



Research Article

Managing the Effects of Introduced Predators on Hawaiian Endangered Seabirds

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ABSTRACT Introduced predators are one of the greatest threats facing seabirds worldwide. We investigated the effects of multiple introduced predators on 2 endangered seabirds, the Newell's shearwater (*Puffinus newelli*) and the Hawaiian petrel (*Pterodroma sandwichensis*), on the island of Kaua'i, Hawai'i, USA. Between 2011 and 2017, we recorded 309 depredations of which 35.6% were by feral cats, 50.2% by black rats (*Rattus rattus*), 10.4% by pigs (*Sus scrofa*; feral pigs), and 3.9% by barn owls (*Tyto alba*). Cats were the most destructive of the predators because they killed more breeding adults than chicks, which had repercussions on breeding probability in following years. Cats and rats were also the most prevalent of all the predators, depredating birds at all of the sites under consideration regardless of how remote or inaccessible. We also considered the effectiveness of predator control over the study period. Reproductive success at all sites increased once predator control operations were in place and depredations by all species except barn owls decreased. Furthermore, we modeled population trajectories for all sites with and without predator control. Without predator control, population trajectories at all sites declined rapidly over 50 years. With predator control operations in place, populations at all sites increased; thus, controlling introduced predators at endangered seabird colonies is important for their management. © 2020 The Wildlife Society.

KEY WORDS *Felis catus*, Hawaiian petrel, introduced predators, Kaua'i, Newell's shearwater, *Pterodroma sandwichensis*, *Puffinus newelli*, *Rattus*, seabird.

Introduced predators have been identified as one of the most significant causes for the decline of seabird populations on islands worldwide (Courchamp et al. 2003, Croxall et al. 2012, Doherty et al. 2016, Dias et al. 2019, Rodríguez et al. 2019). Whereas the species vary on an island by island basis, the most destructive and well-known introduced seabird predators are feral cats (*Felis catus*), rats (*Rattus* spp.), and pigs (*Sus scrofa*; feral pigs). Feral cats are considered to be a particularly destructive introduced predator in the Pacific (Hess and Banko 2006, Hess et al. 2009, Duffy and Capece 2012) and have a clearly identified effect on seabird populations worldwide (Imber et al. 1994, Johnston et al. 2003, Bonnaud et al. 2012) and indirect effects that include spreading fatal diseases such as toxoplasmosis (*Toxoplasmosis gondii*; Medina et al. 2014). Examples of the effect of rats include direct depredation of seabird eggs (Jones et al. 2005), chicks (Thibault 1995, Igual et al. 2006, Caut et al. 2008), and in smaller species, even adults (Moors and Atkinson 1984, Bertram 1995, Martin et al. 2000). Lastly feral pigs have been identified as the primary predator responsible for the near extinction of multiple seabird species including the

Bermuda cahow (*Pterodroma cahow*; Carlile et al. 2012, Madeiros et al. 2012) and the rapid decline of others (Harris 1970, Cuthbert et al. 2001, Cuthbert and Davis 2002).

Cats, rats, and pigs are the main introduced predators threatening seabird populations on the Hawaiian Islands, but several other mammalian species have been identified as being significant threats. These include the small Indian mongoose (*Herpestes javanicus*; Munro 1941, Harrison 1990, Hays and Conant 2007) and feral or domestic dogs (Byrd and Telfer 1979, Byrd et al. 1985, Towns et al. 2011). Ironically, it was because of a hunting dog depredation incident that the breeding grounds of the Newell's shearwater (*Puffinus newelli*) were rediscovered on Kaua'i, Hawai'i, USA, in 1967 (Sincock and Swedberg 1969). Lastly, the barn owl (*Tyto alba*) is the only non-native avian predator present in the Hawaiian Islands. Introduced to Kaua'i by the Hawaiian Department of Agriculture in the 1960s to control rats (Tomich 1962, Au and Swedberg 1966), it has become a serious threat to seabird species across the Hawaiian island chain (Byrd and Telfer 1980, Raine et al. 2019).

Recent historical population trends show a 94% population decline for Newell's shearwater and a 78% decline for Hawaiian petrel (*Pterodroma sandwichensis*) on Kaua'i between 1993 and 2013 (Raine et al. 2017) and their range

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has contracted across the Hawaiian Islands. The reason for these declines are particularly because of collisions with powerlines (Cooper and Day 1998, Podolsky et al. 1998, Ainley et al. 2001, Raine et al. 2017, Travers et al. 2019), the attraction of fledglings to artificial lights (Reed et al. 1985, Telfer et al. 1987, Ainley et al. 1997, Cooper and Day 1998), and habitat modification within breeding colonies due to invasive plants and pigs (Duffy 2010, VanZandt et al. 2014). This combination of factors has led to the Hawaiian petrel being globally listed under the International Union for Conservation of Nature Red List as vulnerable (BirdLife International 2019a) and the Newell's shearwater being listed as endangered (BirdLife International 2019b).

To assess the effect of introduced predators on these species, we considered data from 7 years of seabird monitoring at 6 remote seabird management sites in the northwest sector of the island of Kaua'i. We evaluated the key predators affecting the species, quantified the long-term effect to the colonies by introduced predators, and considered the effectiveness of predator control operations within the colonies.

STUDY AREA

We collected data between 2011 and 2017 at 6 endangered seabird colonies on the island of Kaua'i, the northern-most

island within the Main Hawaiian Islands. Sites included the Upper Limahuli Preserve (a 153-ha fully protected conservation area owned by the National Tropical Botanical Gardens) and 5 sites in Hono O Nā Pali Natural Area Reserve (NAR; a large 1,448-ha conservation area owned by the State of Hawaii): Pihea, Pōhākea, North Bog, Hanakāpī'ai, and Hanakoa (Fig. 1). All were located within the northwestern portion of Kaua'i, at an elevation of between 500 m and 1,300 m above sea level. All sites consisted of intact wet montane forest, criss-crossed with deep drainages, narrow ridgelines, and steep valley walls, and were dominated by native species such as 'Ōhi'a (*Metrosideros polymorpha*), lapa'apa (*Cheirodendron platyphyllum*), and tree ferns (*Cibotium* spp.) in the canopy and large patches of uluhe fern (*Dicranopteris linearis*) in the understory. The climate was tropical, with an average annual precipitation of 263–398 cm. Mean July temperature across the 6 sites was 18°C, and mean January temperature was 14.9°C.

All sites had ongoing seabird monitoring projects coupled with active management, consisting primarily of predator control operations, which varied in terms of date when control started and techniques used. Upper Limahuli Preserve was protected by an ungulate-proof fence (and was thus free of feral pigs) and had predator control operations

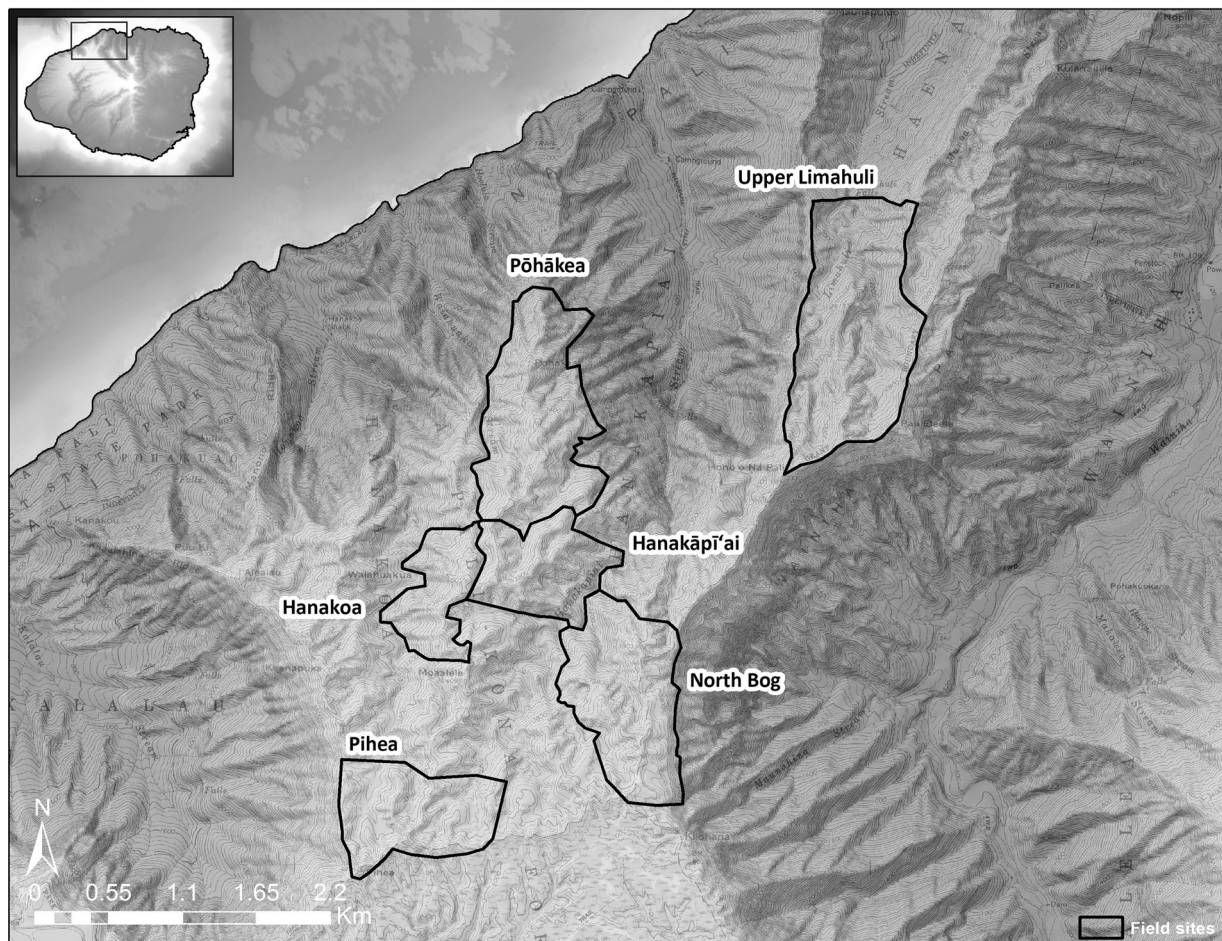


Figure 1. Locations of the 6 study sites for Newell's shearwater and Hawaiian petrel, located on the island of Kaua'i, Hawaii, USA, 2011–2017.

in place since 2011, with the project increasing in scope, staff time, and available trapping techniques each year to the present day (2019). The 5 sites in Hono O Nā Pali NAR were protected on 1 side by a large ungulate-proof fence that separated the NAR from the adjacent Alaka'i Swamp and more recently installed wing fences that cut off all other access routes to pigs, but as of 2019 the area is not entirely free of pigs (although active pig control, through the use of snares and hunts, has been ongoing since 2013). Predator control operations began at 3 of the NAR sites (Pihea, Pōhākea, and North Bog) in 2012, whereas at Hanakāpī'ai and Hanakoa predator control began in mid-2016.

METHODS

Throughout this study we acted in accordance with the guidelines for the ethical use of wild birds in research as outlined by the North American Ornithological Council (Fair et al. 2010). All work was conducted under State Migratory Bird Master Permit (MB673451-0) and Section 6 Co-operative Agreement between the United States Fish and Wildlife Service and the State of Hawaii Division of Land and Natural Resources.

Burrow and Camera Monitoring

All sites have been part of a long-term seabird monitoring project, with Upper Limahuli starting in 2011, Pihea, North Bog, and Pōhākea in 2012, and Hanakāpī'ai and Hanakoa in 2015. We undertook colony monitoring trips nearly monthly throughout the breeding season from March to December, with site access either by foot (Pihea) or helicopter (Upper Limahuli, North Bog, Pōhākea, Hanakāpī'ai, Hanakoa).

We searched each site for active seabird burrows throughout the study period. We marked all burrows located within each colony with a unique identification tag (colored and numbered cattle ear tags) and recorded their locations using a handheld global positioning system (GPS; Garmin Rino 650, Olathe, KS, USA). We identified each burrow to species wherever possible, although in some cases where burrows were too convoluted to see the bird, we recorded the species as unidentified procellariid because it could have been either Newell's shearwater or Hawaiian petrel. During burrow checks, we inspected each burrow to assess breeding status. For deep burrows where direct visual inspection was not possible, we used a handheld camera (Panasonic LUMIX, Olympus Tough TG-3 or TG-4, Olympus America Inc, Center Valley, PA, USA) in an attempt to take photos into the back of the burrow to assess burrow contents.

At each check, we made notes on any signs of activity within or around the nest. This included the presence of adult, egg, or chick; scent, signs of digging, or trampling; or presence of feathers, guano, or egg shell. We calculated reproductive success annually for each site by dividing the number of burrows where a chick successfully fledged by the number of burrows where we confirmed breeding. This represented a subset of burrows because breeding did not occur at some burrows (i.e., inactive burrows, prospectors)

and could not be confirmed at others because of the depth of the burrow or inconclusive sign.

We also recorded any signs of depredation such as a dead adult or chick in front of burrow or inside burrow, chewed feathers, egg shells, or the presence of scats or prints that indicated that a predator had been in the vicinity of the nest. In instances where we located a seabird carcass, we photographed it, and removed it for further inspection. Wherever possible, we identified the predator involved in the depredation event to species based on the disposition of the carcass, injuries sustained, portions of the carcass consumed, and other field characteristics. We attributed depredations to feral cats if there were large chunks eaten out of the body of the carcass, the back of the head was consumed, and if feathers were strewn about the depredation area. We identified rat depredations if there were gnaw marks on eggs, if small chicks were dragged out of burrows but only partially consumed (differentiating them from cats, which would eat small chicks whole), or if chicks were killed inside the burrow but not dragged out. We identified instances as barn owl depredations if the carcass was lying on its back with the keel stripped neatly of flesh, and if the head was entirely missing, or if the carcass was lying on the top of vegetation. Lastly, we identified events as pig depredations if the burrow was dug up, or if we found carcasses with multiple bones broken and severe trauma caused to the carcass in general. We also recorded incidences of depredation (or signs of introduced predators) away from known nesting burrows when we observed them during trips to each area, with locations logged using a handheld GPS. We reported all depredation events immediately to predator control teams to help direct predator control activities.

We monitored a subset of ≥ 30 burrows at each colony using cameras (Reconyx Hyperfire PC900s, Hyperfire HP2X and/or Reconyx Ultrafire XP9s, Holmen, WI, USA), with the number deployed at each site based on availability of camera units. We mounted cameras on poles located 1–1.5 m away from the burrow entrance, with the camera pointed directly at the burrow mouth to catch all activity (seabird and predator) at the burrow mouth. We set cameras on a rapid-fire setting (motion sensor activated, with a trigger speed of 0.2 seconds in the latest models). We switched out memory cards each month and reviewed images to look for seabird and predator activity. Data collected on predators included date, time, species, predator activity (passed burrow, investigated burrow, entered burrow), and depredation events.

Predator Control Techniques

Predator control operations at the project sites increased in scope, intensity, trap hours, and available techniques each year throughout the study. Most sites (apart from Hanakāpī'ai and Hanakoa) had some level of predator control in the first year of monitoring, although these operations were greatly limited. For the purposes of the comparisons carried out in this study, we considered the results of the first year of seabird monitoring at each site as being typical of a seabird colony on Kaua'i where no or

extremely limited predator control operations were occurring (i.e., yr zero), and the results of the last year as being typical of areas with high-level predator control operations (i.e., yr 2017). The techniques outlined below were all used in high-level predator control operations on Kaua'i in 2017.

We used walk-in live-capture traps (Tomahawk Live Trap, Hazelhurst, WI, USA) at all sites and checked and rebaited traps every 1–2 days. We typically set traps on or near a trail with the base of the trap covered with leaves and dirt to simulate the trail surface. We camouflaged traps with leaves, sticks, and ferns or left them uncovered. We used 76-cm and 91-cm live-cage traps with both single and double door designs. Double door traps were primarily unbaited, and set in trails (blind set). Single door traps were baited with a variety of baits including scent and food-based lures. Cats were the primary target of the larger traps (the mesh size allowed rodents to escape), whereas the smaller traps targeted cats and rodents (but may have been less appealing to larger cats).

Body-grip traps (Belisle Trap, Belisle Pieges, Canada) are spring-driven lethal traps targeted at cats, although they are also capable of capturing rats. We set body-grip traps with bait or as blind sets and used them only in certain areas deemed to be seabird safe (i.e., it was unlikely that a seabird would be present on the ground in the area). We disabled body-grip traps during certain times of year to avoid harm to seabirds. We used body-grip traps at all sites, primarily 220 or 280 size.

Goodnature® A24 traps (goodnature, Sonoma, CA, USA) are a proprietary, self-resetting, lethal rodent trap (targeted at black rat [*Rattus rattus*], Polynesian rat [*R. exulans*], brown rat [*R. norvegicus*], and house mouse [*Mus musculus*]) and are powered by carbon dioxide cartridges. We set A24s preferably at the base of a tree approximately 10 cm off the ground but also used a wooden stake if no suitable trees were present. These traps can be triggered up to 24 times before needing a new carbon dioxide cartridge, although at all sites, we typically refreshed bait before the carbon dioxide cartridge was empty. We set A24s in grids around key seabird areas with supplemental trapping near burrows. We used different baits over the years, but in the most recent year all traps had the auto-lure pumps installed using the chocolate bait formula.

Snap traps included Victor® Easy Set® Rat Traps (BM205, Woodstream Corporation, Lancaster, PA, USA) soaked in linseed oil to weatherproof the wood, and Ka Mate Medium Snap Traps (MT01, Ka Mate Traps, Nelson, New Zealand). We added snap traps to trapping stations to provide supplemental rodent control. We deployed snap traps only inside seabird-safe enclosures built in-house out of fluted polypropylene plastic boxes or hardware cloth cages. We baited snap traps with a variety of pastes and solid baits.

Population Trend Modeling

We evaluated the effectiveness of predator control operations within the 6 sites using 2 population simulation

models (with and without predator control) through the program Vortex 10 (Lacy et al. 2005). Model inputs used a combination of biological variables already known for the 2 seabird species through data collected by the Kaua'i Endangered Seabird Recovery Project (KESRP) if available and, when these were not available, biological variables from previously published works on Newell's shearwater and Hawaiian petrel, or biological variables from closely related procellariid species (predominantly Manx shearwater [*Puffinus puffinus*] and short-tailed shearwater [*Puffinus tenuirostris*]). Although the 2 study species differed in terms of certain aspects of their breeding ecology, we combined Newell's shearwater and Hawaiian petrel; thus, model outputs relate to the 2 endangered seabirds as a single unit for the purposes of modeling. We considered this to be a reasonable approach for assessing the large-scale effects of predator management within our study sites because the species-specific inputs into the model were very similar and the 2 species breed close to each other within the study area; thus, the effects of introduced predators were likely to be similar.

In the population model, we considered the reproductive system to be long-term monogamous in which males and females had an age of first reproduction equal to 6. We assumed this was the earliest age both species would return to breed and successfully fledge a chick based on previously published works on Hawaiian petrel (Simons 1984) and Newell's shearwater (Ainley et al. 2001). We selected a maximum lifespan of 36 years, which represents the maximum age observed among similar shearwater species (Bradley et al. 1989) and this age also represented the maximum age of reproduction in both sexes. We set the maximum number of broods per year and the maximum number of progeny per brood to 1. We set the default sex ratio to 1:1 because there are no data to suggest a sex bias in the population.

When calculating reproductive rate, we considered all monitored burrows across all sites where there was >1 year of data and followed them annually after the first confirmed breeding attempt to assess the likelihood that breeding was attempted in the following year. We determined that 98.6% of the time established breeders initiated breeding in the following year (i.e., most birds never skipped a year). The only time breeding was not attempted in the following year in our data set was if 1 of the pair was known to have been depredated, which was assessed by the presence of a depredation event outside or inside the burrow. To account for this, we assumed that if 1 of the pair disappeared (through predation or old age), then breeding was not attempted in the following year. We thus adjusted the reproductive rate by multiplying 98.6% by the annual survival rate (92.4%, see below) minus the site-specific percentage of adults predated each year after the predation scenario took effect. For the predator control management scenario, this resulted in a final annual site-specific reproductive rate of 88.8–91.1% and for the no predator control scenario a reproductive rate of 83.9–91.1%. This is similar to the 89% described for Hawaiian petrels by Simons (1984).

We set survival to breeding age at 25.0% based on data obtained from a satellite tracking project on Newell's shearwater fledglings (KESRP, unpublished data). This low juvenile survival is similar to that calculated previously for Hawaiian petrel (Simons 1984) and that published for other seabirds (Hudson 1985, Mougín et al. 2000). We applied an adult annual survival rate of 92.4% after reaching breeding age based on the average of adult survival rates presented in a number of studies undertaken on Manx shearwater (Harris 1966, Perrins et al. 1973, Brooke 1977) and Hawaiian petrel (Simons 1984, 1985). Site fidelity among seabirds is typically high (Warham 1980; e.g., Manx shearwater [Harris 1966, 1972; Perrins et al. 1973], streaked shearwater [*Calonectris leucomelas*; Sugawa et al. 2014]). The juveniles of some shearwater species, however, do appear to exhibit a degree of emigration to new breeding colonies (e.g., short-tailed shearwater [Serventy and Curry 1984]) and there may even be a degree of difference between sexes (Ristow et al. 1990, Thibault 1993). To take into account this interspecies variation, we used a site fidelity of 90% to account for returning juveniles in our model. Initial population sizes at each site were based on current breeding population estimates for both species combined (Raine et al. 2018) to get the total number of breeding adults in each colony and then using 0.637 as the proportion of the population that was of breeding age (Ainley et al. 2001) to get the number of non-breeders at each site.

Using the above variables, we used population simulation models to consider the effectiveness of predator control by considering 2 scenarios: population trajectories at each site without predator control using depredation rates recorded at each site prior to the implementation of fully functioning predator control operations (yr 1 of monitoring) and population trajectories at each site with a fully functioning predator control project in place using depredation rates in the most recent year of monitoring (yr 2017). For both scenarios, we assessed depredation as harvest to isolate its effect on seabird populations from general mortality. We calculated rates as 2 types: rates of depredation at breeding age (adults) and rates of depredation prior to breeding age (egg or chick depredations).

Finally, to account for the fact that cats continue to appear with regularity at predator control sites (because there are currently no predator-proof fences in any of these areas) and occasionally kill birds before being caught, we also added a CATastrophe element to the model for both scenarios. In this event, cats killed birds at 15% of all burrows at the site. This is the highest level of cat depredation ever recorded over the last 3 years across the 4 longest term management sites. Of these depredations, 62.7% involved the depredation of an adult and 37.3% of a chick (see Results). For modeling purposes for sites with predator control, we set the interval of a CATastrophe at 12 years (because this occurred at 1 of 4 sites in a 3-yr period, as outlined above), whereas for sites without predator control we set the interval for this event at 3 years (because this event occurred at the Pōhākea site once over a 3-yr period). We set the interval as more frequent for sites without predator control because cats are

recorded at all management sites every year, and if there is no predator control, a CATastrophe is much more likely to occur in any given year.

Aside from differing rates of depredation (harvest) and different starting populations at each site, all other model inputs were identical. We ran each simulation for 500 iterations over 50 years. We omitted inputs related to genetics, state variables, density dependence, and population supplementation to focus attention solely on the effects of introduced predators. Likewise, because the point of the exercise was to isolate the effects of predator control, we did not attempt to model the effects of other threats to the species, which are significant and include powerline collisions (considered to be the biggest cause of mortality of endangered seabirds on Kaua'i; Raine et al. 2017, Travers et al. 2019) and light attraction. Thus the results of the models should be considered as an assessment of the effect of predator control only.

RESULTS

By the end of 2017, we monitored 1,071 seabird burrows annually across the 6 colonies, consisting of 160 Newell's shearwater, 588 Hawaiian petrel, and 323 unidentified procellariid burrows. We confirmed 309 endangered seabirds as killed by introduced predators over the 7-year study period, consisting of 57 Newell's shearwaters, 208 Hawaiian petrels, and 44 unidentified procellariids. Of the 309 depredations, 110 (35.6%) were by cats, 155 (50.2%) by black rats, 32 by pigs (10.4%), and 12 (3.9%) by barn owl.

Predators targeted different age classes of seabirds (Fig. 2). Cats depredated adults (62.7%) and chicks (37.3%), black rats depredated chicks (79.4%) and eggs (20.6%), barn owls depredated only adults (100.0%), and pigs destroyed entire burrows, eating adults (68.6%), chicks (3.1%), and eggs (28.1%). The level of depredation caused by different predator species also varied between sites. At Pihea, Pōhākea, and Hanakoa, cats caused the most depredations (59.1%, 50.0%, and 48.8%, respectively), whereas at Hanakāpī'ai and North Bog black rats were the most prevalent predators (82.6% and 73.5%, respectively). Only cats and black rats caused depredations at all 6 sites, whereas pigs and barn owls each caused depredations at 66.6% of sites.

Of the 309 depredations, 159 occurred at burrows where we monitored the burrow in the year immediately after the depredation occurred; thus, we could assess subsequent breeding activity. In the case of burrows depredated by black rats, the majority were active in the year following depredation (chick depredated: 93.5%, egg depredated: 94.7%) and the majority had breeding attempts (chick depredated: 88.3%, egg depredated: 84.2%). In the case of burrows depredated by cats, 93.8% were active and 87.5% had breeding attempts the following year if the chick was depredated, but only 58.8% were active and 35.3% had breeding attempts if an adult was depredated. Only 14.3% of burrows destroyed by pigs were active in the following year and in only 1 of these was there a breeding attempt (7.1%).

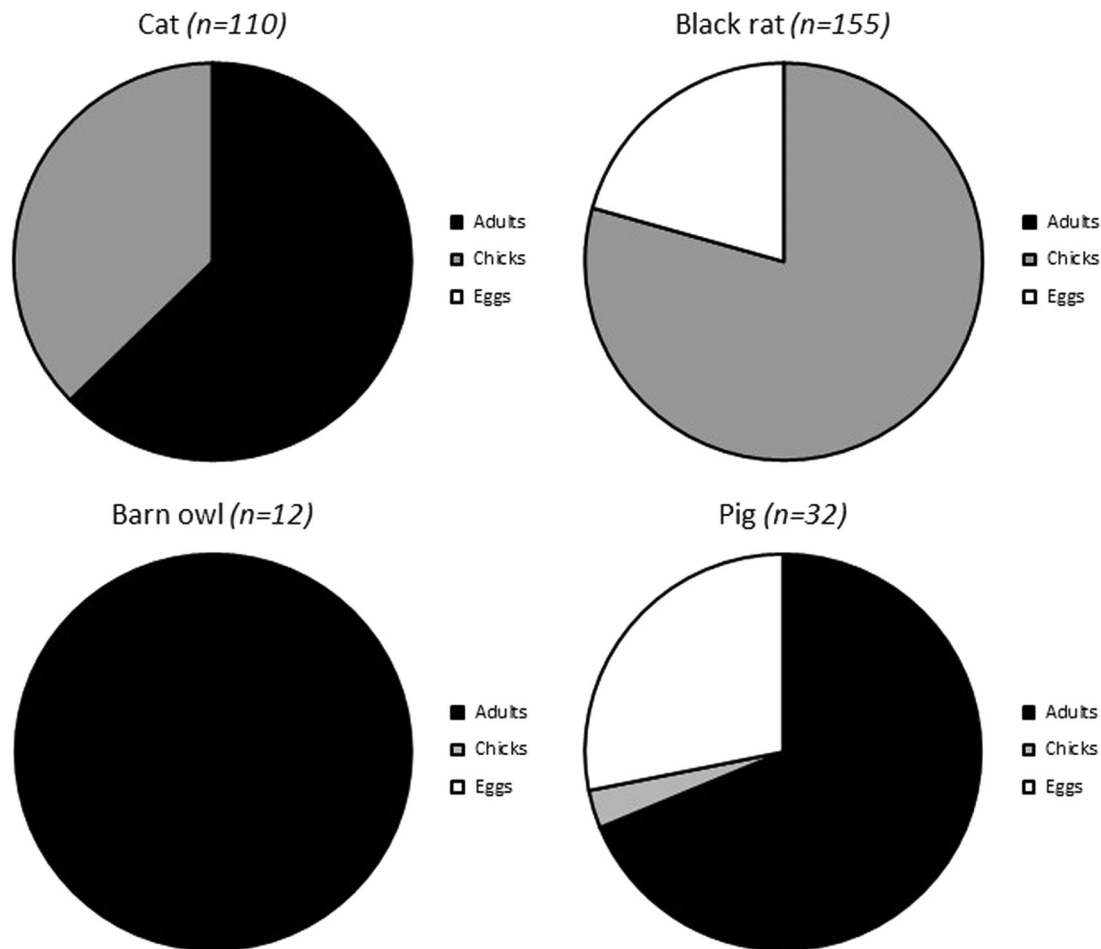


Figure 2. Age classes of Newell's shearwater and Hawaiian petrel (both species combined) targeted by different introduced predators at 6 monitored colonies on Kaua'i, Hawaii, USA, 2011–2017.

Effectiveness of Predator Control

Depredated seabirds were found at all 6 study sites on the very first visit to the area, indicating that introduced predators were present at all sites prior to human visitation and the initiation of management and monitoring activities. To consider the overall effectiveness of predator control, we compared the percentage change in reproductive success rate at monitored burrows at each site in the first year of monitoring (yr zero) with the most recent year when predator control operations were most refined (yr 2017). Reproductive success rate increased at all sites by a mean of 48.5% (range = 22.5–100.0%) for Hawaiian petrel and 35.8% (28.8% and 42.9%, respectively, for the 2 sites with monitored burrows of this species) for Newell's shearwater. We also compared the percentage of burrows depredated by each of the predator species between year zero and year 2017. The percentage of burrows depredated in 2017 was significantly lower than in year zero for cats (percent change; -68.1% , $\chi_1^2 = 5.03$, $P = 0.025$), black rats (percent change; -86.2% , $\chi_1^2 = 23.21$, $P \leq 0.001$), and pigs (percent change; -100.0% , $\chi_1^2 = 15.09$, $P \leq 0.001$; Fig. 3). We considered barn owls separately because we recorded very few depredations directly at a burrow and the majority were of kills found on trails or on top of vegetation. The

number of barn owl kills ($n = 8$) was highest in 2017 when compared with all other years of monitoring (range = 0–1), although this could not be tested statistically due to the small sample size.

Population modeling indicated if colonies did not receive predator control, population trends for all sites showed a rapid decline (Fig. 4; stochastic r , $\bar{x} = -0.039$, min. = -0.027 , max. = -0.059). If colonies received predator control at the current 2017 level, all populations increased over the 50-year period (Fig. 5; stochastic r , $\bar{x} = 0.050$, min. = 0.002 , max. = 0.015).

DISCUSSION

Introduced predators are a serious conservation challenge for seabird species around the world, and Kaua'i is no exception. We recorded depredations of endangered seabirds at all of the study sites on the very first visit to the site before the advent of trails, or any human activity. For example, the first expedition to the Pihea site in 2012 recorded 5 freshly killed adult Hawaiian petrels, all depredated by cats. The first expedition to Hanakāpī'ai recorded multiple depredations of both seabird species by 3 different predators: black rats, cats, and pigs. Therefore, it is clear that the threat of introduced predators is widespread throughout even the

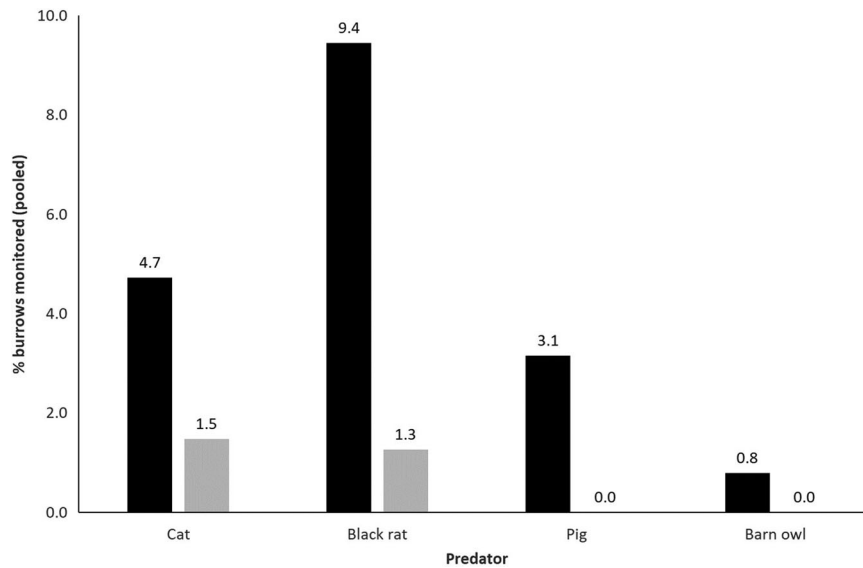


Figure 3. Percentage of Newell's shearwater and Hawaiian petrel burrows monitored (pooled across sites) that were depredated by each introduced predator species on Kaua'i, Hawaii, USA, 2011–2017 in the first year of monitoring at each site (black bars) and the most recent year of monitoring (2017, gray bars).

most remote seabird colony, regardless of site accessibility and location.

Predator control operations are critical to preventing the loss of seabird colonies on Kaua'i and these operations are an integral facet of seabird management on the island. The effectiveness of these predator control operations within managed colonies was evident; at all sites, reproductive success increased significantly from the year of first monitoring to the most recent year, whereas depredations

decreased (apart from barn owl). Population modeling also demonstrated the importance of predator control. Without predator control, all colonies declined. Conversely, populations increased over time with predator control. As these modeled projections show, leaving colonies without management invariably led to population declines towards extinction.

The most destructive of the introduced predators were cats. Cats caused depredations at all sites and were

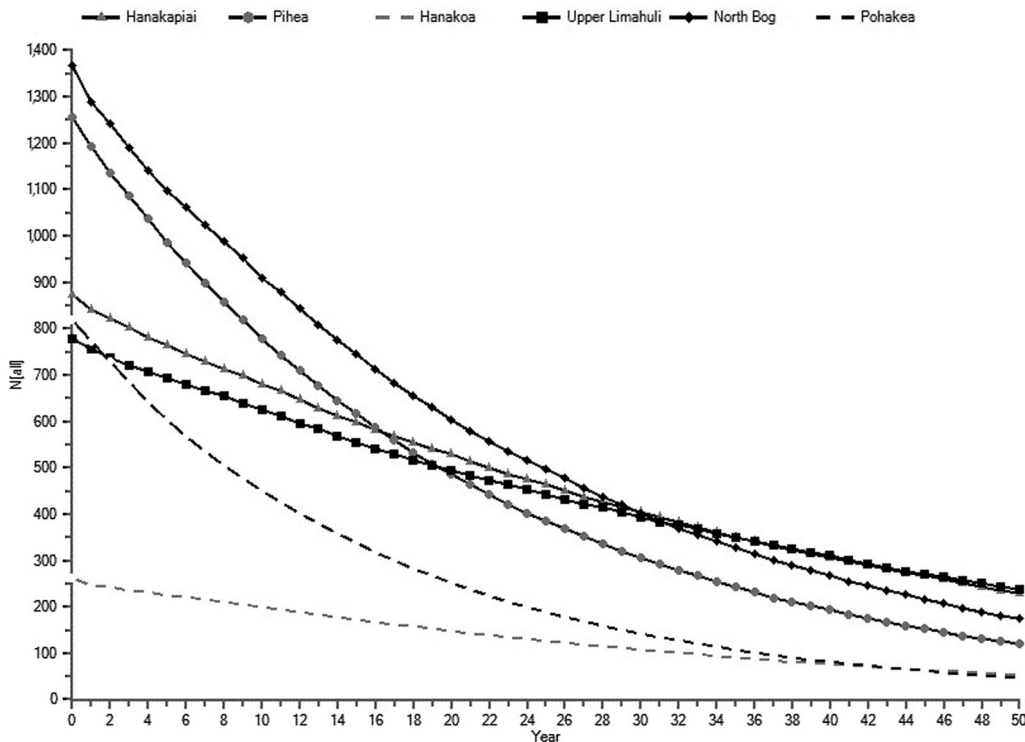


Figure 4. Population growth rates ($N[all]$; Newell's shearwater and Hawaiian petrel combined) as projected by the program Vortex at all colonies on Kaua'i, Hawaii, USA, if no predator control was undertaken (i.e., based on predation rates the first year predator control began). Models should be viewed as the response of the colonies to predators only.

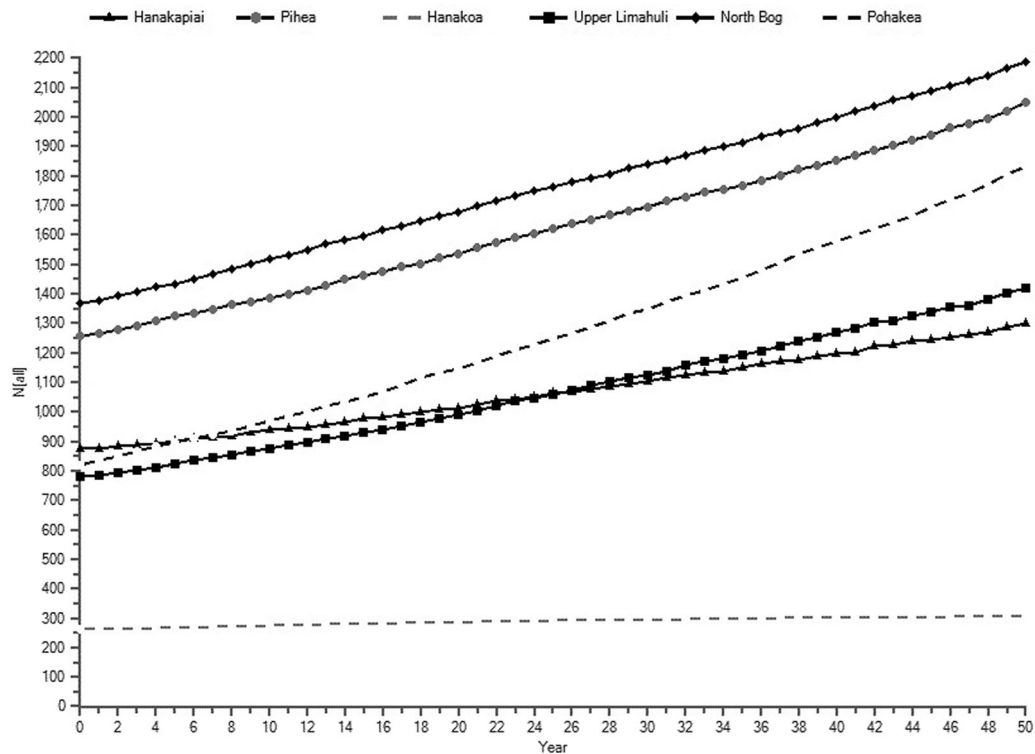


Figure 5. Population growth rates ($N[all]$; Newell's shearwater and Hawaiian petrel combined) as projected by the program Vortex at all colonies on Kaua'i, Hawaii, USA, if predator control continued at the existing 2017 level. Models should be viewed as the response of the colonies to predator control only.

responsible for 35.6% of all recorded depredations. Cats targeted breeding adults more than other age classes, which highlights the damage this species can do on endangered seabird populations. As can be seen in the modeling inputs of this and other studies (Simons 1984), breeding adults contribute more to population trends than any other cohort. Burrows where adults were depredated were much less likely to be active in the following year, and even less likely to initiate breeding. Because none of the managed colonies are currently protected by a predator-proof fence, cats continue to be recorded at every colony every year and notably begin to appear on burrow and trail cameras within seabird colonies just as the seabird season begins.

Predation by cats is exacerbated by their large home range (Fitzgerald and Karl 1986, Smucker et al. 2000, Edwards et al. 2001, Bengsen et al. 2012) meaning a single individual can affect multiple colonies and a single cat can easily depredate a large number of birds in a very short period of time (Borroto-Paez and Perez 2018). In 1 instance at Upper Limahuli in 2014, we identified the same cat on 9 different seabird burrow cameras over the course of a single day and the cat killed a Newell's shearwater chick at 1 of them. In another instance in Pōhākea in 2015, a cat killed birds at 15% of all monitored burrows over a couple of weeks; this same cat subsequently raised a litter of kittens in 1 of the Newell's shearwater burrows where it had killed both adults, and we saw the cat on camera later in the season bringing its kittens to other active burrows to hunt birds. Cats have been identified as a key predator of other native bird species, including forest birds such as the endangered Palila (*Loxioides bailleui*;

Laut et al. 2003) and waterbirds such as the Hawaiian moorhen (*Gallinula galeata sandvicensis*), Hawaiian duck (*Anas wyvilliana*), nēnē (*Branta sandvicensis*), and Hawaiian coot (*Fulica alai*; Baker et al. 2019). Cat control is an effective conservation tool for seabirds in other parts of the world (Cooper et al. 1994, Nogales et al. 2004, Bellingham et al. 2010, Rauzon et al. 2011).

In terms of numbers, black rats resulted in the highest number of depredations and were also recorded at all 6 sites. Black rats always targeted chicks or eggs. Unlike burrows where the adults were depredated by cats, burrows where there was a depredation by black rats were normally active the following year and the pairs in these burrows attempted to breed in the following year. Black rats are a known predator of seabirds and other bird species throughout the world and are a common target of rat eradication projects (Thibault 1995, Martin et al. 2000, Towns and Broome 2003, Jones et al. 2008, Jones and Kress 2012).

Although feral pig depredations were not as common as those of cats and black rats, when they did occur they were devastating. Pig depredations typically involved the destruction of the entire burrow, which the pigs excavated to access whatever was inside. Once the burrow was excavated, the pigs ate adults, chicks, or eggs and burrows were rarely active again. In the rare cases where adults returned to breed in pig-destroyed burrows, adults and chicks became more vulnerable to future depredation because they had lost structural integrity (and thus protection) of the burrow.

Lastly, barn owls represent a particularly difficult threat to address because they are not dissuaded by fences or

traditional predator control operations and can have large home ranges, meaning they can target multiple colonies. Although the number of depredations by this species were comparatively low, they were the 1 predator for which depredations increased over the study period. Depredations by this species are also hard to locate because they are generally not found near burrows (meaning they are probably under-represented in the data set). We hypothesize 2 main reasons for this. Barn owls could be targeting birds in mid-air on their way back to their burrows and forcing them toward the ground where they are presumably easier to kill (we observed this behavior on several occasions on Kaua'i and Lāna'i) or targeting non-breeding birds. Barn owl depredations of adults are rarely associated with burrows and it is possible that many depredations could involve non-breeding birds, which, while attempting to attract mates, may inadvertently draw attention to themselves from owls through vocalizations and conspicuous ground activity.

This study has demonstrated the serious effects of introduced predators on endangered seabirds on Kaua'i and the importance of predator control in alleviating these effects. In addition to the predator control techniques used in this study, other management techniques are important to consider. Ideally, the most important seabird colonies should also be fenced. Installation of ungulate-proof fences are important to protect native seabirds and entire watersheds. Strategically protecting key colonies with predator-proof fences can be even more effective. Other management tools, such as the use of landscape-level toxicants (including diphacinone and brodifacoum for rats [Townes and Broome 2003, Keitt et al. 2015] and paraaminopropiophenone [PAPP] for cats [Campbell et al. 2011, Johnston et al. 2011, Eason et al. 2014]) should also be carefully considered. Combined with a predator-proof fence, large-scale eradication efforts can bring longer-lasting predator reduction results, although their use may not be appropriate in all circumstances. Lastly, biosecurity at ports and docks should be considered as a first line of defense for predator control throughout the Hawaiian islands to prevent the introduction of new predators to the islands or the spread of existing predators such as the small Indian mongoose to mongoose-free islands like Kaua'i.

MANAGEMENT IMPLICATIONS

Intensive predator control projects are vital and effective in seabird breeding colonies, and can rapidly improve the population trajectories of seabirds breeding at these sites. Conversely, stopping or reducing predator control can have serious consequences for the colonies, causing rapid declines towards extirpation. Predator control operations need to be constant throughout the year, need to have sufficient funding to maintain them annually into the future, and need to have access to all effective predator control techniques. They also need to be coupled with a solid seabird monitoring strategy to ensure that management actions are effective. Furthermore, each introduced predator represents its own set of challenges and has its own population-level effects on seabird populations. Therefore, predator control operations need to be

specifically designed to target each introduced predator species within the colony and require an individually tailored management response. With well-planned predator control and seabird monitoring operations in place within critical seabird colonies, endangered seabird populations on Hawai'i can persist and increase into the future.

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