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THE STATUS AND POPULATION TRENDS OF THE NEWELL'S SHEARWATER ON KAUA'I: INSIGHTS FROM MODELING

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Abstract. We assessed the status of the endemic subspecies of Townsend's Shearwater, hereafter referred to as Newell's Shearwater (*Puffinus auricularis newelli*), on Kaua'i, Hawaiian Islands, where the only sizable population of this species remains. First, to index recent population trends, we analyzed data gathered on the 1,000–2,000 fledglings attracted to lights and picked up annually by the "Save Our Shearwaters" (SOS) Program over a 17-year period, 1978–1994. Second, to calibrate and to provide a demographic context to these data, we quantified breeding productivity and mortality in a mountain colony and mortality due to anthropogenic factors in the urban corridor that encircles the breeding areas during seven years: 1980–1985 (summary of previous study), 1993, and 1994. Finally, we entered rates of productivity and mortality into a Leslie model to integrate these data, to evaluate the demographic importance of different sources of mortality, and to assess the utility of SOS in mitigating mortality from anthropogenic factors.

During 17 years of data collection, an average 1,432 fledglings that were attracted to lights were picked up by SOS each year; 90% were banded and released alive. Considering all of Kaua'i during the study period, more fledglings were picked up, if breeding effort and success were higher, and the full moon occurred in early October well before the mid-month peak of fledging. Overall, the annual totals of fledglings (1) gradually decreased on the southern shore, where the level of urbanization (and lighting) has grown to double that of the entire remainder of the island; (2) remained approximately stable on the eastern shore (moderate urbanization); but (3) increased markedly on the northern shore, where urbanization is low but grew dramatically during the study period. The relationships to urbanization were corroborated by natural experiments when lighting was curtailed. Research in the breeding colony revealed (1) a high incidence of nonbreeding (46% of burrow occupants) even among experienced adults, typical of many petrel species; (2) predation (2.5% of individuals) on subadults and adults in the colonies by introduced house cats (*Felis catus*) and Barn Owls (*Tyto alba*); and (3) breeding success (0.66 chicks/pair) comparable to other shearwaters with stable populations. Research in the urban corridor revealed, conservatively, that (1) about 15% of an estimated 9,600 fledglings produced each year are picked up by SOS, (2) annual mortality of fledglings following light attraction during autumn is about 10%, and (3) annual mortality to adults and subadults from collisions with power lines during spring and summer (without light attraction) is 0.6–2.1%/yr. Only 15 of the 23,000 fledglings (<0.1%) initially banded by SOS have been recovered in subsequent years, but recoveries show that first breeding occurs at about 6 yrs of age and that 1-yr-olds do not visit Kaua'i.

A Leslie model, using parameters determined for the Newell's Shearwater, supplemented by those from the very closely related Manx Shearwater (*P. p. puffinus*), indicated a balanced/stable population when extrinsic mortality of anthropogenic origin was excluded. Factoring in predation on adults and subadults in the colonies and mortality of fledglings and adults/subadults due to collisions with human-made structures produced decadal declines of 30–60% in the population, with variation depending on the parameter values used. The model also showed that the SOS program is critical to reducing the rate of population decline. Predation from introduced animals proved to be the most important cause of decline, but collisions with structures by adults and mortality of fledglings following light attraction were also significant.

Key Words: bird impacts; cat predation; Hawai'i; Kaua'i; light attraction; Newell's Shearwater; oceanic island; population model; *Puffinus auricularis*; transmission line; urbanization.

Many populations of tropical seabirds that nest on oceanic islands with large human populations have been decimated by introductions of mammalian predators, habitat destruction, and urbanization, though the details are known only generally. Several large tropical petrels are now endangered or recently extinct, for example, the Bermuda Petrel (*Pterodroma cahow*), Jamaican Petrel (*Pt. hasitata*), Madeiran Petrel (*Pt. mollis madeira*), Fiji Petrel (*Pt. macgillivrayi*), and Magenta Petrel (*Pt. magentae*, of New Zealand; Croxall et al. 1984, Warham 1990, Ehrlich et al. 1992, Nettleship et al. 1994). Included in this group are those petrels nesting among the main Hawaiian Islands, the endemic subspecies of Townsend's Shearwater (*Puffinus auricularis newelli*), hereafter referred to as Newell's Shearwater, and Dark-rumped Petrel (*Pt. phaeopygia sandwichensis*), both of which are listed by the U.S. Endangered Species Act (USFWS 1982a). Newell's Shearwater and Dark-rumped Petrel have been extirpated from most of their former nesting islands, but on Kaua'i they are still relatively abundant (Telfer et al. 1987, Harrison 1990).

The Newell's Shearwater, or ʻAʻo, was considered extinct as of 1908, but on Kauaʻi in 1947 it was rediscovered and, in 1967, confirmed to be breeding (King and Gould 1967, Sincock and Swedberg 1969). A small breeding population has been confirmed recently on the island of Hawaiʻi (Reynolds et al. 1997a, Reynolds and Ritchotte 1997), and the species may also nest in very low numbers on Molokaʻi and Oʻahu (Harrison 1990). Rediscovery of Newell's Shearwater coincided with rapid growth in urban development on Kauaʻi, when hundreds of fledglings were found, having been attracted to and, typical of all petrels (Reed et al. 1985), apparently blinded by man-made lighting as the birds made their way from nest to ocean on their nocturnal fledgling flight (King and Gould 1967). This annual "fallout" became a major source of mortality, because fledglings die after being run over by cars or colliding with lights, utility poles and wires, and buildings (Byrd et al. 1984, Telfer et al. 1987). Shielding lights reduced attraction by as much as 40% in experimental areas (Reed et al. 1985); for example, a reduction in the intensity of yard lights at the Hanalei Plantation Hotel in 1965 reduced the fallout there significantly (King and Gould 1967). New building codes established in the late 1980s request measures to shield lights (State of Hawaii 1987); however, compliance has been inconsistent (D. Ainley and R. Podolsky, pers. obs.).

Attempting to decrease the mortality associated with fallout, the U.S. Fish and Wildlife Service (USFWS) and the State of Hawaii, Department of Land and Natural Resources (DLNR), organized the "Save Our Shearwaters" (SOS) Program in 1978 (Telfer et al. 1987, Rauzon 1991). Residents who found fallen shearwaters were encouraged, by advertisements in the news media, to place them in bird boxes at "Shearwater Aid Stations." The captured birds were then picked up each morning and taken for release from a coastal cliff. In the 17 years through 1994, about 23,000 shearwaters have been retrieved, banded, and released (T. Telfer, unpubl. data).

The current relatively high abundance and easy access of the Newell's Shearwater on Kauaʻi provided the opportunity to understand the species' ecology in the context of interactions with human activity, and to test the utility of SOS before the species' status becomes desperate and conservation attempts costly. What is learned may help to protect this and similar seabirds as development and tourism spread to more and more tropical islands (e.g., Croxall et al. 1984, Croxall 1991). We report here our findings during a study that included both fieldwork and analysis of existing unpublished data gathered by SOS and by government researchers since the late 1970s. The assembled information provided inputs into a demographic model of population growth under various scenarios of mortality. The model was used to evaluate the impact of three important factors indicated in the field studies: predation of adults from introduced animals, mortality of fledglings after fallout, and mortality of adults from collisions with power lines. In addition, we use the population dynamic model to project long-term stability of the Newell's Shearwater population on Kauaʻi.

METHODS

FIELDWORK

We conducted fieldwork in a mountain colony above Kalāheo (Fig.1), where the species breeding biology was studied in the early 1980s as part of an effort to determine whether Newell's Shearwaters could be cross-fostered by the much more abundant Wedge-tailed Shearwater (*P. pacificus*; Byrd et al. 1984). Access to the colony was difficult but nevertheless was easier by far than to any other colony known for Newell's Shearwater. Elevation of the Kalāheo colony is about 600 m. We searched for burrows among the vegetation on the >65 degree slopes between May and November 1993. Burrows were marked and a line of small sticks was erected across entrances to indicate burrow use when brushed aside by entering or departing birds; we also noted the presence or absence of excrement and feathers. We used a miniature infrared TV camera (Furhman Diversified, Inc.) on a stiff coaxial cable "snaked" down each burrow to determine the presence of eggs or chicks. Once an egg or chick was found, we rechecked the nest's status monthly. We attempted to set up a second study colony at a site called Kaluahonu, on the southern part of the island, but found that few birds still nested there compared with the early 1980s. In 1994, due to a shortfall in funding and a request from the committee overseeing the project (see Acknowledgments), we diminished work in the Kalāheo colony and allocated our efforts elsewhere. Therefore, we checked contents of burrows found the previous year on four occasions between late August and mid-November. We compared our findings on breeding productivity with the results of Telfer (1986), who participated in the cross-fostering studies from 1981 to 1985. Results over the seven seasons were combined in the demographic model described below.

To guard against intrusions of feral cats (*Felis catus*) and rats into our study colony, we placed a network of live-capture traps at the entrance to our ridge-top trails. Traps were baited every three days. In addition, we carried no food of our own into the colony for fear of attracting mammals.

To assess survival from the proportion of colony occupants that may have been banded by SOS (when birds were fledglings), we captured adult shearwaters by blocking the burrow entrance just before dark and waiting nearby. Upon arrival, the birds sat by the entrance and could be picked up easily. We checked

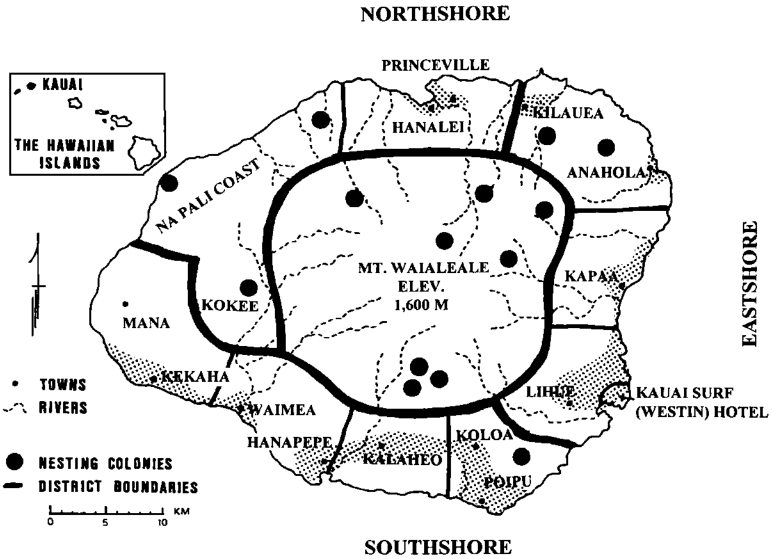

FIGURE 1. Map of Kaua'i, Hawaiian Islands, showing breeding colonies of Newell's Shearwaters (from Ainley et al. 1995) and the 10 districts used by SOS to summarize data (modified from Telfer et al. 1987). Bold boundaries indicate the Southshore, Eastshore, and Northshore areas on Kaua'i into which we combined SOS districts in our analysis. Shading indicates the current extent of urban and suburban areas.

these birds for bands and banded them if none was present. We quantified mortality due to collisions with power lines during summer and to fallout during autumn; results are reported elsewhere (Ainley et al. 1995, Podolsky et al. 1998).

ANALYSIS OF SOS DATA

To assess temporal and regional trends in the number of birds retrieved, we analyzed data contained in annual reports of the SOS program from 1980 to 1993 (project W-18-R, Hawaii DLNR), as well as raw data computerized by SOS from 1987 to 1993. We did not use data from 1978 or 1979 in most analyses because effort by the citizenry was reduced in the first two years of the program relative to subsequent years (citizens learned of the program each fall through advertisements in newspapers and radio).

A ledger on which persons could record the place where each bird was found was provided by SOS at each shearwater station. In 10–15% of cases the specific pickup locality was not recorded, and in some of these (e.g., when a citizen was commuting to/from work) it was likely that birds were turned in at stations some distance from the pickup locality. Beginning in 1982, to determine geographic variation in the relative strength of fallout, SOS divided Kaua'i into ten districts (Fig. 1) and apportioned the birds of unknown locality to the various districts according to the SOS station at which these birds were turned in (Telfer et al. 1987). We combined the districts into broader regions, a procedure that further diluted the effect of any incorrect apportionment. The regions, and the districts/drop-off stations comprising them, were (see Fig. 1): (1) Northshore—Hanalei-Princeville; (2) Eastshore—Kīlauea-Anahola, Kapa'a, Līhu'e, Westin Lagoons (Kaua'i Surf) Hotel; and (3) Southshore—Kōloa-Po'ipū, Kalāheo, Hanapēpē-Waimeae, Mānā-Kekaha (including Barking Sands Naval Air Station). Nāpali-Kōke'e is included in the Northshore, but being mostly wild land, it contributed little to SOS data.

In analyses where year was an important consideration, we did not use data from autumn 1992 or from 1993, because Kaua'i was much different in ways critical to our study. Hurricane Iniki devastated human structures on the island in September 1992, just before the shearwaters had begun to fledge and SOS would have swung into action. The hurricane obliterated all bright lights; all hotels were closed due to damage and fewer than 10% of street lights or power lines were left standing. Life on Kaua'i did not return to normal until summer 1994. Hurricane Iwa, in 1982, did not pass over Kaua'i until November, after shearwater fallout had been completed, so the fallout data were not affected and were included in analyses.

To maintain robust sample sizes in the data, we made some reasonable assumptions to categorize certain data rather than discarding them from analysis. First, dead adults were distinguished from dead fledglings in the 1987–1993 SOS data, but this was not the case in the 1980–1986 data. With no organized search effort in 1987–1990, the average number of dead adults/subadults found was 17/yr (see Results). So, to estimate the number of dead fledglings reported by SOS each autumn, 1980–1986, we assumed that the age ratio and search effort were the same as in 1987–1990 and, therefore, subtracted 17 "adults" from the total number of dead shearwaters reported in each of those years.

Second, dead adults reported during spring and summer were logged by SOS beginning in 1987. It was not until 1991–1992, however, that a concerted search effort for adults/subadults was made, in effect, equal to the effort for fledglings in autumn. In 1991, some especially interested and knowledgeable citizens (C. Berg, C. Orr, and K. Viernes) undertook this task and it was continued by us in 1993 and 1994. We assumed that patterns revealed in 1991–1994 were similar to those in the older SOS data. Next, we assumed that "adults" reported as dead in the SOS data after 15 September of each year included many individuals incorrectly aged for two reasons. First, in SOS records, peaks in number of dead birds recorded as "adults" (many of which are flattened and thus hard to assess) corresponded exactly to peaks of fledglings (Ainley et al. 1995). Second, few adults visit the colonies and no banded adults/subadults have been found after this date (see Results). Adult shearwaters desert their young a week or two before the fledgling departs (see Warham 1990); therefore, we considered all birds found after 15 September (the beginning of the fledging and fallout period) to be fledglings. To be sure, a few adults are found after that date (T. Telfer, pers. comm.).

Finally, it was not until 1982 that stainless steel bands were used by SOS on all fledglings. Prior to then, most were banded with monel bands. Therefore, our analyses based on return rates of banded birds do not include the data for the 1978–1981 cohorts, assuming that the monel bands were lost rapidly as a result of immersion in sea water (Boekelheide and Ainley 1989).

To assess trends in SOS totals in the context of urbanization, we indexed the urbanization of Kaua'i in two ways. Ultimately, we were interested in the number and dispersion of shearwaters, the number and dispersion of lights to attract them, and the number of people available to report birds or carcasses to SOS. Not having direct data on urbanization (e.g., the rate at which building permits were issued), we chose two surrogates. First, we used growth in numbers of year-round human residents (data from the U.S. Census Bureau, 1930–1990), and compared these among the three regions to which the SOS data had been partitioned (Fig. 1). From this population are the persons who participate in SOS, with participation depending only on the acts of encountering a shearwater, picking it up, and delivering it to an SOS station. In the small, close community of residents (currently 48,000 persons), more and more persons would know about SOS as the years passed and the proportion of interested persons would not decrease. Efforts to advertise SOS remained constant throughout the period. Next, to index trends in growth of the infrastructure developed for the tourist industry (i.e., coastal hotels, condominiums, lighted tennis courts and driving ranges, etc.), which would not necessarily track the requirements of permanent residents, we obtained data from the state of Hawai'i on the number of passengers using the Līhu'e Airport each year from 1960 to 1993. This infrastructure (and attendant lights) would be the source of fallout. Tourists would not know about SOS.

The following assumptions were used to relate trends in the SOS data to urbanization. First assumption: the number of fledglings retrieved by SOS in any year is proportional to breeding population size and reproductive success. Reproductive output, or at least SOS totals, appears to have exhibited no continuous trend through time, except for the occasional outlying year (see Results). Second assumption: the number of fledglings reported to SOS is strongly affected by the number and distribution of lights to attract them. This effect of lights, proposed also by Telfer et al. (1987), was verified experimentally when lighting was severely reduced at the Hanalei Plantation Hotel in the 1960s (King and Gould 1967), at the Kaua'i Surf/Westin Lagoons Hotel after 1983, and throughout Kaua'i as a result of Hurricane Iniki during 1992–1993 (see Results). Third assumption: the number of citizens present on Kaua'i also directly affects the number of birds reported. The latter two factors (i.e., number and distribution of lights plus number of persons available to encounter birds) would determine the proportion of fledglings produced that were attracted to lights, went aground, and were picked up. Final assumption: because the shearwater population incurs a cost through mortality from fallout (i.e., some birds die regardless of SOS), the cost, if high enough, can lead to population decline (i.e., too many fledglings die due to effects of urbanization). It is possible that the proportion of fledglings attracted and picked up could become saturated (i.e., an asymptote is reached whereby additional lights and people do not lead to more birds retrieved). This would argue also, however, for fallout cost to reach a maximum early in the growth of urban development (an important consideration; see below).

MODELING

We developed a population-dynamic model for the Newell's Shearwater, using assumptions similar to those used by others in analogous contexts (e.g., Simons 1984, Beissinger 1995, Shannon and Crawford 1999), to project population trajectory with and without mortality due to anthropogenic factors and to quantify the relative impact of those threats. We used a Leslie model (Leslie 1945), which combines age-specific fecundity and survival to estimate population growth rates. Due to lack of information about year-to-year variation in demographic parameters, which is the case for the vast majority of demographic studies of wild, long-lived vertebrates, we assumed average (constant) values for the parameters. Owing to lack of data regarding age-related variation in demographic parameters among shearwaters and other procellariiforms (e.g., Bradley et al. 1989, Wooller et al. 1989), and consistent with the efforts of other researchers, we also made the simplifying assumption of age-constant survival and reproductive success for individuals that have reached adulthood.

Our approach, first, was to determine the combination of parameter values that produced a stable population. Against this, current population parameters could be compared to show that, in the absence of recent anthropogenic activity, Newell's Shearwaters can maintain their numbers. Second, we used conservative, best estimates for each parameter and compared population projections that did and did not include various factors affecting population growth. The factors considered were: (1) mortality of fledglings attracted to lights and subsequently grounded during autumn (fallout), (2) mortality of adults and subadults that collide with utility structures during spring and summer, (3) predation of adults and subadults in the breeding

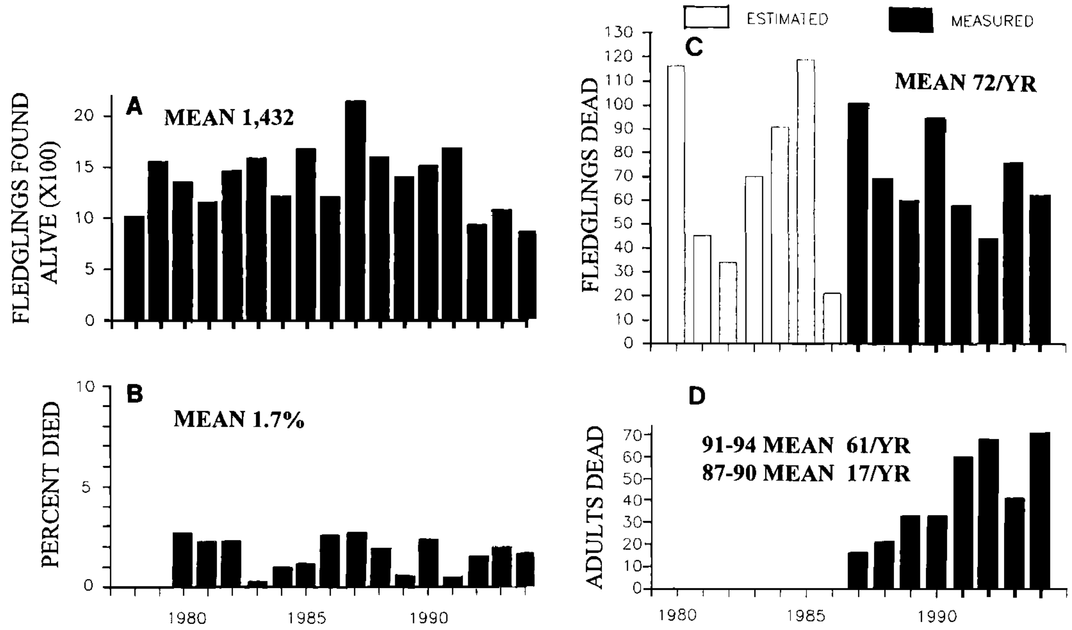

FIGURE 2. Summary of SOS data for Newell's Shearwaters on Kaua'i, Hawaiian Islands: (A) total fledglings retrieved annually, 1980–1994; (B) percentage of fledglings that died in captivity during those years; (C) the number of fledglings, and (D) number of adults, respectively, as reported dead on the road (not retrieved). The number of dead fledglings was estimated for years prior to 1987 (see Methods).

colonies, and (4) reduction of mortality to fledglings as a result of the SOS program in autumn.

For all analyses, we used the computer package STATA (Computer Resource Center 1993). Averages are reported with ± 1 SE.

RESULTS

Breeding Effort and Success

Telfer (1986) monitored 36–47 burrows in the Kalāheo colony during 1981–1985, and we monitored 58–65 burrows, including many in Telfer's sample, in 1993–1994. Among the burrows checked in 1981–1985, the proportion in which breeding adults occurred (i.e., eggs or chicks found) averaged 46.5% ± 6.4% (range 30% to 62%). In 1993, the proportion was 26%, although this is a minimum as some eggs probably were lost before we finished our search for burrows (which took two months). In 1994, our effort was insufficient to derive an estimate of reproductive effort (see Methods). In 1993, 58 burrows were visited by shearwaters (88%); thus, a high level of nonbreeding (no eggs laid) was apparent. Not determined in 1981–1985 was the proportion of burrows that actually were active (i.e., used regularly regardless of whether an egg was laid).

Among nests in which eggs were laid, an average 66.0% ± 6.4% (range 49–75%) succeeded each year, from 1981 to 1985; in 1993 only 27% succeeded and in 1994 81% succeeded. Like Telfer in 1981–1985, we could not ascertain the cause of mortality of most chicks. Only three of the 1994 chicks were from burrows in which eggs were laid in 1993; conversely, among the sites that produced chicks in 1994, 11 were active but none of these produced eggs or chicks in 1993. In total, the Newell's Shearwater produced 0.66 chicks/breeding pair/yr during the 1981–1985 period.

On average, 1,432 fledglings were reported to SOS each year, ranging from 950 (1992) to 2,200 (1987; Fig. 2A). Some of the variation was explained by differences in the timing of moon phases from one year to the next. It appears that when the full moon occurs in mid-October, the peak of fledging (Telfer et al. 1987, Ainley et al. 1997b), as in 1981, the total number of individuals found during all of the fledgling period (mid-September to early November) is much lower than if the full moon occurs at the periphery of peak fledging, i.e., in early or late October (Fig. 3). Breeding effort and success probably also affect the number of fledglings picked up; for instance, 1987 was a year when ocean productivity in the shearwaters' feeding grounds was unusually high (see Discussion) and the number of fledglings picked up was higher than expected. Nineteen eighty-seven

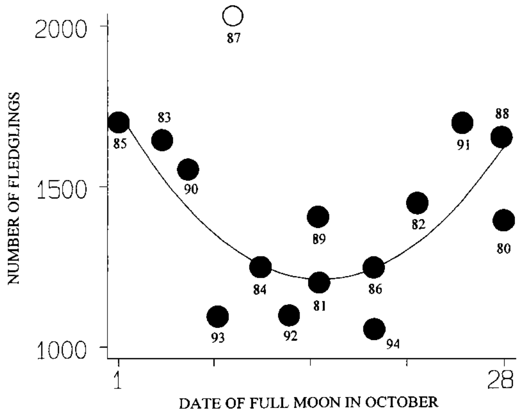

FIGURE 3. The total number of fledgling Newell's Shearwaters on Kaua'i, Hawaiian Islands, retrieved by SOS each autumn (Sept–Nov), 1980–1994, as a function of how closely the full moon coincided with the peak of fledging (mid-October). The point for 1987 was not used to generate the regression line (r^2 = 0.572, $F_{2,11}$ = 7.36, P = 0.009; see text). Number by black and white circles indicates year.

was also a year when the full moon did not occur during the middle of fledging and, thus, the two factors (high ocean productivity, timing of full moon) combined to produce high fallout numbers. Finally, curtailment of lighting, as Hurricane Iniki accomplished in 1992–1993 (and even into 1994 somewhat), brought fewer fledglings to ground (Fig. 2A). The same pattern can be seen locally at the Kaua'i Surf/Westin Lagoons Hotel when lighting was adjusted during renovations in 1983 (Fig. 4B) as subsequent fallout was much lower.

MORTALITY

Breeding colony

We found one fresh adult carcass and six skeletons of adults or subadults in the colony during 1993. In 1994, we found 23 dead shearwaters. All were skeletons of adults that had been killed in the early spring during courtship two months before our first visit, and each had marks on the sternum to suggest eating by a cat. Almost all dead birds were found in the lower two-thirds of the study area indicating that the cat entered the colony from the sugarcane fields below the colony rather than using our access above the colony. Telfer (1986) found cat predation to be significant especially during the second year of his five year study.

We caught one cat and eight rats during 1993, but caught neither rats nor cats in 1994. Each year, we found rat droppings deposited throughout the colony before our arrival. During our work at night in 1993, we often saw or heard introduced Barn Owls (*Tyto alba*). Barn Owls prey on Newell's Shearwaters (Byrd and Telfer 1980), and it was clear that they homed in on the Newell's Shearwater vocalizations that we occasionally played from a tape recorder (Ainley et al. 1995). During the day or evening only, we infrequently saw Short-eared Owls (*Asio flammeus*), but whether they prey on shearwaters is not known.

Urban corridor

The number of fledglings that died each year during SOS processing averaged 1.7% of the total turned in (Fig. 2B). The number of fledglings logged by SOS as dead on the road, but not deposited at SOS stations, averaged an additional 6% of the total each year (Fig. 2C). Almost all of these birds were checked for bands.

During 1991–1994, when a concerted search for dead adults was conducted, 42–72 were found in spring and summer each year (mean = 61 ± 7/yr; Fig. 2D; see also Ainley et al. 1995, Podolsky et al. 1998). Before the directed search, an average 17 ± 2 dead adults were reported per year by SOS (1987–1990). In 1993–1994, among 30 adults that could be sexed (not overly smashed), the male:female ratio was 8:9, and 7 (23%) were breeders. The average mass of dead adults was 381 ± 8 g (N = 35), a value important to our estimate of adult survival (see below).

RATES OF BAND RECOVERIES

Recoveries and band-return rates of fledgling and adult shearwaters were unexpectedly low. None of 15 fledglings banded in 1993–1994 and none of 52 banded in the study colony during 1980–1985 were picked up subsequently by SOS.

In 1993, we captured nine adults in the colony, but none had been banded previously. Only 1 of 30 adults/subadults found dead in 1993–1994 was banded. That one individual had been banded as a fledgling by SOS during fallout on the Southshore. Thus, we found 1 (2.6%) banded birds among 39 adults/subadults examined in the colony in 1993–1994. Similarly low band returns are evident in a sample of 14 adults banded in 1983 (T. Telfer, unpubl. data). These birds were attracted one night to a camp light in the Kōke'e forest (Fig. 1). One of these birds (7.1%) was subsequently recovered upon hitting a power line.

An equally low recovery rate is evident among adults found dead along power lines and roadways. Thus far, only 15 of the 23,000 fledglings banded and released by SOS have been recovered as adults or subadults during subsequent years (Table 1). Excluding data from the

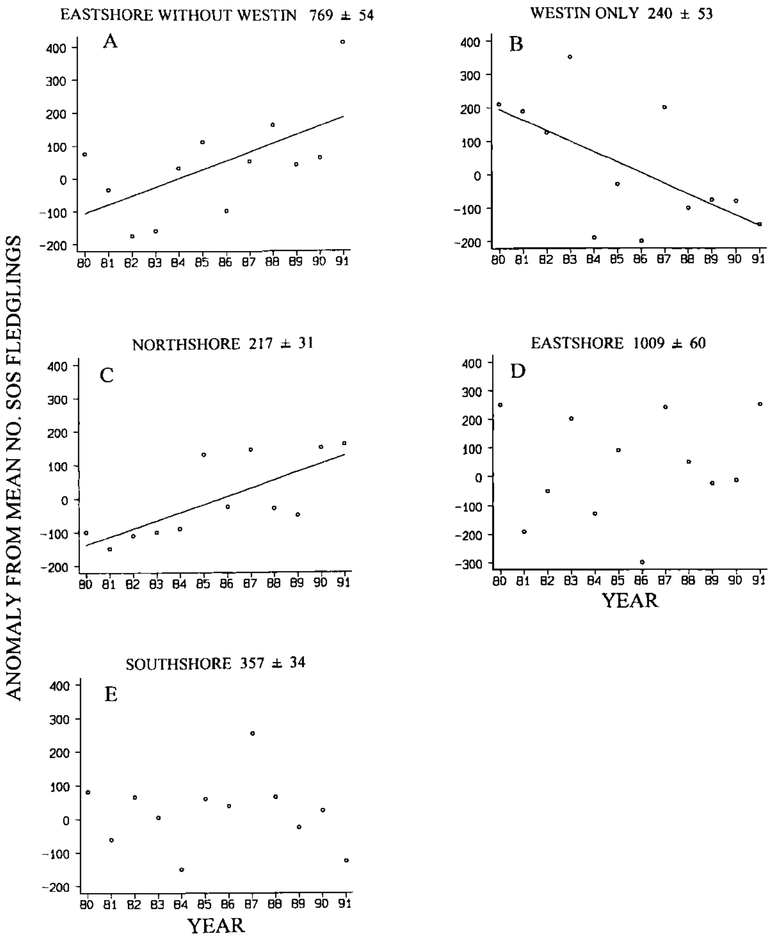

FIGURE 4. Deviations from the mean number of Newell's Shearwater fledglings on Kaua'i, Hawaiian Islands, retrieved by SOS each year, 1980–1994, on the: (A) Eastshore with data from the Kaua'i Surf/Westin Hotel (district) removed [$Y = -2201 + 26.2X$; $r^2 = 0.365$, SE = 10.9, $P = 0.038$]; (B) Kaua'i Surf /Westin Lagoons Hotel only [$Y = 2723–31.6X$; $r^2 = 0.381$, SE = 12.7, $P = 0.032$]; and totals for (C) Northshore [$Y = -2062 + 24.1X$; $r^2 = 0.543$, SE = 6.9, $P = 0.006$], (D) Eastshore [$P = 0.7$], and (E) Southshore [$P = 0.8$].

first few years, when weak monel bands were used, the recovery rate was only 0.1% (12 of 12,443 birds banded in 1982–1990 and recovered in 1989–1994). Looked at in another way, among 351 adults reported to SOS, from 1987 to 1994 (when search effort was quantified), 12 (3.4%) had been banded. Three-fourths of the recoveries occurred during the past four years, when search effort was much greater than it had been (Ainley et al. 1995). No birds <2 yrs of age have been recovered.

POPULATION TRENDS

For all of Kaua'i, numbers of fledglings picked up each year were about the same during the period 1980–1990 (Fig. 2A). Thereafter, even after 1987 numbers declined each year (including years beyond those of this study, through 1997; SOS unpubl. data, T. Telfer, pers. comm.). Results separated by region of retrieval showed a steeply growing number of fledglings for the Northshore (Fig. 4C, D, and E). No sloping trend was evident for the Eastshore (Fig. 4D), unless data for the Kaua'i Surf/Westin Lagoons Hotel were analyzed separately (Fig. 4B). Then, positive growth in the number of fledglings was evident (Fig. 4A). Similarly, no sloping trend was evident for the Southshore overall, although a decline not evident in the other regions is apparent after 1988 (Fig. 4E).

The growing number of SOS-processed birds on the East- and especially the Northshore occurred in concert with the doubling and quadrupling, respectively, of urban development (size

TABLE 1. THE TIME OF YEAR THAT BANDED NEWELL'S SHEARWATERS OF KNOWN AGE WERE RECOVERED ON KAUA'I FROM 1980 TO 1994[a]

Age (Yr)	May			June					July				August				
	<18	18	25	1	8	15	22	29	6	13	20	27	3	10	17	24	31
2–3				1	1	1	1	2	1		1						
4–5	1			2							1						1
≥6	1												1				

[a] Dates represent the first day of one-week periods.

of the human population) since 1970 (Fig. 5A). On the Southshore, where the human population has always exceeded that elsewhere on Kaua'i, it also increased during 1970–1990, but in this case it was returning to a level reached previously in the 1940s. The infrastructure to support tourists (lights included), indexed by the number of persons passing through the Līhu'e Airport, increased more than 12-fold in recent decades (Fig. 5B). We hypothesize that this growth, too, with its accompanying lights, probably affected the ability of urban areas to attract fledglings. Many coastal hotels, restaurants, sporting facilities, etc., have been built to accommodate these tourists and the resident population to service them. To summarize, then, on portions of Kaua'i where urbanization has been increasing recently, more and more fledglings have been recovered by SOS; where urbanization has been even denser and more widely spread for a long time, no trend in SOS retrievals has occurred. We hypothesize that either the proportion of fledglings attracted to lights and the retrieval capabilities of SOS have become saturated in those areas, or an increasingly greater proportion of fledglings are being attracted and the shearwater population has suffered greater mortality due to fallout and, in effect, has declined (see Discussion). In other words, the decline is masked because an increasing proportion of fledglings are being attracted to lights.

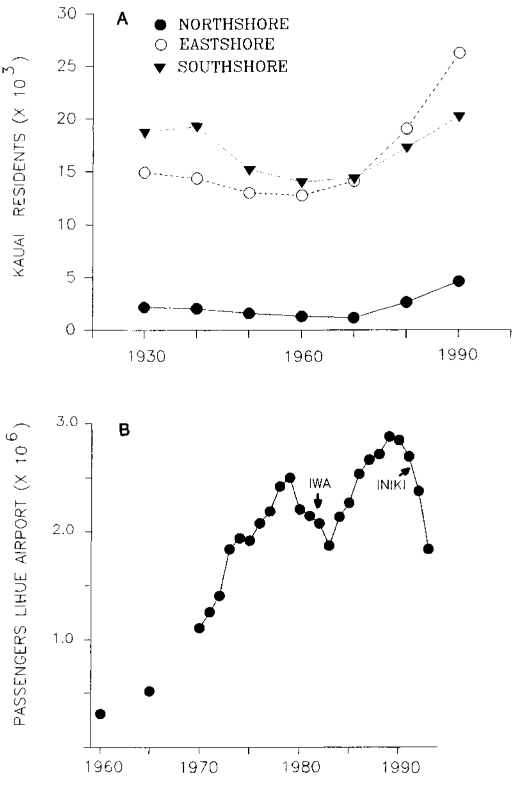

FIGURE 5. Indices to urbanization of Kaua'i, Hawaiian Islands: (A) Number of permanent residents on North-, East-, and Southshores, 1930–1990 (cf. Fig. 1); (B) Number of passengers at Līhu'e Airport (mostly tourists who need to reside at hotels, condominiums, etc.), 1960–1993 (data from State Airports Commission). Another commercial but private airport opened in Princeville ca. 1980 (but no data on passengers are available).

POPULATION MODELING

To put our results into perspective, we developed a Leslie model (Leslie 1945), that incorporates the various parameters of productivity and mortality. Before doing this, and in order to estimate mortality rates, we had to estimate the total number of fledglings produced on Kaua'i. The average 9,636 fledglings/yr was derived by multiplying three values: (1) 84,000, the estimated total population of Hawaiian Newell's Shearwaters (excluding fledglings; Spear et al. 1995); (2) 0.637, the proportion of total population of breeding age, i.e., 6 yrs or older, derived from the stable age distribution (see below); and (3) 0.547, the proportion of adults that bred in any given year (see below). The result was 14,600 breeding pairs, which produced 0.66 fledglings per pair. Our estimate of fledgling numbers does not correct for the few that would occur on Hawai'i (where radar studies indicate far fewer Newell's Shearwaters than on Kaua'i; Ainley et al. 1997b, Reynolds et al. 1997a).

PARAMETERS USED IN THE POPULATION MODEL

Five demographic parameters were required in the Leslie model: survival of adults (i.e., those

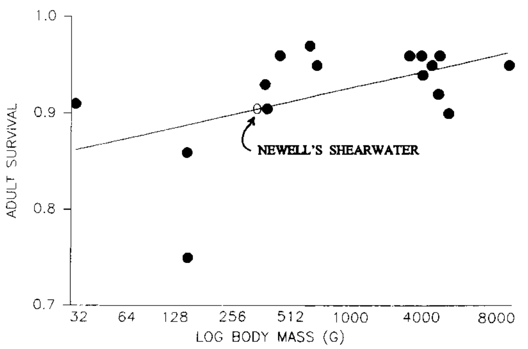

FIGURE 6. Relationship between body mass and annual adult survival among procellariiforms; data extracted from Gaillard et al. (1989) and Dunning (1992). A significant relationship (P = 0.045) exists between log (adult survival) and log (body mass).

birds physiologically mature); survival of juveniles and subadults (i.e., birds between fledging and 12 months of age and those after the first year of life but before adulthood, respectively); age of first breeding; reproductive success; and breeding probability (i.e., the probability that an adult will breed in a specific year). Before discussing model results, we present values for these parameters here, incorporating empirical results and those from the literature.

Annual survivorship

Annual survivorship, as in most seabirds, has not been studied in Newell's Shearwater. We estimated annual adult survival to be 0.905, a value reported for a population of the very closely related Manx Shearwater (*P. p. puffinus*; taxonomy summarized in Ainley et al. 1997a), whose numbers have been stable and which has been exhaustively studied since the 1950s (Brooke 1990). This value is consistent with those reported for procellariiforms of similar mass (Croxall and Gaston 1988) and with an allometric relationship to body mass (381 g; see above) among procellariiforms (Fig. 6). From this regression, the predicted value for adult survival of a Newell's Shearwater was 0.904 ± 0.017, with an approximate 95% prediction interval of 0.870–0.934.

Juvenile and subadult survival

Juvenile and subadult survival also have not been studied in Newell's Shearwater and are poorly known in procellariiforms and most wild birds. The well-studied Manx Shearwater, again, can provide some insight. After adjusting for dispersal, Brooke (1990) estimated that 33.3% of Manx Shearwater fledglings survived from fledging to breeding age (age 6 yrs or older). We incorporated this value into the simulations for Newell's Shearwaters, after considering the following patterns in the few other seabird species for which empirical data are available. Annual survival of juvenile and subadult alcids (e.g., Common and Thick-billed murres [*Uria aalge* and *U. Lomvia*], the size of which is similar to Newell's Shearwater) at ages 1, 2, and 3 yrs, respectively, is 60%, 82–83%, and 95–96% of the adult value; from the fourth year on, subadults have attained 100% of the adult value (Nur 1993, De Santo and Nelson 1995; S. Beissinger and N. Nur, unpubl. data). A similar pattern has been observed among male Western Gulls (*Larus occidentalis*; Spear et al. 1987), South Polar Skuas (*Catharacta maccormicki*; Ainley et al. 1990), also similarly sized to Newell's Shearwater, as well as among the heavier-bodied Adélie Penguin (*Pygoscelis adeliae*; Ainley and DeMaster 1980) and African Penguin (*Spheniscus dermersus*; Shannon and Crawford 1999). This pattern of age-specific survival was maintained by us for the Newell's Shearwater while scaling survival upward to achieve a total survival of 0.333 between fledging and age 6 yrs. The result was annual survival estimates of 0.654, 0.78, 0.89, and 0.905 in the first four years of life, and 0.905 for each year of life thereafter (within 1 SE of 0.904, the value obtained from the allometric regression, above).

These survival values, consistent with those for other seabird species, if anything, may be a bit high rather than too low. For example, survival from fledging to age 6 yrs in a growing population of Cory's Shearwater (*Calonectris diomedea*; Mougin et al. 1987) was estimated to be in the interval 0.230–0.334; Simons (1984) assumed survival from fledging to breeding age of 0.268 for a stable population of Dark-rumped Petrels; and for five alcid species, survival to average breeding age ranged 0.244–0.345 (Hudson 1985). As pointed out below, given an adult survival of 0.905, survival from fledging to breeding age would need to be at least 0.333 to produce a stable population; therefore, we retained this estimate.

Age of first breeding

On the basis of an average age of first breeding in the Manx Shearwater of six to seven years (Brooke 1990) and data presented in Table 1, we assumed that no Newell's Shearwater breeds before age 6 yrs, and from age 6 yrs onward, all individuals breed with probability, *p* (see below). Among 15 banded, known-age Newell's Shearwaters recovered by SOS during the past several years (Table 1), essentially all <5 yr of age were found from the period of late-egg laying onward, suggesting that they did not breed.

Of the two birds 6–7 yrs old, one was found in the prelaying period, consistent with a bird arriving early enough to breed. We further estimated that 1-*p* fraction of 6-yr-old Newell's Shearwaters would not breed in a given year. The result of this assumption is that the actual mean age of first breeding is between 6 and 7 yrs in all of our simulations, which is consistent with values not just for Manx Shearwater but also for the other shearwater species for which empirical data are available: 7 yrs in the Short-tailed Shearwater (Bradley et al. 1989) and 9 yrs in Cory's Shearwater (Mougin et al. 1987).

Longevity

We assumed a maximum age of 36 yrs for Newell's Shearwater. This corresponds to the maximal age observed among other shearwaters (e.g., Bradley et al. 1989).

Productivity

We used a breeding success value of 0.66 fledglings/breeding pair, a value determined in our study, to simulate the current trajectory of the Kaua'i population. In the Manx Shearwater, reproductive success was 0.70 (Brooke 1990), a value consistent with that reported for Short-tailed Shearwater (Wooller et al. 1989). We used 0.70 to simulate a balanced Newell's Shearwater population.

The low numbers of fledglings picked up by SOS during 1992 and 1993 may be due to several factors: (1) strong El Niño conditions that negatively affected food availability and, thus, shearwater breeding success (see below); (2) the possibility that Hurricane Iniki killed many birds, forcing a need for much new pairing and construction of burrows, two factors that result in lower breeding success in other seabirds (but this is unlikely; see above); (3) an absence of bright lights (which attract fledglings) on Kaua'i for many months after the storm (see above); and (4), at least for 1992, the effect of the full moon during fledging (Fig. 3). None of these explanations are likely to explain the pattern entirely, however, because the numbers of fledglings found by SOS continues to decline even through 1998 (SOS, unpubl. data; T. Telfer, pers. comm.). We hypothesize that recently we have begun to see the effects of the costs of fallout and adult mortality on the stability of the shearwater population (see below).

The low number of birds turned in during fall 1978 was certainly a result of the start-up nature of the SOS program. The large number found in 1987 was unusual, but is consistent with that year being at the start of one of the strongest La Niñas of recent decades. At that time, unusually productive waters existed in the eastern tropical Pacific, where Newell's Shearwaters feed (cf. Ribic et al. 1992, Spear et al. 1995). Thus, in 1987, breeding success may have been unusually high, and, in that year, the timing of the full moon would not have decreased the numbers of fledglings found.

It is not known whether the fewer fledglings found in some years, as a function of moon phase, is due to their greater ability to see structures in the moonlight (hence, fewer crashes), or whether fledglings are attracted away from civilization by the very bright moon (as suggested by Reed et al. 1985). The moon is clearly the brightest light source around and is low on the horizon just after sunset; our surveys indicated that most fallout occurs during the three hours after sunset (Ainley et al. 1995). Also hypothesized as a possibility by Reed et al. (1985), but determined to be false by us, is that moon phase affects the fledging rate, i.e., young may not fledge during the bright full moon (Ainley et al. 1995).

Breeding probability

The breeding probability parameter refers to the proportion of adults occupying a burrow in which no egg is laid. In Newell's Shearwater, 46% of occupied burrows produced an egg during the 1981–1985 period. Some of these burrows were surely occupied by prebreeding individuals. Assuming that (1) all 4- and 5-yr-old Newell's Shearwaters occupied burrows but did not breed (see above), (2) all individuals >5 yr of age occupied burrows and bred with probability *p* (see above), and (3) 4- and 5-yr-olds composed 15.9% of all individuals 4 yr or older (as determined from simulations described below), we can solve for the fraction of breeding-aged individuals that bred. Dividing 46% by 84.1% (proportion of burrow-holding population that has the potential to breed) yields an annual breeding probability of 0.547. In the Manx Shearwater, 20% of adults that had bred previously do not breed in a given year (Brooke 1990); in Short-tailed Shearwater, 12% of adults do not attend the colony and 19% maintain burrows but do not lay an egg (i.e., breeding probability is 0.69; Wooller et al. 1989).

There are two sources of uncertainty concerning our estimate of breeding probability. First, sampling error is associated with the estimate of 46% of pairs breeding among those occupying burrows (SE = 0.035; 95% CI = 0.39–0.53). Second, uncertain is our assumption that 15.9% of burrows are occupied by prebreeding individuals (i.e., that all 4- and 5-yr-olds occupy burrows but do not breed and that 2- and 3-yr-olds do not occupy burrows). If 3-, 4- and 5-yr-olds occupy burrows, this implies that 22% of bur-

TABLE 2. PARAMETER ESTIMATES USED IN LESLIE MODELS UNDER DIFFERENT SCENARIOS

		Best estimate: Newell's Shearwater		
	Balanced: Manx Shearwater	W/O Power line mortality, predation, or fallout	W/Power line mortality, predation, and fallout	W/Power line mortality, and fallout, but W/O predation
Survival: adult	0.909	0.905	0.896	0.904
Survival: fledgling to adulthood	0.333	0.333	0.239	0.327
Age first breeding	6–7	6–7	6–7	6-7
Breeding success	0.70	0.66	0.634[a]	0.634[a]
Breeding probability	0.80	0.547	0.547	0.547
λ	1.000	0.968	0.939	0.963

[a] 0.66 chicks fledge per breeding pair but 4% of fledged chicks die in fallout (not rescued by SOS); therefore, 0.66 × 0.96 = 0.634.

rows are occupied by prebreeders; alternatively, if only 5-yr-olds occupy burrows, this implies that 11% of burrows are occupied by prebreeders. In turn, this implies that breeding probability may vary between 0.60 (if only 5-yr-olds hold burrows) and 0.50 (if 3-, 4- and 5-yr-olds all hold burrows). We used 80% breeding probability for simulating a balanced population (Manx Shearwater), but 54.7% for simulating the contemporary Newell's Shearwater population.

The factors that affect breeding probability in Newell's Shearwater are not known for certain. Why reproductive effort was so low especially in 1993 is difficult to ascertain. As in 1983, the year that Telfer (1986) found the fewest burrows with eggs, 1993 was a year of major El Niño. Characteristic of such years, seabirds forgo reproduction because of a lack of food reserves (Schreiber and Schreiber 1984, Ainley and Boekelheide 1990). The 1993 breeding season also closely followed the devastation of Hurricane Iniki (September 1992). We saw some evidence of terrain slumping and a few uprooted trees at Kalāheo. Thus, the high level of nonbreeding could have been related to storm damage, but we saw little evidence of major burrow excavation, and many burrows used in 1993–1994 was not unusual for this population. It is not clear why breeding probability is low in the Newell's Shearwater (54%), but it may result from a high level of mate loss (itself a result of excessive mortality, see below) because, among seabirds, breeders who have lost their mates usually cannot obtain a new one quickly (e.g., Ainley and DeMaster 1980, Boekelheide and Ainley 1989). It could be, too, that our estimates are biased.

SIMULATION OF A BALANCED POPULATION

Incorporating values from the Manx populations (Table 2), our model produced a population that was nearly balanced but still declined slowly at 0.65% per year (λ, the finite population growth rate = 0.994). Thus, after 10 years, the population will have declined by 6.3%. Increasing adult survival from 0.905 to 0.909, however, produced a stable population: λ = 1.000. An adult survival rate of 0.909, within 1 SE of Brooke's (1990) estimate of 0.905, is statistically reasonable.

Substituting a breeding probability of 0.547 and a reproductive success of 0.66 in the model, i.e., Newell's Shearwater values, produced a population that declined at 3.2%/yr (λ = 0.968). This is our best estimate of the current population trajectory of the Newell's Shearwater in the absence of additional mortality due to fallout, collisions with power lines, or from introduced predators (see below). In other words it is an idealistic scenario. The main factor affecting the declining growth rate was the fact that breeding probability was 0.547, rather than 0.8. Substituting 0.547 into the model was by itself sufficient to reduce population growth rate from 1.000 to 0.978. A breeding success of 0.66 (versus 0.70) and adult survival of 0.905 (versus 0.909) were of minor influence in lowering population growth rate, accounting for an additional drop from 0.978 to 0.968.

POPULATION STABILITY WITH MORTALITY OF FLEDGLINGS DURING FALLOUT

We next added mortality to fledglings during fallout to the simulation, i.e., attraction to lights and subsequent death owing to a complex of factors (see Introduction). This mortality occurs in spite of the efforts of SOS.

On the basis of the SOS data gathered by an opportunistic effort, the percent of fledglings that died annually, among those encountered by SOS, was 7.7% (see above; Fig. 2). However, on our night surveys in which search effort was quantified, 43% of fledglings were found dead (Ainley et al. 1995, Podolsky et al. 1998). The discrepancy with SOS must be due partly to different areas being surveyed, our sampling of areas that were less frequented by citizens (e.g.,

TABLE 3. FLEDGLING MORTALITY AS A FUNCTION OF MORBIDITY AND DISCOVERY RATES[a] OF NEWELL'S SHEARWATERS ON KAUA'I, HAWAIIAN ISLANDS

Morbidity rate	Discovery rate 100%	80%	67%	50%
7.7%	0.011	0.014	0.017	0.023
15%	0.022	0.028	0.033	0.044
25%	0.037	0.046	0.056	0.074
43%	0.064	0.080	0.096	0.127

[a] Morbidity = percentage dead among downed fledglings; discovery = percentage of downed fledglings found by SOS.

TABLE 4. POPULATION GROWTH RATES (λ) IN RELATION TO FLEDGLING MORTALITY, ADULT, AND SUBADULT MORTALITY AND PREDATION OF NEWELL'S SHEARWATER ON KAUA'I, HAWAIIAN ISLANDS

Fledgling mortality	Adult/subadult power line-caused mortality None	Low	Medium	High
Without predation from introduced animals:				
0.02	0.966	0.965	0.963	0.962
0.04	0.965	0.963	0.962	0.960
0.06	0.964	0.962	0.960	0.959
0.08	0.963	0.961	0.959	0.958
0.10	0.961	0.960	0.958	0.957
With predation from introduced animals:				
0.02		0.941	0.939	
0.04		0.939	0.938	
0.06		0.938	0.937	
0.08		0.937	0.936	
0.10		0.936	0.934	

sugarcane fields, secondary roads), and the reluctance of the public to salvage dead birds for SOS. The true mortality could be approximated better if we knew the number of birds that citizens rescued from our circuits each night before we passed through. Our regular checks of SOS shearwater drop-off stations in the vicinity of our circuits, however, revealed a few (1–5) but not disproportionately large numbers of additional live birds. Clearly, a greater proportion of each year's fledgling cohort dies than is revealed by SOS data. This hypothesis is supported by the fact that SOS reported none of 44 dead birds tagged and left in place by us during autumn 1993 and 1994 (Ainley et al. 1995, Podolsky et al. 1998). Thus, the true morbidity, i.e., probability that a downed fledgling dies, is likely between 7.7% and 43% of all fledglings. In our simulations, we considered these extremes as well as intermediate values of 15% and 25%.

Finally, we estimated the proportion of all downed fledglings encountered by the public and (if alive) brought to SOS stations, i.e., discovered. An extreme assumption would be that citizens discovered (and recorded) all downed fledglings. This scenario is unlikely, because some fledglings fall in inaccessible areas, such as sugarcane fields (which occupy a huge proportion of Kaua'i's coastal plain and are crossed by many kilometers of power lines), as well as other factors that could prevent discovery (e.g., birds moved by predators, birds hiding in the bushes). On the other hand, without recording them, some citizens find birds and release them into the ocean at the beach (probably jeopardizing the shearwaters, which are not anatomically prepared to deal with surf). The proportion of individuals that escape on their own are not our concern here. Therefore, we have considered four scenarios: 100%, 80%, 66.7%, and 50% of all downed fledglings are discovered by SOS.

Combining four levels of morbidity and four levels of discovery yields 16 combinations of total fledgling mortality (Table 3). We recognize that the two dimensions, morbidity and discovery, are likely related: the more fledglings that come down in areas not covered efficiently by citizens, the higher the level of morbidity, since many fledglings will not be able to recover (e.g., it would take days, if ever, for a shearwater to extricate itself from the tall, dense foliage of a sugarcane field). However, our intention is merely to indicate the range of fledgling mortality likely to be sustained by this population. Total fledgling mortality due to fallout for the 16 different combinations of morbidity and discovery ranged 1.1% to 12.7%. Thus, in the most optimistic scenario, 1,432 out of 9,636 fledglings are downed and 7.7% of the 1,432 die (110/9,636 = 0.011). In the most pessimistic scenario, 2,864 fledglings are downed and 43.1% of these die (1,232/9,636 = 0.128).

We simulated the effects of fledgling mortality due to fallout, allowing the fraction of fledglings dying to vary from as low as 0.02 to as high as 0.10, where all other parameter values corresponded to our best estimate model (Table 2). High fledgling mortality (0.10) lowered λ by 0.5%, compared to low fledgling mortality (0.02; Tables 4, 5; Fig. 7A).

POPULATION STABILITY WITH SUBADULT AND ADULT MORTALITY DUE TO POWER LINE COLLISIONS

As indicated above, about 61 subadults and adults have been found dead as a result of power line collisions each year. This by no means includes all such individuals, as an adequate search of inland power lines, of which there are about 40 km across sugarcane fields, was beyond our resources (Ainley et al. 1995, Podolsky et al. 1998). We assumed true island-wide mortality to be either 122 birds (i.e., twice the measured level: "low power line mortality"), 244

TABLE 5. COMPARISON OF POPULATION GROWTH RATES (λ) AT DIFFERENT LEVELS OF SPONTANEOUS ESCAPEMENT BY DOWNED NEWELL'S SHEARWATER FLEDGLINGS ON KAUA'I, HAWAIIAN ISLANDS, WITH AND WITHOUT PREDATION FROM INTRODUCED ANIMALS AND WITHOUT THE SOS PROGRAM

Fledgling mortality	25% of downed fledglings escape		0% of downed fledglings escape	
	Population Growth rate	Difference[a]	Population Growth rate	Difference[a]
Low-level power line mortality for adults/subadults, without predation:				
0.02	0.958	0.0071	0.955	0.0096
0.06	0.955	0.0073	0.952	0.0099
0.10	0.952	0.0075	0.949	0.0102
Low-level power line mortality for adults/subadults, with predation:				
0.02	0.934	0.0062	0.932	0.0085
0.06	0.932	0.0063	0.930	0.0087
0.10	0.929	0.0066	0.926	0.0091

[a] Absolute difference in λ, comparing population growth rate for a population with (see Table 4) and without SOS program (in which 25% or 0%, respectively, of the 1,432 fledglings turned in each year would escape on their own).

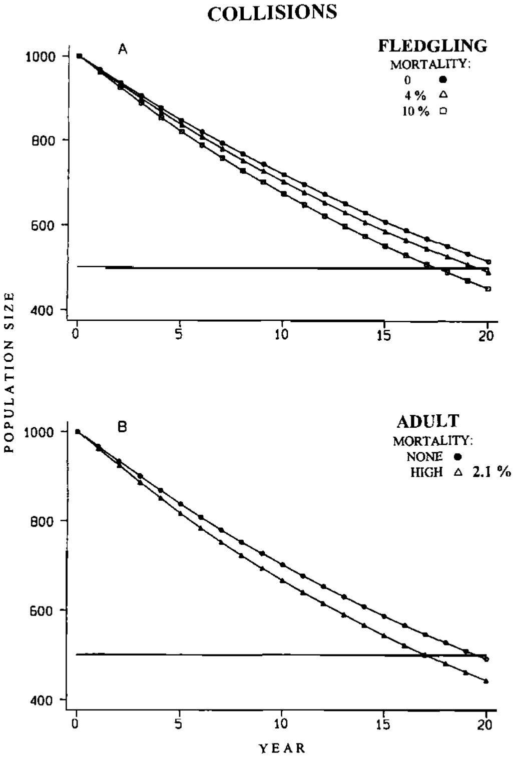

FIGURE 7. Results of simulations showing effects on population growth in the Newell's Shearwater caused by: (A) fledgling mortality of 0, 4, and 10% due to fallout; and (B) no versus high adult/subadult mortality due to collisions with power lines. The horizontal line indicates 50% population level.

birds (i.e., 4 × 61, "medium power line mortality"), or 350 dead birds ("high power line mortality"; see Ainley et al. 1995, Podolsky et al. 1998, for derivation). In addition, such mortality is apparently age specific: subadults appear more vulnerable than breeding adults. First, as noted above, 20% of the birds found and necropsied by us were active breeders, yet an estimated 35% of such birds exist in the population (on the basis of the model, 0.637 × 0.547). Second, an additional sample of 15 known-aged (banded) subadult and adult individuals killed by power lines (Table 1) indicated that only two (13%) were 6 yrs of age or older (i.e., of breeding age); the remainder were 2–5 yrs of age (subadults). Thus, the two samples yielded similar adult:subadult ratios.

On the basis of these data, we assumed either 24, 48, or 70 dead breeders per year (122, 244, or 350 × 0.2). Dividing 24, 48, and 70 by the total number of adults at the colony yielded mortality rates of 0.046%, 0.092%, and 0.131%, respectively, for the three levels of power line mortality. For subadults ages 2–5 yrs (Table 1), depending on the level of power line mortality, we derived mortality rates of 0.60%, 1.20%, and 1.72%, respectively.

We simulated population growth rate incorporating these levels of subadult and adult mortality, together with a range of fledgling (fallout) mortality values (Table 4). The effect of high subadult and adult power line mortality compared to no such mortality was to lower population growth rate by 0.5% for a given level of fledgling mortality. Low and intermediate subadult and adult power line mortality generated intermediate levels compared to high and no power line mortality. It appears that the magnitude of the effect of power line mortality on population growth rate is roughly comparable to the estimated effect of fledgling mortality (i.e., depressing the population growth rate by as much as 0.5%). We considered the high level of power line mortality to be the best estimate of such (Ainley et al. 1995, Podolsky et al. 1998). Nevertheless, for analyzing effects of predation and efficacy of the SOS program, to err on the side of caution given the uncertainties involved, we used our most conservative estimates of power line mortality.

POPULATION STABILITY WITH PREDATION OF BURROW OCCUPANTS

Mortality due to predation from introduced animals should be considered additional to mortality already discussed, since most studies of shearwaters have been conducted at sites where predation of subadults and adults is low. Some Manx Shearwaters are taken by Great Skuas (*Catharacta skua*) and large gulls (*Larus* spp.), but numbers of these avian predators are extremely low because of control programs (Furness 1987). Predation by humans had a marked effect on the Cory's Shearwater population (Mougin et al. 1987).

We found 30 dead subadults and adults among the estimated 600 individuals in the Kalāheo colony (about 150 burrows × 2 yrs × 2 individuals/burrow/yr; Ainley et al. 1995). This yielded a crude estimate of 5% mortality among burrow holders. We modeled this as an extra 2.5% morality averaged over all adults and subadults (excluding 1-yr-olds). We chose to use 2.5% mortality (rather than 5%) to reflect the fact that some individuals killed might have been transients and not burrow holders, and some nonbreeders of breeding age might not have been present at the burrows at all, as in the Short-tailed Shearwater (Wooller et al. 1989; see above). As shown below, even 2.5% mortality of subadults and adults has a dramatic effect on population growth rate. We have not considered mortality of adults or chicks due to predation by rats, for we have no data on rat predation, a most difficult factor to quantify (Thompson 1987, Seto 1995, Seto and Conant 1996).

We also considered that predation, especially from owls, is age specific. Active breeders are inconspicuous, so we assumed that they incurred a very low predation rate, whereas 4- and 5-yr-olds, who attempt to gain both a burrow and a mate, are most conspicuous of all and suffered the highest predation rate. We assumed that inactive breeders (individuals that bred in a previous year, but not the current year) and 2-and 3-yr-olds incur intermediate levels of predation. Taking into account our subjective assessment of predation risk, 2- and 3-yr-olds were assigned a mortality rate due to predation of 5%; 4- and 5-yr-olds a rate of 10%; and breeding age individuals (whether active or inactive) a predation rate of 1%. Averaged over all individuals 2 yrs of age or older, mortality due to predation was 2.5%.

The effect of predation on population growth was dramatic (Tables 4, 5). Simulations indicated a decline of 0.023–0.024 in the finite population growth rate, depending on the level of mortality assumed for fledglings, subadults, and adults. Thus, the two most important factors in determining population growth (and in this case, decline) were the low breeding probability compared with that of stable shearwater populations (0.547 versus 0.80) and the apparently high mortality rate due to introduced predators. The two may well be related; loss of mates (due to predation, hurricanes, or power line collision, see above) may lead to a reduced breeding probability for the current or subsequent breeding season.

POPULATION STABILITY WITH SOS REDUCTION OF FLEDGLING MORTALITY

There is little information regarding the number of fledglings that come to ground but then, in the absence of SOS, spontaneously escape to the sea. Here, to assess the impact of SOS, we consider two possibilities: 0% and 25% of downed fledglings escape on their own. Telfer et al. (1987) proposed that few fledglings that fallout would be capable of survival on their own. In fact, we observed two fledglings who took off after being grounded (it was windy and they were in a large, unobstructed expanse—empty parking lots; Ainley et al. 1995).

In the simulations (Table 5), 2.0–10.0% of all fledglings were assumed to have died as a result of hitting power lines, etc., just as was implemented in the simulations shown in Table 4, and then an additional 1,432 (due to not being rescued by SOS participants, assuming 0% spontaneous escape) or 1,074 (assuming 25% spontaneous escape) fledglings die. The decline in population growth rate in the absence of SOS was 0.62–0.75% if 25% of downed fledglings escaped on their own, and ranged 0.85–1.02% in the absence of spontaneous escape. Therefore, the SOS program has had a significant effect on population growth of the Kaua'i population: fledgling mortality, in the presence of SOS, lowered the population growth rate by 0.12–0.62% but, in the absence of SOS, lowered it by an additional 0.62–1.02%.

MODELED POPULATION TRAJECTORIES

Finally, we modeled the population trajectory for the Kaua'i population of Newell's Shearwaters under four scenarios, assuming an arbitrary starting population size of 1,000 individuals (of all ages >1 yr; Fig. 8A). All scenarios assumed a "low" level of subadult and adult mortality due to power lines and 4% mortality of fledglings due to fallout (see above). Scenarios 1 and 3 assumed the continued operation of the SOS program, but scenarios 2 and 4 assumed no such program, and further assumed that 25% of downed fledglings spontaneously escape (see above). Scenarios 1 and 2 included no provision for mortality due to introduced predators; scenarios 3 and 4 included such mortality.

We also considered results for these scenarios with values of breeding probability and reproductive success from the Manx Shearwater (Table 2, Fig. 8B; Brooke 1990). After all, Newell's Shearwater eggs raised in the absence of pred-

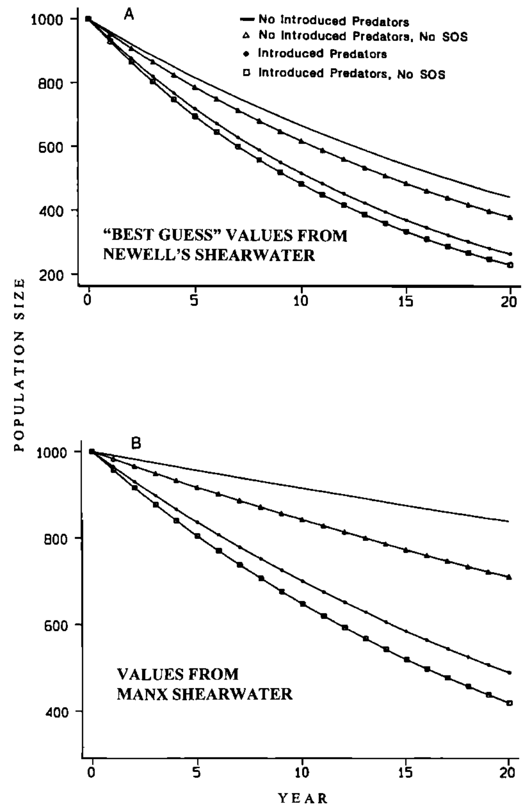

FIGURE 8. Results of simulations showing effects on population growth of shearwaters in the face of low-level mortality to fledglings due to fallout (SOS in operation), low levels of mortality to adults/subadults due to collisions, and low levels of predation on adults/subadults in the breeding colonies, assuming: (A) demographic parameters estimated currently for the Newell's Shearwater, and (B) demographic parameters estimated for the Manx Shearwater.

ators (by Wedge-tailed Shearwaters) attained a success equal to that of the Manx Shearwater (Byrd et al. 1984). Moreover, Manx values, when combined with other parameter values, produced a population declining slightly, whereas Newell's values produced a population declining steeply (see above). If one concludes that the Newell's population is declining slightly rather than steeply, one should adopt Manx values. Whatever values one uses, however, qualitatively similar results are produced: the cessation of the SOS program would accelerate the decline of the Newell's Shearwater population by two fold (in the absence of predation).

DISCUSSION

Comparing the spatial and temporal patterns in the SOS data with those evident in urbanization, as well as modeling results, we interpret the trends seen in fallout as follows. The shearwater population on the Southshore is decreasing. The increased urbanization there, which is compensated somewhat by the slightly increased use of shielded lights (since 1987), should lead to more shearwaters being found, all else being equal. The opposite pattern observed, however (no increase in fallout), is consistent with an added cost (mortality that is not uncompensated) and a declining population. The severe reduction in the size of the Southshore colony at Kaluahonu (few occupied burrows present in 1992–1993 compared to the early 1980s; Ainley et al. 1995) is consistent with this trend. In fact, because our inputs to the demographic model were gathered on the Southshore (Kalāheo colony, routes to quantify mortality), our model results duplicate well what we propose is happening to the Southshore Newell's shearwater population on the basis of SOS results.

In contrast to the Southshore, shearwater colonies on the Eastshore and Northshore are facing increased urbanization (well beyond historical levels; Fig. 5A) and, as predicted with more lights, more birds are being reported to SOS (Fig. 4A, C). The very recent growth in urbanization is so dramatic that the increased use of shielded lights (although still minimal) must be having little compensatory effect on shearwater fallout. Due to mortality and ensuing population decline, the fallout pattern for the North- and Eastshore eventually should duplicate the trend seen on the Southshore: level or decreasing fallout. Indeed, following our study, the number of fledglings found in 1995, 1996, 1997, and 1998 (T. Telfer, pers. comm.) continued the "unexplained" gradual lowering of SOS totals that began in 1992 (or even 1987).

In the absence of fallout, power line-caused mortality, and introduced predators, the model showed that the Kaua'i population of Newell's Shearwaters should be able to maintain its numbers, i.e., no other important factors affect population instability. The SOS program goes far to reduce one of these mortality factors, death of fledglings due to fallout. Even with SOS, however, there is significant mortality of fledglings; >2% and as much as 10% or more of fledged shearwaters likely die as a result of fallout. Mortality of subadults and adults due to power line collisions also depresses population growth, but depending on the actual rates obtained, it may or may not be as important. Firm quantification of the significance of power line-caused mortality among subadults and adults awaits further study. In the absence of the SOS program, however, fallout-caused mortality of fledglings would likely be more important than power line-caused mortality of subadults and adults.

Evidence points clearly to two factors that importantly affect population growth of the Newell's Shearwater: low breeding probability and high rates of predation on adults and subadults. The cause of the low breeding probability are not readily apparent, but rates would be exacerbated by mortality of breeders and prebreeders due to predation, disturbance by predators, and collisions with power lines. Otherwise, even if the Newell's Shearwater breeding population is not currently declining (i.e., the model is wrong and the SOS results are not a valid index of population size), our results indicate the vulnerability of the Newell's Shearwater population. A reduction in the production and survival of fledglings will only be felt many years later, at the time when such fledglings would have begun breeding. Remember, the longevity of this species is about 30 yrs, and not even one generation has passed since urbanization began to expand rapidly. We ask, Are the low SOS totals continuing past 1987 and the unusually low banded-bird recovery rates finally indicating decreased survival? Seen in this context, mortality of adults and subadults due to collisions is still of great concern for recovery of Newell's Shearwater (see USFWS 1982a).

Alternative hypotheses exist, of course, to explain some of the trends revealed by our research and simulations. The regional difference in trends could be a result of an increasing population of shearwaters on the Northshore due either to immigration from colonies on the Southshore (in turn to help explain the decrease there) or much better breeding success on the Northshore than on the Southshore. A shift from the Southshore to the Northshore is problematic given the high degree of philopatry characteristic of procellariiforms (Warham 1990). The very low recovery rate of shearwaters initially banded as fledglings by SOS could be a result of a lower-than-natural survival rate of these birds (deemed to have been "rescued" by SOS only because they were able to fly away). Another possibility is that the large majority of fledglings picked up by SOS were produced on the Northshore—and eventually recruited to Northshore colonies as adults—but having reached the sea were attracted back to land by coastal lights on the more brightly lighted South- and Eastshores. Until 1995, the Northshore had lacked the power lines that effectively "sample" adults and subadults in the population, although following completion of our study high, deep arrays of lines have been installed. Thus, sampling efficiency may have increased and we can see whether or not the number of banded birds found also increases. Additional research in the colonies on the Northshore also could easily determine whether many banded shearwaters nest there.

In conclusion, then, the population of Newell's Shearwaters on Kaua'i appears to be declining. On the basis of demographic modeling, the prospects appear to be poor for the continued existence of a robust population of this species on this island. A reversal of the indicated population trends will be possible only with more strict controls of lighting (such as on the Big Island, where the astronomical observatories require minimal upward light radiation), fencing and predator control in several important shearwater breeding areas, and, possibly, the burying of power lines in a few especially critical areas (Ainley et al. 1997a, Podolsky et al. 1998).

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