies of both species are concentrated in areas that are remote and difficult to access, particularly in the northwestern section of Kaua'i (Ainley and Holmes 2011, Kaua'i Endangered Species Recovery Program [KESRP], <http://kauaiseabirdproject.org/index.php/the-birds/>). However, monitoring population trends is critical for an understanding of the current conservation needs of the 2 species and to assess whether the significant population declines of the Newell's Shearwater described between 1993 and 2001 (Day et al. 2003a) have continued. It is equally important to assess long-term population

trends for the Hawaiian Petrel because recent genetic work has indicated strong genetic differentiation between populations on the islands of Hawaii and Kaua'i (Wiley et al. 2012), increasing the importance of understanding the population trends of this species at an island level. Remote nesting sites and nocturnal habits make it challenging to monitor these populations, but radar has proved to be a highly effective method (e.g., Day and Cooper 1995, Cooper and Day 2003, Day et al. 2003a, 2003b, Gauthreaux and Belser 2003, Burger et al. 2004, Cooper et al. 2006, Bertram et al. 2015). This technique also has been used extensively in the past for surveying both Hawaiian Petrels and Newell's Shearwaters on most of the southeastern Hawaiian Islands, including Kaua'i (Day and Cooper 1995, Reynolds et al. 1997, Cooper and Day 2003, Day et al. 2003a, 2003b, Swift and Burt-Toland 2009). Here, we combine radar data used by Day et al. (2003b) and more recent data from contemporary radar surveys to assess long-term trends for the 2 species on Kaua'i.

We also use a second, complementary dataset to assess long-term population trends of Newell's Shearwaters based on the "fallout" of fledglings collected over 37 yr by the "Save Our Shearwaters" (SOS) program on Kaua'i. The SOS is a citizen conservation program created by the State of Hawaii's Department of Land and Natural Resources, Division of Forestry and Wildlife, in 1979; its primary focus has been to collect and release seabirds grounded by light pollution, which fledgling Newell's Shearwaters are particularly affected by (Reed et al. 1985, Telfer et al. 1987, Ainley et al. 1997, Cooper and Day 1998). Hawaiian Petrels also are found by the project, but in such low numbers annually that they do not provide useful trend data.

The objectives of this study were threefold. First, we assessed whether the long-term population decline of the Newell's Shearwater found in previous studies continued in the following 2 decades. Second, we assessed whether the Hawaiian Petrel followed a similar declining trend on Kaua'i. These analyses update those presented in Ainley et al. (2001) and Day et al. (2003b). Finally, we used the most recent radar data collected to assess the contemporary distribution of the 2 species on the island, to allow us to focus future conservation planning and effort.

METHODS

Visual Sampling

We conducted visual sampling at 6 of the radar survey sites (Kekaha, Waimea, 'Ele'ele, Wailua, Keālia, and Hanalei; Figure 1) in 2012 and 2013 to count and identify all birds passing overhead. Observers detected birds and, during daylight hours, used binoculars as needed for identification purposes. After dark, night-vision goggles (model PVS-7, Generation 3, 40° field of view, 1× magnification; U.S.

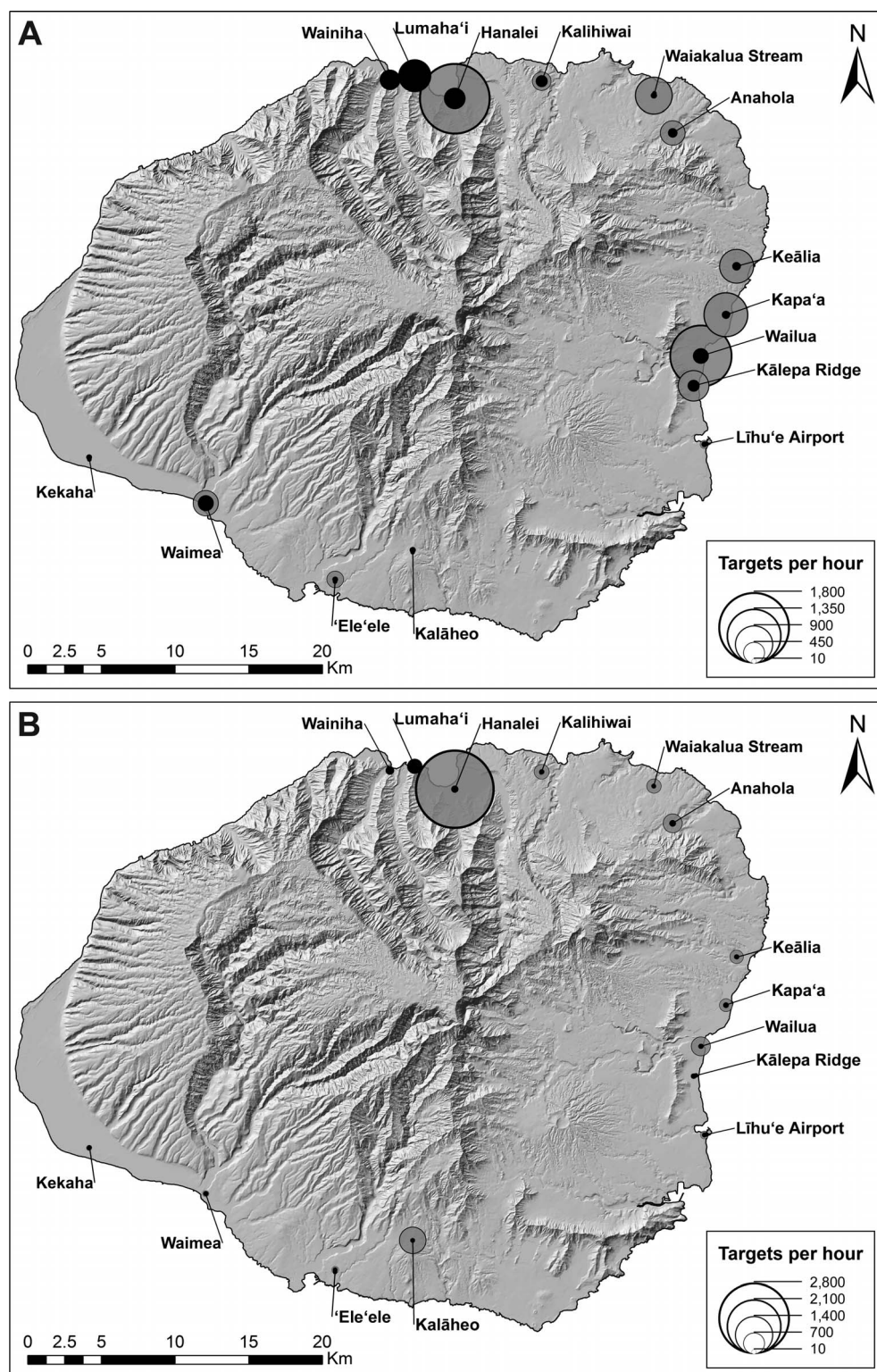


FIGURE 1. (A) Mean movement rate (targets hr^{-1}) of radar targets during session 2 (Hawaiian Petrel) recorded at each survey site on Kaua'i Island, Hawaii, USA, in 1993 (gray circles) and 2013 (black circles). (B) Mean movement rates (targets hr^{-1}) of radar targets during sessions 3 and 4 combined (Newell's Shearwater) recorded at each survey site on Kaua'i Island in 1993 (gray circles) and 2013 (black circles). See Figure 2 for explanation of radar sessions. Note that no data are available for Wainiha and Lumaha'i in 1993. Contemporary breeding distributions of both species are now concentrated in the northwest of the island.

Night Vision, Roseville, California, USA) were used to identify and count birds passing overhead. Near-infrared illuminators (Raymax 300 Platinum; Raytec, Ashington, Northumberland, UK) were used to increase night-vision capabilities and helped to ensure consistent light levels and night-vision monitoring across sites and nights that varied in ambient light levels. We standardized the area sampled by only counting birds that flew between 2 measured points (adjacent power poles). All birds that flew between the poles were included, regardless of flight altitude (i.e. birds flying high, but between the poles, were also counted). The monitoring distance was deliberately kept narrow (100–200 m) so that observers could effectively monitor the entire airspace, regardless of light levels or optical tool being used, thus ensuring that detection distance was not biased toward daylight hours or a particular species. Visual surveys were conducted in the same manner as radar surveys (see below), starting 15 min before sunset and running for 2 hr, divided into 4 consecutive 30-min sampling sessions (sessions 1–4). Unlike the radar surveys, they were conducted continuously throughout the whole 2-hr period. Surveys were conducted by the same 3 observers in both years.

Birds were identified to species whenever possible by observers trained in identification techniques for all species likely to be found on Kaua'i. Birds were counted only if they were deemed to be in transit—that is, flying in a direct and steady route over a long distance (the same characteristics used for radar surveys). We did not count birds observed to take off or land. Species, time, and flight direction were noted using voice recorders to allow the visual observers to watch the sky continuously. We used these data to assess when peak movement rates occurred for Hawaiian Petrels and Newell's Shearwaters.

Radar Sampling

On Kaua'i, ornithological radar has been used to monitor the summer movement patterns of Hawaiian Petrels and Newell's Shearwaters at 13 sites since 1993 (Figure 1), with repeat surveys occurring in 1999–2001, 2004–2010, and 2012–2013. In 1999, we added 2 radar sites on the North Shore (Lumaha'i and Wainiha) to obtain more data from the northern part of the island, where some of the largest populations of these species remain (Ainley and Holmes 2011, <http://kaua seabirdproject.org/index.php/the-birds/>, R. Day and B. Cooper personal observations). Following Day and Cooper (1995), radar sites were located at the mouths of all accessible major drainages around the island. The only area on Kaua'i that was not covered by these surveys was the northwestern part of the island (the Nāpali coast, where Newell's Shearwater colonies are known to exist; <http://kaua seabirdproject.org/index.php/the-birds/nesh-fact-sheet/>), due to its inaccessibility to a truck-mounted radar unit.

Radar operation and target identification followed the protocol outlined in Day and Cooper (1995) and Day et al. (2003b). We used an FR1510MK3 radar unit (FURUNO, Camas, Washington, USA) mounted horizontally on top of a truck and tilted upward at an angle of 10°, with a 38.1-cm (15-in) radar screen inside the vehicle. This was an X-band radar transmitting at 9.410 GHz, with a peak power output of 12 kW (10 kW in 1993). The pulse setting was set to 0.07 μ sec, the antenna spun at a rate of 24 rpm, and the range setting was 1.5 km.

Surveys were conducted each year from late May to mid-July. Based on burrow-monitoring data from colonies on Kaua'i, this period covered the egg laying, incubation, and early hatching stages of both species on the island (<http://kaua seabirdproject.org/index.php/the-birds/>). Surveys prior to 2006 started at 1900 hours (typically 10–25 min before sunset). For analysis we recalculated these data from 15 min before sunset for 2 hr. Surveys from 2006 onward started 15 min prior to sunset, thus standardizing the 2-hr survey period to timing of sunset, avoiding bias associated with variability in available light. From 2006 onward, we also surveyed a subset of 7 of the 13 sites on 3 nonconsecutive nights to estimate among-night variation in movement rates; for these surveys, the average number of targets over the 3 surveys was used in regression analyses. Due to the 1-mo period in which all surveys had to be conducted, we could not survey all sites for 3 nights each.

Each survey consisted of 4 consecutive 30-min sampling sessions (sessions 1–4). We used the first 5 min of each sampling session to collect weather data, then counted targets for 25 min. Targets were recorded only when moving at a velocity ≥ 48 km hr⁻¹, which is the ground-speed of >99% of all Newell's Shearwaters and Hawaiian Petrels unless they are climbing steeply, and also excluded other bird species potentially flying in the area during the radar period (Day and Cooper 1995). For all targets recorded, we collected time, number of targets, cardinal transect crossed (north, south, east, west), flight direction (to the nearest 10°), minimum distance from the radar truck (to the nearest 100 m), velocity (to the nearest 8 km hr⁻¹), and flight behavior (straight-line, erratic, or circling; for examples of these flight behaviors, see Day et al. 2015:370). For analysis, we only included targets flying inland.

The only exceptions to this protocol were at the 3 northernmost sites (Hanalei, Lumaha'i, and Wainiha), where steep terrain lies immediately adjacent to the ocean. Here, visual observations have indicated that seabirds transiting over these areas need to gain elevation rapidly, and thus appear to fly more slowly than elsewhere on Kaua'i (Day and Cooper 1995, Ainley et al. 1997). At these sites, the projected speed on radar can sometimes appear to be <48 km hr⁻¹ because the radar's 2-dimensional

screen projects only horizontal distance covered and not total horizontal plus vertical distances combined. At these 3 sites, targets moving at 40 km hr^{-1} were also included when their behavior indicated that they were seabirds moving inland.

Clear plastic transparencies were overlaid on the radar screen, and major features of topography, radar shadows, and bird traffic were drawn in most years of radar surveys. These transparencies were compared for all sites between the earlier surveys and surveys after 2006 to assess whether there were any significant changes in radar coverage that might have affected counts of targets. The only site where radar coverage changed was Hanalei, where the location of the survey site had to be moved to the east $\sim 1.5 \text{ km}$ because the original location eroded into the sea. To account for this change, the subsequent data collection strategy required using only half of the radar screen to ensure that only the portion of the original flyway covered in earlier surveys was sampled. To test any impact on results, we undertook analyses with and without the Hanalei site.

We did not survey when rain or other forms of clutter such as insects obscured potential radar targets (i.e. if $>20\%$ of the display screen was obscured for more than 1 min). During these conditions, we stopped surveys until conditions improved. If $<10 \text{ min}$ of sampling time (excluding the collection of weather data) was conducted between 15 and 45 min after sunset, we canceled the entire sampling session and returned the following day.

"Save Our Shearwaters" Data

The SOS program is a state-run project based at the Kaua'i Humane Society. The ongoing project collects and releases endangered seabirds and other bird species. The SOS program was initiated in 1979; thus, it represents a continuous dataset of 37 yr, with 30,552 fledgling Newell's Shearwaters collected to date. We used this second, independent dataset to assess long-term population trends of Newell's Shearwaters from fledglings collected annually. Adults are less attracted to lights on the coast (Ainley et al. 2001, Duffy 2010), and are only sporadically recovered by SOS. Likewise, too few Hawaiian Petrel fledglings or adults are collected every year to allow for any meaningful trend analysis.

Data Analyses

We conducted all statistical analyses with Excel 2013 (Microsoft, Redmond, Washington, USA) and SPSS Statistics 23 (IBM, Armonk, New York, USA).

For the radar data, we calculated linear regressions on log-transformed data to test for change in mean movement rates by year over the 20-yr period and for each site individually over the entire 20-yr period, and used paired t -tests to compare mean movement rates at each site

between the first and last years of the study. We conducted linear regression analyses on log-transformed data with and without the Hanalei radar site. We also conducted the linear regression analysis with and without data from 1993, the year after Hurricane Iniki devastated Kaua'i. Day and Cooper (1995) and Day et al. (2003a) suggested that seabird populations may have had unusually high productivity in 1993 following the poor 1992 breeding season caused by the hurricane, potentially resulting in abnormally high numbers that year.

For the SOS data, we calculated linear regressions on log-transformed data to test for changes in the numbers of fledgling Newell's Shearwaters collected by the project every fall season during 2 periods: (1) 1979 to 1991 (pre-Hurricane Iniki), and (2) 1992–2015 (post-Hurricane Iniki).

We present the slope for site-specific regressions by back-transforming the slope from regression equations. For all tests, we used $\alpha = 0.05$ for statistical significance. Means are presented \pm standard error (SE).

RESULTS

Visual Data

Observers recorded 1,279 birds during visual surveys between May and October of 2012 and 2013. Of these, 114 were identified as Hawaiian Petrels, 678 were Newell's Shearwaters, and 487 were nonseabird targets, including 347 Cattle Egrets (*Bubulcus ibis*), 124 songbirds of various species, and 16 Hawaiian Ducks (*Anas wyvilliana*). Bird movements during session 1 consisted primarily of non-seabird targets, which were the numerically dominant birds in the sky between 15 min before and 20 min after sunset; they composed 95% of all targets during session 1. No Hawaiian Petrels were observed prior to sunset, and only 6% and 14% of all Hawaiian Petrels were recorded by 10 and 15 min after sunset, respectively. No Newell's Shearwaters were observed prior to 20 min after sunset. By 21 min after sunset, all movement was numerically dominated by either Hawaiian Petrels or Newell's Shearwaters (Figure 2). Peak movement of Hawaiian Petrels was centered on the end of civil twilight (23 min after sunset), when the sun is 6° below the horizon, whereas the peak movement of Newell's Shearwaters was centered on nautical twilight (52 min after sunset), when the sun is 12° below the horizon.

We excluded session 1 data from further analysis because it contained mainly nontarget bird species and did not encompass the movement periods of petrel and shearwater targets, apart from the very end of that session, when Hawaiian Petrels began moving. Session 2 constituted the vast majority of Hawaiian Petrel targets and included the peak period of this species' inbound movements (with Newell's Shearwater movements beginning toward the end

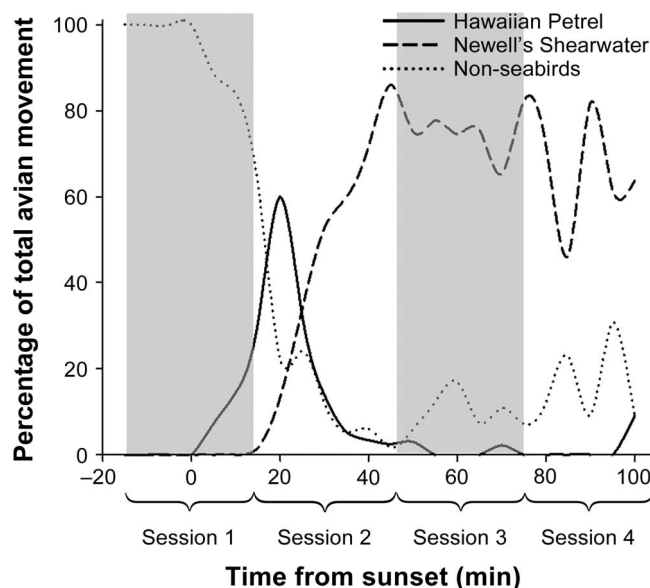


FIGURE 2. Percentages of avian movement by time, based on visual observations, on Kaua'i Island, Hawaii, USA, 2012–2013. Sampling (visual and radar surveys) started 15 min before sunset and ran for 2 hr, divided into 4 consecutive 30-min sampling sessions. Shaded and unshaded areas depict, in order, session 1 (which was excluded from all further analysis because it consisted almost entirely of nontarget species), session 2, session 3, and session 4.

of the session). Sessions 3 and 4 consisted almost exclusively of Newell's Shearwaters. We used data from session 2 to assess trends in radar detections for Hawaiian Petrels and data from sessions 3 and 4 to assess trends in radar detections for Newell's Shearwaters. Because similar patterns in the timing of movements of both species were recorded on Kaua'i in the 1990s (Day and Cooper 1995), we assume that species-specific timing of movement did not change over the time series.

Radar Trends—Hawaiian Petrel

Movement rates of Hawaiian Petrels in 2013 were highest on the North Shore (Figure 1A). The 3 sites with the highest movement rates in 2013 were Hanalei, Wainiha, and Lumaha'i, all on the North Shore. The 3 sites with the lowest movement rates were 'Ele'ele, Kekaha, and Kalāheo, all on the South Shore. To examine the change in passage rates from 1993 to 2013, we included the 13 sites surveyed over the entire study period (i.e. excluding Lumaha'i and Wainiha, which were not surveyed in 1993). The overall mean movement rate across all 13 sites combined dropped ~78%, from 654 ± 145 targets hr^{-1} in 1993 to 143 ± 36 targets hr^{-1} in 2013. A paired t -test revealed a significant decline for individual sites ($t_{24} = 3.43$, $P < 0.002$).

A linear regression showed a strongly significant decline over the period 1993–2013 ($y = -0.028x + 2.811$, $r^2 = 0.71$, $F_{11} = 26.26$, $P < 0.001$; Figure 3). Back-transforming the

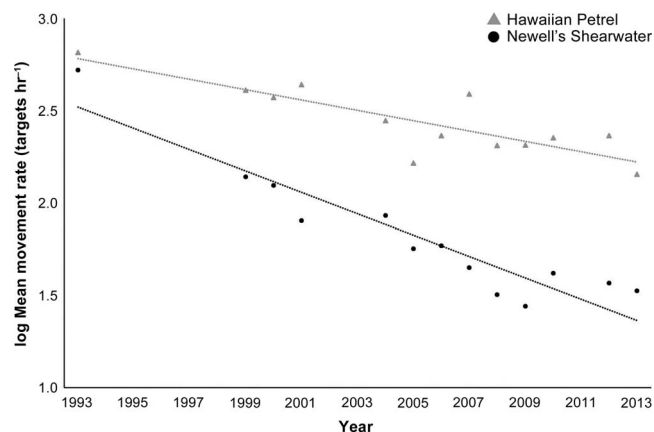


FIGURE 3. Linear regressions of log-transformed mean movement rates (targets hr^{-1} from 13 sites surveyed since 1993) recorded by radar during session 2 (Hawaiian Petrel) and sessions 3 and 4 combined (Newell's Shearwater). See Figure 2 for explanation of sessions.

slope gave a lambda of 0.938, or an average decline of ~6% per year. The same decline remained significant when Hanalei was removed from the analysis ($F_{11} = 21.14$, $P = 0.001$). Removing 1993 as a potential outlier from the analysis also did not change the relationship ($F_{10} = 12.44$, $P = 0.005$). Eight of 13 (62%) sites showed significant declines across the entire study period (Table 1). Three southern sites (Kalāheo, Waimea, and Kekaha) did not show significant differences in movement rates over the time period, presumably because movement rates at these sites were already low when the surveys began in 1993.

Radar Trends—Newell's Shearwater

As with Hawaiian Petrels, movement rates of Newell's Shearwater in 2013 were highest on the North Shore (Figure 1B). The 3 sites with the highest movement rates in 2013 were Lumaha'i, Wainiha, and Hanalei, all on the North Shore. The 3 sites with the lowest movement rates were 'Ele'ele, Kalāheo, and Kekaha, all on the South Shore. To examine the change in passage rates from 1993 to 2013, we included the 13 sites surveyed over the entire study period (excluding Lumaha'i and Wainiha). The overall mean movement rate across all 13 sites dropped ~94% from 524 ± 207 targets hr^{-1} in 1993 to 34 ± 9 targets hr^{-1} in 2013. A paired t -test revealed a significant decline for individual sites ($t_{24} = 2.37$, $P = 0.03$).

A linear regression on the log-transformed data showed a strongly significant decline over the period 1993–2013 ($y = -0.058x + 2.577$, $r^2 = 0.88$, $F_{11} = 81.64$, $P < 0.001$; Figure 3). Back-transforming the slope gave a lambda of 0.875, or an average decline of ~13% per year. The same decline remained statistically significant when the Hanalei site was removed from the analysis ($F_{11} = 54.30$, $P < 0.001$). Removing 1993 as a potential outlier from the analysis also

TABLE 1. Results of individual site linear regressions of log-transformed radar targets recorded during session 2 (Hawaiian Petrel) and sessions 3 and 4 combined (Newell's Shearwater) on Kaua'i Island, Hawaii, USA, between 1993 and 2013. *ns* = not significant. See Figure 2 for explanation of sessions.

Site	Hawaiian Petrel			Newell's Shearwater		
	Slope	r^2	P	Slope	r^2	P
Hanalei	0.925	0.72	<0.001	0.833	0.85	0.001
Kalihiwai	0.956	0.62	0.002	0.811	0.68	0.001
Waiakalua Stream	0.889	0.61	0.005	0.822	0.51	0.01
Anahola	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>
Keālia	0.926	0.61	0.002	0.870	0.82	<0.001
Kapa'a	0.943	0.61	0.002	0.922	0.43	0.02
Wailua	0.940	0.36	0.03	0.881	0.52	0.008
Kālepa Ridge	<i>ns</i>	<i>ns</i>	<i>ns</i>	0.919	0.59	0.01
Līhu'e Airport	0.953	0.31	0.06	0.896	0.61	0.005
Kalāheo	<i>ns</i>	<i>ns</i>	<i>ns</i>	0.839	0.54	0.01
'Ele'ele	0.917	0.44	0.01	0.855	0.62	0.001
Waimea	<i>ns</i>	<i>ns</i>	<i>ns</i>	0.911	0.35	0.03
Kekaha	<i>ns</i>	<i>ns</i>	<i>ns</i>	0.911	0.64	0.02

indicated a significant negative relationship between 1999 and 2013 ($F_{10} = 48.35$, $P < 0.001$). Twelve of 13 (92%) sites showed statistically significant declines across the entire study period (Table 1).

SOS Fallout Data

A total of 30,552 Newell's Shearwater fledglings was collected by the SOS program between 1979 and 2015. Before Hurricane Iniki in 1992, annual numbers varied between 2,235 and 1,141 (average: $1,511 \pm 79$), but with no trend ($r^2 = 0.003$, $F_{11} = 2.26$, $P > 0.05$; Figure 4). From 1992 (the year of Hurricane Iniki) to 2015, numbers declined strongly, from 955 to 157 annually ($r^2 = 0.91$, $F_{22} = 250.25$, $P < 0.001$; Figure 4).

DISCUSSION

Long-term monitoring data are critical for making informed decisions about threatened species (Yoccoz et al. 2001), and monitoring should be undertaken over biologically relevant timeframes (Beltran et al. 2014). For long-lived species with low fecundity, like many seabirds, decades of repeated measurements may be required before biological trends become evident. We were able to use 21 yr of radar data and 37 yr of data on fledglings rescued by the SOS program to assess trends in the abundance of 2 endangered seabirds on the island of Kaua'i. Ornithological radar surveys provided insights into the annual numbers of adult Hawaiian Petrels and Newell's Shearwaters flying from the ocean to inland breeding grounds during the peak seasonal period of incubation. Likewise, analysis of trends from the 37-yr dataset of the SOS program highlighted changes in the numbers of fallout-related fledglings of Newell's Shearwaters (i.e. reproductive output). These 2 datasets offered an island-scale view over

multiple generations, allowing us to determine population trends and the current conservation status of these 2 species.

Radar data clearly indicated that both seabird species have experienced long-term population declines across the island during the last 21 yr, regardless of whether data from the (possibly) high production year of 1993 were included in the analysis. By stratifying these data into periods that encapsulated nightly movement patterns for each species, we were able to conclude that the decline was not restricted to Newell's Shearwaters but was also occurring in Hawaiian Petrels. For survey session 2, which included most of the Hawaiian Petrel movements recorded during visual surveys, radar sites experienced a 78%

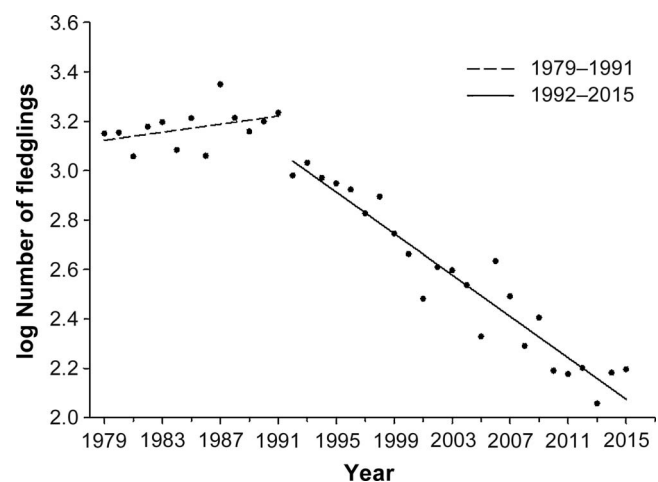


FIGURE 4. Linear regressions showing the annual numbers of fledgling Newell's Shearwaters recovered by the "Save Our Shearwaters" program on Kaua'i Island, Hawaii, USA, before Hurricane Iniki (1979–1991) and from the year of the hurricane onward (1992–2015).

reduction in radar targets between 1993 and 2013. For sessions 3 and 4 combined, which encompassed the movements of most of the Newell's Shearwaters, radar sites experienced a 94% reduction in radar targets over the same period. These patterns were true both for the entire 21-yr period and for 1999 onward (i.e. with the initial, possibly high, production year of 1993 removed). In all instances, radar detections were recorded primarily at radar sites in the western part of northern Kaua'i, particularly in the Wainiha, Lumaha'i, and Hanalei valleys. This part of Kaua'i is known to be the primary remaining stronghold of both species on the island. In contrast, radar sites in the southern parts of the island recorded few targets. Several formerly large colonies in these areas, such as those at Kalāheo and Kaluahonu, have declined dramatically in recent decades and now face localized colony extinction (A. Raine and N. Holmes personal observations).

For the Newell's Shearwater, the markedly steep decline is consistent with earlier published work (i.e. Ainley et al. 1997, 2001, Day et al. 2003b). For the Hawaiian Petrel, however, the results of our analyses differ from those of Day et al. (2003a), who suggested that populations of this species had possibly increased over the period 1993–2001. Our revised results reflect the reanalysis of the early dataset to ensure that the starting times for all radar sessions were standardized relative to sunset. This approach standardized the radar data on a nightly basis, and thus changed the overall time periods encompassed by the radar sessions. As highlighted by our data collected by visual observers, 95% of the session 1 radar data was composed of nontarget birds, and thus data from this session were excluded. Session 2 clearly encapsulated the peak of inbound movements of Hawaiian Petrel targets, and sessions 3 and 4 primarily captured Newell's Shearwater movements. Therefore, we suggest that our reanalysis of the data more accurately reflects Hawaiian Petrel trends through time. That the Hawaiian Petrel population on Kaua'i is suffering a decline comparable with that of the Newell's Shearwater is not surprising. On Kaua'i, this species nests in habitats similar to those used by the Newell's Shearwater and faces the same suite of threats.

The decline in radar-based population counts for both species is dramatic and indicates 2 decades of decline on Kaua'i. The decline in radar-based counts of Newell's Shearwaters is also mirrored in the numbers of fledgling Newell's Shearwaters recovered by the SOS program since its inception in 1979. In the 1980s, the project was processing on average 1,495 fledglings yr^{-1} , with a high of 2,235 fledglings in 1987. That number has declined since then by an order of magnitude, with an average of only 146 fledglings yr^{-1} processed since 2010. The SOS data also suggest that the decline may have commenced in earnest

after Hurricane Iniki hit the island in 1992. While it is unlikely that the hurricane itself caused direct mortality of adults, as it struck the island during the day while adults were out at sea, it could have had knock-on effects on these seabird populations. These effects could include increased impacts of introduced predators (by opening up ingress routes into the remote interior), habitat modification (by encouraging the spread of introduced plants into the interior), and powerline collisions (due to infrastructure change, or the removal of considerable vegetation shielding powerlines after large trees were blown over).

It is appropriate to assess whether other factors may be responsible for the apparent trends. For the radar data, methodologies and equipment capabilities have remained constant throughout the time series, radar operators have been trained with the same protocols, and vegetation and topography have remained constant at all but one site (i.e. there have been no significant changes in tree heights that could have added new radar shadows to the sites). Only the Hanalei site changed to some degree, and overall population trends were the same with or without this location. Thus, we do not expect our results to be an artifact of methodology or survey site changes over time.

For the SOS data, an alternative hypothesis is that reduced numbers of Newell's Shearwater fledglings collected over time reflect reduced light pollution threat (i.e. levels of light pollution have decreased over time, thereby decreasing fallout). Although it is true that, in recent years, some private businesses and Kaua'i County itself have decreased light pollution in certain areas through shielding, removed "problem" lights where many birds were grounded, and reduced overall light intensity (particularly during the fledging period), recent analyses of light levels on the island of Kaua'i continue to show high levels of artificial light around coastal areas (Troy et al. 2011, 2013). Hence, there still are very few places on Kaua'i where a fledgling seabird would not be exposed to artificial light as it headed out to sea (Troy et al. 2013). In addition, the correlation of radar as a second independent dataset counters this hypothesis and strongly indicates that the decline of Newell's Shearwater is a real trend.

During our study period, several conservation projects to benefit both species were undertaken, such as control of introduced predators and powerline- and light-minimization projects; however, significant threats still exist. Predator control will reduce predation, but will not eliminate it (Cromarty et al. 2002), and mortality does still occur at seabird colonies receiving this conservation intervention, albeit at a lower rate (Raine and Banfield 2015a, 2015b). Both species are also targeted regularly by introduced Barn Owls, which are frequently seen hunting for seabirds over breeding colonies when the 2 focal species are returning inland to their burrows (A. Raine, N. Holmes, R. Day, and B. Cooper personal observations).

Recent monitoring of powerline collisions in key areas indicates that this remains a critical threat to the species as well, particularly at cross-island powerlines (Ainley et al. 2001, Travers et al. 2016). Therefore, while each of these conservation actions represent an important positive contribution toward the recovery potential of these threatened seabirds, they must be increased in scope, scale, and impact to reverse the declines and allow recovery.

Radar surveys will continue to be an important method for assessing island-wide population trends for both species on Kaua'i into the future. The inclusion of the Nāpali Coast (which is known to hold large colonies of Newell's Shearwater; A. Raine and N. Holmes personal observations) in future radar surveys would be an important addition to this monitoring program. This area is inaccessible to radar mounted on trucks, but could be surveyed by slinging in a radar unit via helicopter and then mounting it on a tripod. Likewise, the SOS program represents both an important monitoring technique and a conservation tool for rehabilitating and releasing downed fledglings that face a high risk of mortality from predation, being run over by cars, or dehydration and starvation if they are not recovered and released at sea.

Conservation efforts should focus on reducing powerline collisions and light-attraction issues, controlling introduced predators, and creating protected colonies within predator-proof fences, and should focus on the locations with the greatest remaining concentrations of birds in northwestern Kaua'i. This effort should include the installation of predator-proof fences encompassing colonies in upper montane areas wherever logistically feasible, and the creation of new colonies within predator-proof fences using assisted-colonization techniques, such as social attraction and chick translocation (Miskelly et al. 2009), in more accessible areas, such as the recent Nihoku Ecosystem Restoration Project at Kilauea National Wildlife Refuge on the northern shore of Kaua'i. Continued and long-term investment in conservation actions at both montane colonies and lowland translocation sites is critical for the success of these important conservation measures. Finally, refugia free of lights, powerlines, and predators should also be considered via the eradication of introduced predators and assisted colonization techniques at locations such as Lehua Islet and Moku'ae'ae Rock Islet, to ensure that a component of the population can persist in areas free of nonnative predators, powerlines, and artificial light sources.

ACKNOWLEDGMENTS

We thank the hard work and dedication of Jessi Hallman Behnke, Kyle Wright, Amy Shipley, Tom Savre, Harrison Hyatt, Emily Haber, and Trevor Joyce, all of whom spent many

nights out in the radar truck collecting data. Matthew Boone, Amy Shipley, and Margaret Massey helped with aspects of data analysis and mapping. Work from 2006 onward was undertaken as part of the Kaua'i Endangered Seabird Recovery Project, which is a joint project of the Pacific Cooperative Studies Unit (PCSU) of the University of Hawaii and the Department of Land and Natural Resources, Division of Fish and Wildlife (DOFAW). We thank all staff at DOFAW and PCSU who helped to ensure that this work went ahead as planned, especially David Duffy at PCSU and Thomas Ka'iakapu at DOFAW. We also thank Tracy Anderson, Maddy Jacobs, and the staff at Save Our Shearwaters for their dedication in rescuing and rehabilitating endangered seabirds and other species on Kaua'i. This manuscript has been improved by the efforts of David Ainley, 2 anonymous reviewers, and the Associate Editor.

Funding statement: Funding for radar work carried out from 2006 onward was via a State Wildlife Grant from the U.S. Fish and Wildlife Service (USFWS). The Save Our Shearwaters project is currently (as of 2004) funded by the Kaua'i Island Utility Cooperative (KIUC) under their Short-term Habitat Conservation Plan and is based at the Kaua'i Humane Society. Prior to 2004 it was operated by the State of Hawaii. B.A.C.'s and R.H.D.'s research originally was funded by Kaua'i Electric, KIUC, USFWS, and the State of Hawaii. None of our funding organizations had any influence on the content of the submitted or published manuscript, and none required approval of the final manuscript to be published.

Ethics statement: All work carried out during the course of collecting the data for this paper was undertaken with full ethical consideration for the species under study and did not result in either direct or intentional harm to the study species. All radar work was completed under a license of Radio Station Authorization by the Federal Communications Commission, FCC Registration Number 0001513464.

Author contributions: All authors conceived the idea, design, and experiment, performed the experiments (collected data, conducted the research), wrote the paper or substantially edited the paper, and developed and/or designed the methods; A.F.R. analyzed the data; and A.F.R., N.H., B.A.C., and R.H.D. contributed substantial materials, resources, and/or funding.

LITERATURE CITED

- Ainley, D. G., and N. Holmes (2011). Species accounts for three endemic Hawaiian seabirds on Kaua'i: Hawaiian Petrel, Newell's Shearwater, and Band-rumped Storm-Petrel. H.T. Harvey & Associates Final Report to U.S. Fish and Wildlife Service, Pacific Islands Fish and Wildlife Office, Honolulu, HI, USA (unpublished report).
- Ainley, D. G., R. Podolsky, L. DeForest, and G. Spencer (1997). New insights into the status of the Hawaiian Petrel on Kauai. *Colonial Waterbirds* 20:24–30.
- Ainley, D. G., R. Podolsky, L. DeForest, G. Spencer, and N. Nur (2001). The status and population trends of the Newell's Shearwater on Kaua'i: Insights from modeling. In *Evolution, Ecology, Conservation, and Management of Hawaiian Birds: A Vanishing Avifauna* (J. M. Scott, S. Conant, and C. Van Riper, III, Editors). *Studies in Avian Biology* 22:108–123.

- Ainley, D. G., W. A. Walker, G. C. Spencer, and N. D. Holmes (2014). The prey of Newell's Shearwater *Puffinus newelli* in Hawaiian waters. *Marine Ornithology* 44:69–72.
- Beltran, R. S., N. Kreidler, D. H. Van Vuren, S. A. Morrison, E. S. Zavaleta, K. Newton, B. R. Tershy, and D. A. Croll (2014). Passive recovery of vegetation after herbivore eradication on Santa Cruz Island, California. *Restoration Ecology* 22:790–797.
- Bertram, D. F., M. C. Drever, M. K. McAllister, B. K. Schroeder, D. J. Lindsay, and D. A. Faust (2015). Estimation of coast-wide population trends of Marbled Murrelets in Canada using a Bayesian hierarchical model. *PLoS ONE* 10:e0134891. doi:10.1371/journal.pone.0134891
- BirdLife International (2016a). Species factsheet: *Pterodroma sandwichensis*. <http://www.birdlife.org>
- BirdLife International (2016b). Species factsheet: *Puffinus newelli*. <http://www.birdlife.org>
- Burger, A. E., T. A. Chatwin, S. A. Cullen, N. P. Holmes, I. A. Manley, M. H. Mather, B. K. Schroeder, J. D. Steventon, J. E. Duncan, P. Arcese, and E. Selak (2004). Application of radar surveys in the management of nesting habitat of Marbled Murrelets *Brachyramphus marmoratus*. *Marine Ornithology* 32:1–11.
- Cooper, B. A., and R. H. Day (1998). Summer behavior and mortality of Dark-rumped Petrels and Newell's Shearwaters at power lines on Kauai. *Colonial Waterbirds* 21:11–19.
- Cooper, B. A., and R. H. Day (2003). Movement of the Hawaiian Petrel to inland breeding sites on Maui Island, Hawai'i. *Waterbirds* 26:62–71.
- Cooper, B. A., M. G. Raphael, and M. Z. Peery (2006). Trends in radar-based counts of Marbled Murrelets on the Olympic Peninsula, Washington, 1996–2004. *The Condor* 108:936–947.
- Cromarty, P. L., K. G. Broome, A. Cox, R. A. Empson, W. M. Hutchinson, and I. McFadden (2002). Eradication planning for invasive alien animal species on islands – The approach developed by the New Zealand Department of Conservation. In *Turning the Tide: The Eradication of Invasive Species. Proceedings of the International Conference on Eradication of Island Invasives* (C. R. Veitch and M. N. Clout, Editors). Occasional Paper of the IUCN Species Survival Commission No. 27, IUCN SSC Invasive Species Specialist Group, IUCN, Gland, Switzerland. pp. 85–91.
- Day, R. H., and B. A. Cooper (1995). Patterns of movement of Dark-rumped Petrels and Newell's Shearwaters on Kauai. *The Condor* 97:1011–1027.
- Day, R. H., B. A. Cooper, and R. J. Blaha (2003a). Movement patterns of Hawaiian Petrels and Newell's Shearwaters on the island of Hawai'i. *Pacific Science* 57:147–159.
- Day, R. H., B. A. Cooper, and T. C. Telfer (2003b). Decline of Townsend's (Newell's) Shearwaters (*Puffinus auricularis newelli*) on Kauai, Hawaii. *The Auk* 120:669–679.
- Day, R. H., J. R. Rose, A. K. Prichard, and B. Streever (2015). Effects of gas flaring on the behavior of night-migrating birds at an artificial oil-production island, Arctic Alaska. *Arctic* 68:367–379.
- Derraik, J. G. B. (2002). The pollution of the marine environment by plastic debris: A review. *Marine Pollution Bulletin* 44:842–852.
- Duffy, D. C. (2010). Changing seabird management in Hawai'i: From exploitation through management to restoration. *Waterbirds* 33:193–207.
- Gauthreaux, S. A., Jr., and C. G. Belser (2003). Radar ornithology and biological conservation. *The Auk* 120:266–277.
- Gilman, E., D. Kobayashi, and M. Chaloupka (2008). Reducing seabird bycatch in the Hawaii longline tuna fishery. *Endangered Species Research* 5:309–323.
- Harrison, C. S. (1990). *Seabirds of Hawaii: Natural History and Conservation*. Cornell University Press, Ithaca, NY, USA.
- Hodges, C. S. N., and R. J. Nagata, Sr. (2001). Effects of predator control on the survival and breeding success of the endangered Hawaiian Dark-rumped Petrel. In *Evolution, Ecology, Conservation, and Management of Hawaiian Birds: A Vanishing Avifauna* (J. M. Scott, S. Conant, and C. Van Riper, III, Editors). *Studies in Avian Biology* 22:308–318.
- Kain, E. C., J. L. Lavers, C. J. Berg, A. F. Raine, and A. L. Bond (2016). Plastic ingestion by Newell's (*Puffinus newelli*) and Wedge-tailed Shearwaters (*Ardenna pacifica*) in Hawaii. *Environmental Science and Pollution Research* 23:23951–23958.
- Miskelly, C. M., G. A. Taylor, H. Gummer, and R. Williams (2009). Translocations of eight species of burrow-nesting seabirds (genera *Pterodroma*, *Pelecanoides*, *Pachyptila*, and *Puffinus*: Family Procellariidae). *Biological Conservation* 142:1965–1980.
- Podolsky, R., D. G. Ainley, G. Spencer, L. Deforest, and N. Nur (1998). Mortality of Newell's Shearwaters caused by collisions with urban structures on Kauai. *Colonial Waterbirds* 21:20–34.
- Raine, A. F., and N. Banfield (2015a). Monitoring of Endangered Seabirds in HNP NAR II: Pohakea Annual Report 2014. Kaua'i Endangered Seabird Recovery Project, State of Hawai'i, Department of Land and Natural Resources, Division of Forestry and Wildlife, Lihue, HI, USA (unpublished report).
- Raine, A. F., and N. Banfield (2015b). Monitoring of Endangered Seabirds in HNP NAR III: North Bog Annual Report 2014. Kaua'i Endangered Seabird Recovery Project, State of Hawai'i, Department of Land and Natural Resources, Division of Forestry and Wildlife, Lihue, HI, USA (unpublished report).
- Reed, J. R., J. L. Sincok, and J. P. Hailman (1985). Light attraction in endangered procellariiform birds: Reduction by shielding upward radiation. *The Auk* 102:377–383.
- Reynolds, M. H., B. A. Cooper, and R. H. Day (1997). Radar study of seabirds and bats on windward Hawai'i. *Pacific Science* 51: 97–106.
- Rodríguez, A., N. D. Holmes, P. G. Ryan, K.-J. Wilson, L. Faulquier, Y. Murillo, A. F. Raine, J. Penniman, V. Neves, B. Rodríguez, J. J. Negro, et al. (2017). A global review of seabird mortality caused by land-based artificial lights. *Conservation Biology*. Accepted Author Manuscript. doi:10.1111/cobi.12900
- Sileo, L., P. R. Sievert, M. D. Samuel, and S. I. Fefer (1990). Prevalence and characteristics of plastic ingested by Hawaiian seabirds. In *Proceedings of the Second International Conference on Marine Debris*, 2–7 April 1989, Honolulu, Hawaii (R. S. Shomura and M. L. Godfrey, Editors). U.S. Department of Commerce NOAA Technical Memorandum NMFS NOM-TM-NMFS-SWFSC-154. pp. 665–681.
- Simons, T. R. (1985). Biology and behavior of the endangered Hawaiian Dark-rumped Petrel. *The Condor* 87:229–245.
- Sincok, J. L., and G. E. Swedberg (1969). Rediscovery of the nesting grounds of Newell's Manx Shearwater (*Puffinus puffinus newelli*), with initial observations. *The Condor* 71: 69–71.

- Spear, L. B., D. G. Ainley, N. Nur, and S. N. G. Howell (1995). Population size and factors affecting at-sea distributions of four endangered procellariids in the tropical Pacific. *The Condor* 97:613–638.
- Swift, R., and E. Burt-Toland (2009). Surveys of procellariiform seabirds at Hawaii Volcanoes National Park, 2001–2005. Pacific Cooperative Studies Unit Technical Report 163, University of Hawai'i at Mānoa, Department of Botany, Honolulu, HI, USA.
- Telfer, T. C., J. L. Sincock, G. V. Byrd, and J. R. Reed (1987). Attraction of Hawaiian seabirds to lights: Conservation efforts and effects of moon phase. *Wildlife Society Bulletin* 15:406–413.
- Travers, M., D. Golden, A. Stemen, and A. F. Raine (2016). Underline Monitoring Project 2015 Annual Report. Kaua'i Endangered Seabird Recovery Project, State of Hawai'i, Department of Land and Natural Resources, Division of Forestry and Wildlife, Lihue, HI, USA (unpublished report).
- Travers, M. D., A. Shipley, M. Dusch, and A. F. Raine (2014). Underline Monitoring Project 2013 Annual Report. Kaua'i Endangered Seabird Recovery Project, State of Hawai'i, Department of Land and Natural Resources, Division of Forestry and Wildlife, Lihue, HI, USA (unpublished report).
- Troy, J. R., N. D. Holmes, and M. C. Green (2011). Modeling artificial light viewed by fledgling seabirds. *Ecosphere* 2:1–13.
- Troy, J. R., N. D. Holmes, J. A. Veech, and M. C. Green (2013). Using observed seabird fallout records to infer patterns of attraction to artificial light. *Endangered Species Research* 22: 225–234.
- USFWS (U.S. Fish and Wildlife Service) (1983). Hawaiian Dark-rumped Petrel and Newell's Manx Shearwater Recovery Plan. U.S. Fish and Wildlife Service, Portland, OR, USA.
- VanderWerf, E. A., and L. C. Young (2016). Juvenile survival, recruitment, population size, and effects of avian pox virus in Laysan Albatross (*Phoebastria immutabilis*) on Oahu, Hawaii, USA. *The Condor: Ornithological Applications* 118:804–814.
- VanZandt, M., D. Delparte, P. Hart, F. Duvall, and J. Penniman (2014). Nesting characteristics and habitat use of the endangered Hawaiian Petrel (*Pterodroma sandwichensis*) on the island of Lāna'i. *Waterbirds* 37:43–51.
- Warner, R. E. (1968). The role of introduced diseases in the extinction of the endemic Hawaiian avifauna. *The Condor* 70: 101–120.
- Wiley, A. E., A. J. Welch, P. H. Ostrom, H. F. James, C. A. Stricker, R. C. Fleischer, H. Gandhi, J. Adams, D. G. Ainley, F. Duvall, N. Holmes, et al. (2012). Foraging segregation and genetic divergence between geographically proximate colonies of a highly mobile seabird. *Oecologia* 168:119–130.
- Yoccoz, N. G., J. D. Nichols, and T. Boulinier (2001). Monitoring of biological diversity in space and time. *Trends in Ecology & Evolution* 16:446–453.