Assessment of demographic risk factors and management priorities: impacts on juveniles substantially affect population viability of a long-lived seabird

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Abstract

Predicting population-level effects from changes in demographic rates of different life stages is critical to prioritize conservation efforts. Demographic modeling and sensitivity analysis in particular, has become a standard tool to evaluate how management actions influence species' survival. Demographic analyses have resulted in the robust generalization that, for long-lived species with delayed reproduction, population growth rates will be most sensitive to changes in survivorship of older-aged individuals. Although useful in guiding management, this simple maxim may limit options for conservation by causing managers to overlook actions that, although possibly not the most effective in terms of increasing a population's growth rate in an ideal world, can nonetheless more feasibly and rapidly slow a population's decline. We examine the population-level benefits of increasing chick survival in a long-lived seabird, the Laysan albatross *Phoebastria immutabilis*. Specifically, we use a simple deterministic modeling approach to evaluate the impact of chick mortality (from ingestion of lead-based paint) on the population growth rate (λ) for Laysan albatross that breed on Sand Island, Midway Atoll (part of the Hawaiian Archipelago). We estimate that up to 7% of chicks on Sand Island fail to fledge as a result of lead poisoning, which will create a 16% reduction in the Laysan albatross population size ($\sim$190 000 less birds) at 50 years into the future. We demonstrate how straightforward management actions that increase juvenile survivorship (e.g. removal of lead-based paint) can help slow population declines while efforts are underway to reduce politically and logistically challenging threats to adult survivorship (e.g. mortality from international fisheries bycatch). Our work exemplifies a situation where over-generalizations about demography can stifle useful conservation actions and highlights the need to consider the population-level benefits from multiple management strategies.

Introduction

Conservationists are often forced to prioritize management strategies for rapidly declining species. Selection of an optimal management plan involves complex trade-offs between the logistical feasibility of improving different aspects of demographic performance and the sensitivity of population viability to improving demographic rates. One key conservation development has been the adoption of demographic modeling and especially the use of sensitivity analysis (Wisdom, Mills & Doak, 2000; Caswell, 2001; Morris & Doak, 2002; Ellner & Fieberg, 2003; Baxter *et al.*, 2006) all seek to address the

relationship between changes in age- or stage-specific demographic rates (e.g. survival, growth, reproduction), which can be directly targeted through management actions, and the resulting impacts on population growth or extinction risk. Methods that quantitatively tie alternative actions to population persistence have been widely used to justify and prioritize management plans (e.g. Crouse, Crowder & Caswell, 1987; Drechsler, Burgman & Menkhorst, 1998; Haydon, Laurenson & Sillero-Zubiri, 2002).

While sensitivity analysis has been applied in many targeted conservation studies, efforts to draw broader lessons from these methods have also led to the formulation of generalities about the most important life stages or

demographic rates to target when attempting to stabilize or increase populations. These include the observation that for all but the most short-lived and highly fecund species, population growth is more sensitive to changes in survival than reproduction and that, for long-lived species, decreases in adult survival are of far greater importance than decreases of the same magnitude in survival of younger life stages (Croxall & Rothery, 1991; Heppell, 1998; Cortes, 2002). Numerous demographic assessments have supported these useful generalizations (Croxall & Rothery, 1991; Doak, Kareiva & Kleptetka, 1994; Hunter & Caswell, 2005; Awkerman *et al.*, 2006), which are valuable in cases where we know little besides a species' general life-history pattern, yet need to anticipate the relative effects of different management interventions.

Even though these generalities about sensitivity patterns are robust, the implications of these patterns for conservation management planning have in some cases been elevated to the level of dogma, potentially hindering effective prioritization and conservation planning. In particular, the observation that population growth rates are influenced more heavily by the same proportional change in survival of adults than of young age classes has sometimes been misinterpreted to mean that only adult survival rates have meaningful influences on growth rates and hence should be the sole targets of conservation action. While no scientist well trained in demographic methods would make such assertions, this over-simplification is widespread enough that we have seen it muddle thinking about conservation planning and management (M. Finkelstein & D. Doak, pers. obs.). Here, we address a particular case where this perspective on demography and management is likely to be inappropriate and use it as a case study to highlight the need for a more nuanced use of demographic tools.

Our case study concerns the Laysan albatross *Phoebastria immutabilis*, one of the three North Pacific albatross species that breeds primarily within the Hawaiian archipelago and has a global population of *c.* 2.5 million (Whittow, 1993*b*). Similar to most albatross species, Laysan albatross populations are believed to be declining, with their status listed as vulnerable by the International Union for Conservation of Nature (IUCN, http://www.iucnredlist.org). Fisheries bycatch mortality is considered a key threat to Laysan albatross (BirdLife International, 2008) and a main conservation focus has been to estimate, understand and mitigate for these effects. However, an additional anthropogenic mortality source is lead poisoning of Laysan albatross chicks on Sand Island, Midway Atoll (Sileo & Fefer, 1987; Work & Smith, 1996; Finkelstein, Gwiazda & Smith, 2003) where *c.* 45% of the global population breeds [US Fish and Wildlife Service (USFWS), unpubl. data]. Finkelstein *et al.* (2003) reported that chicks ingest lead-based paint from abandoned military buildings and that many chicks were severely lead poisoned (blood lead $> 100 \, \mu g \, dL^{-1}$) compared with adults (blood lead $\sim 1 \, \mu g \, dL^{-1}$). Indeed, Finkelstein *et al.* (2003) found substantial numbers of Laysan albatross chicks exhibited overt signs of lead toxicity (peripheral neuropathy, droopwing, Fig. 1). Chicks with droopwing will

Figure 1 Lead poisoned Laysan albatross chick *Phoebastria immutabilis* on Sand Island Midway Atoll exhibiting overt signs of toxicity, peripheral neuropathy (droopwing). Droopwing is a lethal condition as chicks with droopwing will never be able to fly (fledge). Our previous work indicated that $> 80\%$ of chicks ($n = 21$) sampled near buildings between 2000 and 2001 had blood lead levels high enough ($> 100 \, \mu g \, dL^{-1}$) to cause droopwing or other symptoms of severe clinical toxicity [e.g. encephalopathy (Goyer, 1996)] (Finkelstein *et al.*, 2003).

never fly and as a result will die either at the end of the breeding season (when their parents stop feeding them), or sooner from other lead-induced complications [e.g. renal failure, encephalopathy (Goyer, 1996)]. While thousands of Laysan albatross chicks may die from lead poisoning each year, the concept that only adult mortality is important for population persistence of these long-lived birds has stymied efforts to initiate lead-based paint remediation (M. Finkelstein, pers. obs.).

We used population viability analysis (PVA) to explore the impact of chick lead poisoning on the Laysan albatross population growth rate (λ). As fisheries bycatch is deemed the primary threat to Laysan albatross survival (Gales, 1998; BirdLife International, 2008), our demographic model included effects from lead poisoning of chicks and bycatch mortality of adults. We evaluate how a 'minor' rate of juvenile mortality, which has been considered to have a negligible effect on population growth, may be important for long-lived species with low fecundity. In particular we discuss the benefits of immediate management actions that,

although perhaps not the most effective in terms of proportional increases in population growth, can help 'buy time' while more biologically effective, but also more complex and difficult, conservation actions are being initiated. In this context, we highlight the value of including time delays and feasibility of change when prioritizing multiple management actions.

Methods

Laysan albatross life history

Laysan albatrosses are monogamous, forming strong pair bonds that are usually only broken by death or disappearance (Whittow, 1993*b*). Females lay one egg per clutch, one clutch per year and do not lay a replacement if their egg is lost (Whittow, 1993*b*). Laysan albatrosses typically return to the same nest in successive years (Fisher, 1976) and their chicks tend to recruit as breeders to the area where they were raised (Tickell, 2000).

Demographic model structure

We constructed a deterministic nine-stage female-based Lefkovitch matrix with one chick, three juvenile, two immature, two sub-adult age classes and one adult stage class (Table 1, Fig. 2). We follow a post-breeding census design; our model starts directly post-laying so the youngest age class is a newly laid egg. Thus, the first age class spans the egg to 1 year old and age classes continue in 1 year increments through 8 years of age, after which birds are considered to be mature breeding adults (aged 8 +) (Fig. 2).

Similar to previously published demographic models of albatross population dynamics (Weimerskirch, Brothers & Jouventin, 1997; Lewison & Crowder, 2003; Arnold, Brault & Croxall, 2006), we did not incorporate senescence in our model structure. Additionally, our model did not include density dependence as there is no direct evidence of density dependence for Laysan albatross, nor is it believed to be a strong regulating factor for other albatross populations (Weimerskirch *et al.*, 1997; Lewison & Crowder, 2003; Arnold *et al.*, 2006; Awkerman *et al.*, 2006).

Demographic parameters

Parameter rates used in this deterministic model (Table 1) were based on published Laysan albatross demographic data (Fisher, 1975, 1976; Van Ryzin & Fisher, 1976) from birds banded between the 1930s and 1960s and re-sighted during the 1960s and 1970s. The model-derived deterministic λ (1.048) based on these historic demographic data was far higher than the average λ based on recent census data (0.995) collected on Midway Atoll during the 1991/1992–2006/2007 breeding seasons (Data used were from direct nest counts conducted on Midway Atoll for the following breeding seasons: 1991/1992, 1996/1997, 2000/2001, 2001/2002, 2003/2004, 2004/2005, 2005/2006, 2006/2007. The USFWS reported that their direct count method

Table 1 Laysan albatross *Phoebastria immutabilis* population matrix and parameter values used in our deterministic model

	S_{one}	S_j	S_j	S_j	S_i	S_i	S_{sa}	S_{sa}	S_a
	0	0	0	0	0	0	0	0	0.366
	0.482	0	0	0	0	0	0	0	0
	0	0.840	0	0	0	0	0	0	0
	0	0	0.840	0	0	0	0	0	0
$N_{i,t}$	0	0	0	0.840	0	0	0	0	0
	0	0	0	0	0.906	0	0	0	0
	0	0	0	0	0	0.906	0	0	0
	0	0	0	0	0	0	0.945	0	0
	0	0	0	0	0	0	0	0.945	0.916

Survivorship values, including egg to fledge, were modified (multiplied by 0.954) from published demographic data (Fisher, 1975) such that the model-derived deterministic λ (0.995) approximated the average lambda from census data between the years 1992 and 2006 (USFWS, unpubl. data). $N_{i,t}$ is the age-specific population size at time *t*. The youngest class in this post-breeding model is newly laid eggs: survival over the next year of life, S_{one}, comprises $S_c \times S_{\text{fledge}}$, where S_c is the survival of an egg to fledge (0.526) and S_{fledge} is the probability of surviving from fledge to 1 year old (0.917) and then continues with three juvenile age classes (S_j), two immature age classes (S_i), two sub-adult age classes (S_{sa}) and one adult age class (S_a) with a probability of surviving to the next year of 0.840, 0.906, 0.945 and 0.916, respectively (Fig. 2). Fecundity (*F*) for adult birds 8+(0.366) is defined as follows: $F_{8+} = f \times b \times S_a$ where *f* is the proportion of the population that is female (assumed to be 0.5), *b* is the probability of breeding (0.80) (Fisher, 1976) and S_a is the probability that an adult female survives for the year in order to lay an egg.
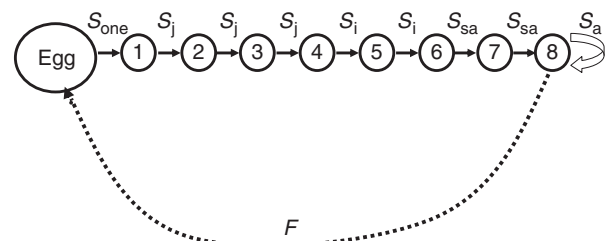

Figure 2 Diagram of post-breeding census model developed for Laysan albatross *Phoebastria immutabilis*. The model begins with newly laid eggs. The first year encompasses an egg to 1 year old, S_{one}, and then continues in 1-year increments with three juvenile age classes (S_j), two immature age classes (S_i), two sub-adult age classes (S_{sa}) and one adult age class (S_a) with a probability of surviving to the next year of 0.482, 0.840, 0.906, 0.945 and 0.916, respectively (Table 1). *F* is the fecundity of mature adults (aged 8 + , 0.366, see Table 1).

had an observer error of 1.76% in 2007.) [USFWS, unpubl. data; calculated using linear regression (Dennis, Munholland & Scott, 1991; Morris & Doak, 2002)]. Therefore, to reduce the model-derived λ such that it approximated the average λ based on recent census data, we multiplied each annual survivorship value (including egg to fledge) by a
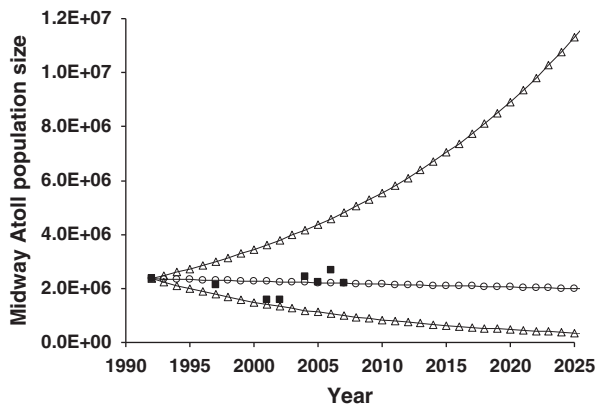
Figure 3 The model-derived total population size for Laysan albatross *Phoebastria immutabilis* on Midway Atoll from 1992 through 2025, based on the average λ (0.995, circles with solid line) and 70% confidence intervals (triangles with solid line) calculated by linear regression (Dennis *et al.*, 1991; Morris & Doak, 2002) using Midway Atoll Laysan albatross census data between the years 1992 and 2006 (USFWS, unpubl. data). Census data (number of breeding pairs) were converted to total population size (filled squares) by using the annual probability of breeding (0.80) (Fisher, 1976), and the stable age distribution from the deterministic matrix (Table 1). Note that the total population size presented represents Midway Atoll, which encompasses, three islands – Sand, Spit and Eastern. Census data were obtained through direct nest counts conducted on Midway Atoll; in 2007 the USFWS determined that their direct count method had an observer error of 1.76%.

single multiplier (0.954). Notably, although we used the average λ from census data to calibrate rates for our model, the uncertainty associated with this value encompasses a λ value equal to 1 ($\pm$70% confidence intervals are 0.944 and 1.049), limiting our ability to precisely predict future sizes of the population (Fig. 3).

The Laysan albatross starting population size (1 528 220) used for model projections was calculated from the number of breeding pairs on Sand Island, Midway Atoll during the 2006/2007 breeding season (277 732 pairs, USFWS, unpubl. data), the annual probability of breeding (0.80) (Fisher, 1976), and the stable age distribution (from the deterministic matrix, Table 1).

Lead-induced chick mortality

To estimate population-wide lead exposure, we conservatively assumed that all Laysan albatross chicks within 15 m of structures with lead-based paint were at risk while those further away were not. We believe this is a conservative assumption because (1) chicks are exposed by directly eating paint chips, not through contact with contaminated soil (Finkelstein *et al.*, 2003); (2) chicks are highly mobile for $\sim$1–2 months before they fledge, easily traveling up to 15 m from their nests in order to find shade, such as that provided by structures; (3) wind can move paint chips considerable distances ($>$15 m) from deteriorating structures (M. Finkel-

stein, pers. obs.); (4) there is no clear evidence of a decreasing linear relationship between how far a chick's nest is from a structure and that chick's lead exposure (most likely due in part to points 1–3 above).

A survey of 41 buildings on Sand Island (May 2006) recorded $\sim$1450 chicks within $\sim$5 m of buildings with an average of 35 ± 26 SD chicks per building. As there are $\sim$95 structures with lead-based paint on Sand Island (USFWS, unpubl. data), *c.* 3325 chicks nest within 5 m of buildings, and, given a fairly uniform nesting density, $\sim$10 000 chicks wander within 15 m of buildings. We assumed that all chicks that wander within 15 m of structures, and as such could encounter and ingest lead-based paint, are at risk for exposure. Although we took a simple approach to estimate the number of chicks within 15 m of buildings, we were constrained by the lack of data available and the multiple variables (e.g. temperature, terrain) that dictate how far a chick will wander and be exposed to lead-based paint. Reassuringly, using different metrics (total area of the island potentially contaminated by lead and island-wide nesting density), an estimate by one of us (J. Klavitter) conducted in 2004 arrived at a similar number of chicks per year ($\sim$6750) at risk for exposure from lead-based paint on Sand Island. For our model projections, we assumed that all chicks at risk for exposure did not survive to fledge. We made this assumption as $>$80% of chicks nesting near buildings had blood lead levels high enough ($>$100 μg dL^{-1}, Finkelstein *et al.*, 2003) to cause droopwing (Fig. 1) or other symptoms of severe clinical toxicity (e.g. encephalopathy, Goyer, 1996) which would either prevent the chick from fledging (chicks with droopwing cannot fly) or almost certainly prevent the chick from surviving to reproductive maturity. Furthermore, exposure to lower levels of lead, although not always indicative of overt toxicity, is known to cause neurological and immune impairment in avian species (Redig, Dunnette & Sivanandan, 1991; Dey *et al.*, 2000); therefore, even chicks not exhibiting clinical symptoms of lead toxicity are likely suffering toxicological effects that could impair their survival.

The estimated annual percentage of chicks that fail to fledge due to lead poisoning used in model scenarios (7%) was calculated assuming 10 000 chicks on Sand Island fail to fledge due to lead poisoning, the 2006 USFWS census data for Sand Island (277 732 breeding pairs), and survivorship data [egg to fledge: 0.526 (modified from Fisher, 1975), S_c, Table 1] as follows: $277\,732 \times 0.526 \approx 146\,000$, the number of eggs producing chicks that survive to fledge; $10\,000 \div 146\,000 = 0.07 = 7\%$, the percentage of chicks that fail to fledge due to lead poisoning. Note that we assumed the egg to fledge survivorship value (0.526) did not incorporate mortality from lead-based paint; consequently the 10 000 chicks that fail to fledge from lead poisoning were treated as a percentage of the chicks that would otherwise have fledged. Thus, egg to fledge survivorship that incorporates 7% lead mortality of chicks is 0.489 ($0.526 \times (1 - 0.07)$). Our treatment of lead-induced mortality as independent of natural mortality is reasonable because by time the chicks are old ($\sim$2 months) and healthy enough to move around, exhibit inquisitive behavior and ingest paint

chips, they have survived most natural mortality risks (e.g. survival from egg-to-hatch ∼60%).

Chick mortality from lead-based paint was not incorporated in the average growth rate (0.995) calculated from censuses of breeding adults because (1) the United States Navy left Midway in 1997 at which time there was an acceleration of lead-based paint deterioration due to lack of maintenance; (2) Laysan albatross life history dictates that effects from lead-based paint on chick survival will not be translated into changes in the number of breeding adults for at least a decade.

We recognize that there is a large degree of uncertainty in our estimate of the number of chicks that die per year from lead poisoning, but there are insufficient data to provide a more specific number. As such, we ran a subset of the model projections with a lower and higher rate of lead-induced mortality (3.5 and 14% of chicks fail to fledge per year) to represent a realistic range of possible outcomes from lead poisoning on Laysan albatross population dynamics. We assumed the percentage of chicks that fail to fledge each year is static (i.e. does not change over time) and given our observations of increasing lead-based paint deterioration on Sand Island structures, we feel this is a conservative assumption. We also assumed that clean-up of lead-based paint from Sand Island includes removal of paint chips from contaminated soil around buildings. Thus, chick mortality from lead-based paint is zero in model projections following clean-up of lead-based paint.

Fisheries bycatch mortality

Although Laysan albatrosses are impacted by fisheries bycatch (BirdLife International, 2008), the number of birds killed annually in global fishing operations is unknown. To examine population effects from changes in bycatch mortality, we subtracted and added annual bycatch mortality in 1% increments (from $+5$ to -3%, where $+5\%$ is a 5% increase in bycatch mortality and -3% is a 3% reduction in bycatch mortality) to adult (aged $8+$) survivorship. Conservatively, our model did not account for the change of a chick's survivorship due to changes in their parents' bycatch rates. Given that fisheries bycatch rates of black-footed albatross *Phoebastria nigripes*, a sympatrically breeding (Whittow, 1993*a,b*) North Pacific species, were estimated to be between 1.9 and 5.0% (Lewison & Crowder, 2003), our approach was reasonable for approximating how changes in bycatch mortality could affect Laysan albatross population dynamics.

Elasticity analysis to compare different management actions

To estimate the time delay with which an immediate cessation of chick deaths from lead-based paint would equal the benefit, in terms of population size, to a 1% reduction in annual bycatch mortality of older-aged individuals (aged $8+$), we used two approaches. First, we simply simulated stage-structured population growth with altered matrices.

Second, to provide a more general approach to estimate the benefits of immediate versus delayed management methods, we calculated deterministic elasticity and sensitivity values (Morris & Doak, 2002) for bycatch reduction and lead-based paint elimination, and then applied them to estimate future population sizes with different time delays in management implementation. Specifically, we derived the following equation for population growth on a log scale:

$$\log(N_T) = \log(N_0) + T\log(\lambda_c) + (T - L)E_v\Delta_{\log(v)} \quad (1)$$

where N_T is the population size at time T given the initiation of management action (elimination of lead-induced chick mortality or 1% reduction in bycatch of birds aged $8+$) in year L; N_0, the current population size; L, the number of years until management action is adopted (assuming instantaneous and not gradual reduction of mortality); λ_c, the current population growth rate (before management action is implemented); E_v, the elasticity of population growth to changes in a vital rate v; and $\Delta_{\log(v)}$, the difference in the logged values of the altered vital rate before and after management (i.e. egg to fledge survivorship for eliminating lead-induced chick mortality and survivorship of birds aged $8+$ for reducing bycatch mortality by 1%). We used this equation to find the number of years one could wait (the time delay) before the implementation of bycatch to get the same population at the end of 50 years as an immediate cessation of lead-based paint mortality (assuming 7% of chicks per year currently fail to fledge from lead poisoning). To do this, we solved the following equality:

$$\begin{aligned} T\log(\lambda_c) + (T - L_{\text{lead}})E_{\text{fledgling}}\Delta_{\log(\text{fledgling})} \\ = T\log(\lambda_c) + (T - L_{\text{bycatch}})E_{\text{adult}}\Delta_{\log(\text{adult})} \end{aligned} \quad (2)$$

where $T = 50$, $L_{\text{lead}} = 0$, and solved for L_{bycatch} with fledgling or adult representing the vital rate (v) for egg to fledge or adult (aged $8+$) survivorship, respectively. While this approach ignores unstable population structure and assumes that over the range of changing vital rate values the relationship between $\log(\lambda)$ and $\log(\text{vital rate})$ is reasonably linear, in our case it gives an answer that closely approximates that of our simulations (difference in population size at end of 50 years $\leq 0.5\%$ for lead or bycatch reduction). For situations in which the relationship between λ and vital rate is more closely linear, the following equation can be used instead:

$$\begin{aligned} \log(N_T) = \log(N_0) + T\log(\lambda_c) \\ + (T - L)\log(1 + E_v\Delta_v/V_0) \end{aligned} \quad (3)$$

where Δ_v is the difference between the new and old vital rate value, and V_0 is the initial vital rate value. For our example, the amount of change is so small that equations (1) and (3) produce nearly the same answer [time delay (years) within ∼3% of each other].

Results

Effects of lead poisoning on population growth and future population size

We determined that lead-induced annual mortality of 7% of chicks causes a decrease in the Laysan albatross population growth rate on Sand Island from 0.995 to 0.991. The range of estimates (3.5, 7 or 14) for the percentage of chicks that fail to fledge per year due to lead poisoning indicate that lead-based paint could reduce the total Laysan albatross population size on Sand Island within 50 years by 8, 16 or 30%, respectively (Fig. 4a). Removal of lead-based paint and immediate cessation of lead-induced chick mortality would thus create a buffer for the Laysan albatross population by increasing the number of birds in 50 years by ~100 000–360 000 over the projected total population size given no lead remediation (Table 2).
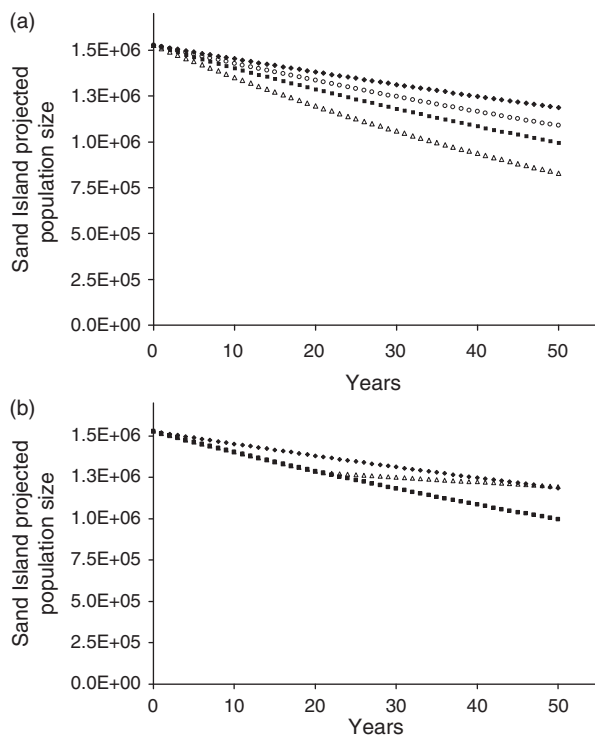

Figure 4 Laysan albatross *Phoebastria immutabilis* projected population sizes over the next 50 years on Sand Island Midway Atoll with (a) removal of lead-based paint at year = 0 and immediate cessation of lead-induced chick mortality (diamonds), no lead-based paint removal and continual chick mortality for either 3.5% (open circles), 7% (squares) or 14% (open triangles) of chicks failing to fledge per year due to lead poisoning (b) simulated population growth with removal of lead-based paint at year = 0 and immediate cessation of lead-induced chick mortality (diamonds), no lead removal with 7% of chicks failing to fledge per year due to lead poisoning (squares), or no lead removal with 7% of chicks failing to fledge per year due to lead poisoning with, at year 21 (time delay of 21 years), a 1% reduction in bycatch mortality for adult birds (aged 8 +) (open triangles).

Time delay between alternative management actions assuming 7% of chicks fail to fledge per year from lead poisoning

Even though immediate removal of lead-based paint will have about half the impact on the population growth rate (λ) as reducing adult (aged 8 +) bycatch mortality by 1% (λ increases from 0.991 to 0.995 for lead removal and to 0.998 for bycatch reduction), increasing chick survivorship now can be as effective as increasing adult survivorship at some point in the future. We determined that the time delay for achieving the same population benefit (in terms of total population size at 50 years) between immediate lead-based paint elimination and reduction of bycatch mortality by 1.0% is 21 years. As such, the Laysan albatross population size at the end of 50 years with these two management actions – lead remediation today versus bycatch reduction in 21 years – is within 0.7% of each other (Fig. 4b).

Relative effects of lead poisoning and fisheries bycatch

At the mid-level estimated rate of lead poisoning of chicks (7% year^{-1}), and a current unknown level of fisheries bycatch mortality, the population growth during the time required for first reproductive effort (8 years) is 0.930 (Fig. 5). Complete elimination of lead-induced chick mortality accompanied by a 1% reduction in bycatch mortality (i.e. 1% reduction in mortality for birds aged 8 +) would stabilize the population (λ ~1.0). However, if there is a twofold increase in lead-induced chick mortality – which is reasonable given the increasing state of deterioration of the structures on Sand Island – a reduction in bycatch mortality by ~2% (i.e. from 3 to 1% of birds aged 8 +) would be required to achieve a stable Laysan albatross population.

Discussion

We examined the quantitative benefit of increasing chick survivorship for a long-lived species with low fecundity, the Laysan albatross, and found that immediate elimination of lead-induced chick mortality would result in ~100 000–360 000 more birds in 50 years, given current survivorship rates (Table 2, note that the increased numbers of birds are projected based on a deterministic model). We also showed that elimination of lead-based paint, a logistically straight-forward (albeit relatively expensive) action, has the same effect on population size (at the end of 50 years) as a 1% reduction in bycatch mortality, a logistically challenging action, with a time delay of 21 years (Fig. 4b). Even though our results could be interpreted to suggest that lead-based paint clean-up is only necessary if bycatch reduction cannot be implemented within 21 years, we do not agree. Rather, we argue that conservation management should be precautionary and logistically feasible actions that will measurably improve demographic performance should be implemented. This is especially the case for species such as the Laysan albatross, which are currently impacted by threats for which

Table 2 Projected number of Laysan albatross *Phoebastria immutabilis* added to the total population on Sand Island Midway Atoll if lead-based paint is removed and lead poisoning of chicks ends at year = 0

Year post clean-up	Lead mortality = 3.5% before clean-up	Lead mortality = 7% before clean-up	Lead mortality = 14% before clean-up
10	24 860	49 873	100 389
20	46 861	93 196	184 275
30	66 252	130 627	253 801
40	83 263	162 765	310 850
50	98 103	190 153	357 080

Numbers represent projected increases in the total population at years 10, 20, 30, 40 and 50 post lead clean-up assuming 3.5, 7.0 or 14% of chicks currently fail to fledge due to lead poisoning. For example, if the lead mortality rate for chicks is currently 7%, and lead-based paint is cleaned up today (immediately ending lead mortality), in 30 years our model predicts there will be 130 627 more birds in the total population. Note that even in the absence of lead poisoning, the projected total population size is declining (Fig. 4a).
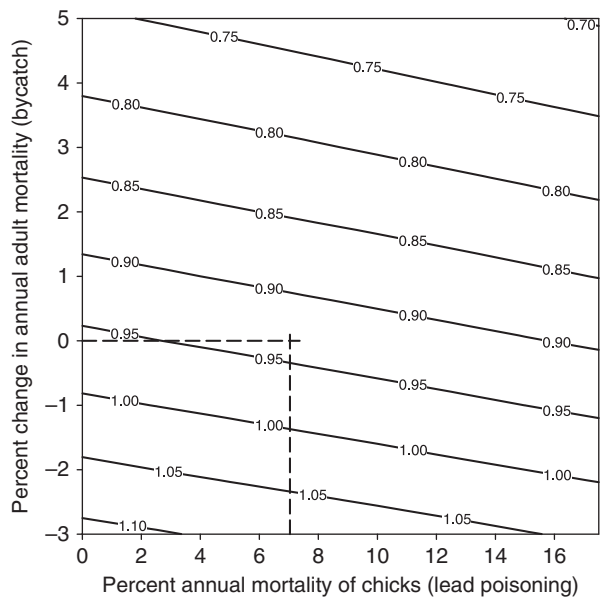

Figure 5 Relative contribution of chick mortality (from lead-based paint) and adult (aged 8 +) mortality (from fisheries bycatch) to Laysan albatross population growth during the time required for first reproductive effort (8 years) (λ^8, denoted by the contour lines). Dashed lines intersect at the population growth (λ^8, 0.930) with the current estimated rate of lead poisoning (7% of chicks) and a current unknown level of mortality from fisheries bycatch (depicted as '0'). Per cent change in annual adult mortality from fisheries bycatch spans from + 5 to −3 where + 5 represents a 5% increase in annual bycatch mortality and −3 represents a 3% reduction in annual bycatch mortality.

our understanding is tenuous at best [e.g. fisheries bycatch (Lewison *et al.*, 2004)] and are at high risk for accelerating impacts in the future [e.g. reduced habitat from sea level rise (Baker, Littnan & Johnston, 2006)].

Prompt clean-up of lead-based paint on Sand Island, in addition to buffering against known and unforeseen threats, is advisable for both logistical and financial reasons. Lead-based paint deterioration is increasing and, with structures subject to extreme weathering processes, the area of the island that is contaminated is almost certainly increasing. A greater area contaminated with lead-based paint translates to a higher percentage of Laysan albatross chicks at risk for lead exposure as well as increased clean-up costs. Even though the USFWS has recently (2005–2008) initiated limited cleanup of lead-based paint on Sand Island at a cost of *c.* US$340 000; thus far conducting lead-based paint removal on *c.* 14 of the 95 structures with lead-based paint, as well as performing an environmental risk assessment for lead (J. Klavitter, USFWS, pers. obs.), this is not enough to significantly change the current impact levels.

A recent proposal has suggested that reduction of on-island threats such as introduced predators, or in our case, contaminants, may be adequate replacements for reductions in fisheries bycatch (Wilcox & Donlan, 2007). We and others have argued that this approach could rarely work for any threatened species (Doak *et al.*, 2007; Finkelstein *et al.*, 2008; Igual *et al.*, 2009; Zydelis *et al.*, 2009), and our analysis here bolsters this point. While there are multiple sources of uncertainty which could change the quantitative and conceivably qualitative results of our model, our results nonetheless predict that Laysan albatross population stability can most easily be achieved with reduction of both bycatch and lead impacts. Fisheries bycatch reduction involves complex political, social and economical issues. Thus, international and widespread adoption of mitigation measures for vulnerable seabirds, such as the Laysan albatross, could require years of dedicated efforts. Removal of lead-based paint can help to buffer the population in the short term while efforts are underway to reduce fisheries bycatch in the long term.

In summary, we emphasize that we do not argue that juvenile mortality is more important than adult mortality for Laysan albatross population viability. Rather, we argue that for Laysan albatross as well as other long-lived species with low fecundity such as rhinoceros *Rhinoceros unicornis* and orcas *Orcinus orca* (Dinerstein, 1991; Brault & Caswell, 1993), management actions targeting juvenile survival can contribute considerably to a population's future growth. Lead-induced mortality of Laysan albatross chicks is a significant, yet manageable threat. Because removal of lead-based paint is logistically feasible in the short term, the immediate benefit to the population from increased chick survival is even more important. We show that for Laysan albatross long-term population recovery, reduction in adult mortality (i.e. bycatch) is mandatory; but eliminating lead-induced chick mortality could slow ongoing declines enough to provide substantially more time to address the complex issues associated with international regulations for fisheries bycatch reduction. We highlight the qualitative rather than quantitative insights provided by our model, which like most PVAs ignores many possible complexities. Nonetheless, our model yields a best guess of what may happen under the

management alternatives we considered (lead-based paint remediation and fisheries bycatch reduction), and although our model does not provide a measure of confidence in that guess, it nevertheless allows us to evaluate likely trade-offs between immediate and future management actions.

Conclusion

Our model results indicate that eliminating lead-induced mortality of chicks could help slow population decline while management strategies can be implemented to reduce other major population threats such as bycatch from fisheries. Others have argued that simple sensitivity analysis methods need to be modified to account not only for the instantaneous relationships between changes in vital rates and population growth, either directly or using elasticities on a proportional scale, but also by the amounts by which vital rates can be improved (Wisdom *et al.*, 2000). Additionally, the incorporation of economic costs in sensitivity analyses has been suggested in order to help evaluate alternative management strategies for increasing population growth (Baxter *et al.*, 2006). Lastly, recent work has demonstrated that sensitivity analysis can inform what life stages are important to monitor; and that the life stage best suited to predict population growth will be dependent upon the time-frame examined (Katzner, Milner-Gulland & Bragin, 2007). We add to these arguments by suggesting that the time-course of management actions must also be considered in designing multi-faceted management plans. Consideration of the feasibility of change – which involves the time delays inherent in enacting policy changes to gain improvements on demographic rates – should be part of any conservation planning effort. Even though we use less elegant methods here, our approach is similar in spirit to the use of formal sensitivity analysis of transient population behavior (Fox & Gurevitch, 2000; Caswell, 2007). Here we have shown that the time required for implementation of different management strategies should be considered when prioritizing management action. More specifically, we illustrate that conservation actions aimed at improving survival of early life stages can be of importance for many long-lived species.

Acknowledgments

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