The albatross of assessing and managing risk for long-lived pelagic seabirds

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ARTICLE INFO

ABSTRACT

Pelagic predators such as albatross have long been of conservation concern, but assessing their status poses numerous challenges. A standard monitoring method for albatross is colony-based nest counts to track numbers of breeders. However, a variable proportion of the population skips breeding in any given year and cannot be quantified by nest counts, creating several complications to efforts in understanding population dynamics. We used stochastic demographic matrix models for black-footed (*Phoebastria nigripes*) and Laysan (*P. immutabilis*) albatross to investigate: i) the potential for the skipping behavior of breeders to create apparent density dependence in nest counts, ii) the limitations to assessing population trends from nest counts and implications for evaluating impacts from fisheries bycatch, including calculating Potential Biological Removal values, and iii) the relative importance of at-sea versus on-island threats to population viability. We found the increased likelihood of these albatrosses skipping breeding following a successful season – a feature common to many seabirds and other taxa – results in substantial negative temporal auto-correlation in the observable population that can be misinterpreted as negative density dependence, with important implications for inferences about population viability. Black-footed albatross appear limited by fisheries bycatch, while Laysan albatross, which have low estimated bycatch mortality, are currently at greater risk from island-based threats. Our results suggest a cautionary approach to managing black-footed and Laysan albatross should be adopted because detecting population declines from nest counts could take decades. Ultimately, we highlight the inherent difficulties in assessing population status and trends in long-lived species such as albatross.

1. Introduction

Several groups of wide-ranging long-lived marine species, such as sea turtles and seabirds, are facing worldwide declines, and effective conservation strategies are a current topic of scientific debate (Read, 2007; Schuyler et al., 2014; Senko et al., 2014). Because these marine species breed on land, they encounter diffuse at-sea threats to adult survival as well as threats to reproductive success concentrated at breeding grounds. Combatting threats on breeding grounds is often more tractable than addressing threats at sea, but increasing reproduction is generally less effective than increasing adult survival for long-lived species with extended pre-reproductive life stages due to the lower sensitivity of the population growth rate to fecundity (Crouse

et al., 1987; Finkelstein et al., 2008; Lebreton and Clobert, 1991). Albatross are a classic example of this type of marine species (Tickell, 2000); all 22 species face potential threats on land and at sea, with the International Union for the Conservation of Nature classifying ~70% at high risk of extinction and the remainder as near threatened (IUCN, 2015). As such, tracking and monitoring albatross species is a high priority for conservation (ACAP, 2015).

Albatrosses are pelagic and spend the majority of their lives foraging across vast areas, precluding population-wide censuses. However, albatrosses are also highly philopatric to breeding colonies (Tickell, 2000), making nest counts, which quantify breeding adults, the standard option for monitoring population trends. Each year some adults skip breeding (Fisher, 1976; Jouventin and Dobson, 2002), such that

nest counts miss a fraction of adults and this fraction varies through time. Skipping behavior is related to environmental conditions (Cubaynes et al., 2011), past breeding performance, and body condition, with skipping more likely for annual breeders in the year after successfully fledging a chick (Fisher, 1976; VanderWerf and Young, 2011; Weimerskirch, 1992). Nest counts also omit pre-breeders, and albatrosses typically spend seven or more years at sea before first returning to breed (Tickell, 2000). As such, annual nest counts and their correlation with total population size are variable, and may not reflect overall population trends, at least over short time periods (Elliott and Walker, 2005; Maxwell and Jennings, 2005; Nichols and Williams, 2006). Inter-annual variability in nest counts also increases the likelihood that counts will exhibit apparent negative density dependence (NDD) even when population growth is density independent (Freckleton et al., 2006), and this effect should be especially pronounced if nest counts are negatively correlated in time due to breeding behavior. Here we investigate the challenges associated with detecting population changes and managing threats for two north Pacific albatrosses – black-footed (*Phoebastria nigripes*, BFAL) and Laysan (*P. immutabilis*, LAAL) – whose conservation status has been assessed primarily based on intermittent nest counts over the past 100 years (Arata et al., 2009; Cousins and Cooper, 2000; US Fish and Wildlife Service, 2011).

Many of the same behaviors that contribute to challenges in assessing the status of species such as BFAL and LAAL also help define their threats. Because albatrosses are extremely wide-ranging, they encounter trans-national threats that are difficult to monitor and manage, including fisheries bycatch (Lebreton and Véran, 2013; Lewison and Crowder, 2003; Véran et al., 2007) and contaminant exposure (Finkelstein et al., 2006; Young et al., 2009a). All reproduction occurs on a limited number of breeding islands, where north Pacific albatrosses nest in dense aggregations and are vulnerable to exploitation. Prior breeding-ground threats have included feather hunting in the early 1900s, thought to have dramatically reduced (i.e., > 90%) populations of LAAL and BFAL, and intentional and unintentional killing of tens to hundreds of thousands of birds due to military activities in the mid-1900s (Arata et al., 2009; Fisher and Baldwin, 1946; Kenyon et al., 1958). Climate change is a growing concern for LAAL and BFAL breeding colonies as some nesting areas are predicted to be inundated by rising sea levels (Storlazzi et al., 2013), and increased storm frequency (Murakami et al., 2013) may create storm surges that reduce reproductive success, especially for beach-nesting BFAL (Arata et al., 2009). Another island-associated threat is the invasive plant *Verbesina encelioides*, which spread across several breeding islands, including Midway and Kure Atolls (VanderWerf, 2013) in the late twentieth century, and lowers chick survival.

The most recent assessment of LAAL and BFAL population status was based on sparse nest count data and concluded that: BFAL were stable or increasing; LAAL were increasing; density-dependent processes may be operating to stabilize numbers of both species; and current fisheries bycatch levels were sustainable (Arata et al., 2009). This assessment has been a primary justification for decisions to down-classify BFAL from endangered to vulnerable in 2012 (BirdLife International, 2011, 2014) and to near threatened in 2013 (BirdLife International, 2013a, 2014) and LAAL from vulnerable to near threatened in 2012 (BirdLife International, 2013b). However, particularly for BFAL, these assessments are inconsistent with predictions of population viability based on limited survivorship data (Lebreton and Véran, 2013).

Because of the challenges inherent to using nest count data to assess population dynamics and threats in albatrosses (Bonnevie et al., 2012; Dillingham and Fletcher, 2011), we re-assessed the status of BFAL and LAAL following a population viability management approach (Bakker and Doak, 2009). In particular, we used updated data to parameterize stochastic demographic matrix models and explicitly modeled threats and management, including parameter uncertainty in key demographic

rates (Bakker and Doak, 2009) to investigate: i) the potential for the skipping behavior of breeders to create apparent density dependence in nest count data, ii) the limitations to assessing population trends from nest count data and implications for assessing impacts from fisheries bycatch, including calculating traditional estimates of the maximum acceptable bycatch mortality (i.e., Potential Biological Removal, Wade, 1998), and iii) the relative importance of at-sea versus on-island threats to population viability. Our results underscore the inherent difficulties in assessing population status and trends in long-lived, slow-reproducing species, such as albatrosses, that are highly dispersed over vast areas for the majority of their life and are monitored via nest counts that only capture a variable and incomplete segment of the population.

2. Methods

2.1. Black-footed and Laysan albatross life history

LAAL and BFAL are generally monogamous, forming strong pair bonds that are typically only broken by mate death or disappearance (Awkerman et al., 2009; Awkerman et al., 2008) or occasionally when a mate skips (Young et al., 2009b). BFAL and LAAL are considered annual breeders, but they will intermittently skip a year (Awkerman et al., 2009; Awkerman et al., 2008). Females lay one egg per breeding attempt, and eggs are not replaced in the event of nest failure (Awkerman et al., 2009; Awkerman et al., 2008). Although post-fledglings of both species forage throughout the north Pacific (Finkelstein et al., 2006; Fischer et al., 2009), they are highly philopatric, with most chicks recruiting as breeders to their natal colony and most adults returning to the same nest area in successive years (Ando et al., 2011; Dierickx et al., 2015; Fisher, 1971; Fisher and Fisher, 1969; Young, 2010).

2.2. Demographic model structure

We built stochastic demographic matrix population models with parameter uncertainty in demographic rates (Bakker et al., 2009), using Matlab (R2016b. Natick, MA: The MathWorks Inc., 2016, Supplement 1). For each species, we used stage + age-based projection matrices with a pre-breeding census for BFAL and a fledging time census for LAAL (and with corresponding differences in the definition of S_0; see Table 3). Both matrices have seven pre-breeder age classes and several breeder stages. For LAAL, we had data on state-dependent breeding probabilities that allowed separation of recruited breeders into four classes: widows, successful breeders, failed breeders, and skippers (Table 1, see Appendix 1 for explanation of these transition rates). We were unable to obtain access to species-specific data on breeding probabilities for BFAL and thus used a simpler structure, with only breeder and widow stages, the latter to allow for indirect effects of bycatch via increased widowing (Finkelstein et al., 2010b; Mills and Ryan, 2005) (Table 2). We incorporated variance in observed breeders by imposing an annual stochastic breeding probability.

We used best estimates for BFAL and LAAL demographic rates, including updated data made available subsequent to Arata et al. (2009) (Table 3). As is typical when parameterizing demographic models, available data represented different samples sizes and were collected across a wide temporal and spatial range (Tables 3, S1–S2). Survival estimates were based on mark-recapture studies and thus represent apparent survival; however, due to the high philopatry of these species (Fisher and Fisher, 1969; Young, 2010), negative bias is assumed to be minimal. In testing our model against historical data (Fig. 1), we imposed known threats, specifically the effects of fisheries bycatch on survival and the effects of *Verbesina* on reproduction. To avoid double-counting of mortality due to fisheries bycatch, we discounted the effects of estimated bycatch mortality (Arata et al., 2009) on all demographic rates and used these "natural" rates as a baseline for exploring scenarios in which bycatch varied in intensity. To allow use of both moderate and high bycatch scenarios of Arata et al. (2009) (see below), we generated

Table 1
Laysan albatross population matrix. See Table 3 for parameter definitions.

	1	2	3	4	5	6	7	8	Widow	Successful breeder	Failed breeder	Skipper
1	0	0	0	0	0	0	0	0	0	RS_0	0	0
2	S_{i_real}	0	0	0	0	0	0	0	0	0	0	0
3	0	S_{i_real}	0	0	0	0	0	0	0	0	0	0
4	0	0	S_{i_real}	0	0	0	0	0	0	0	0	0
5	0	0	0	S_{i_real}	0	0	0	0	0	0	0	0
6	0	0	0	0	$S_{i\_real}(1 - r_5)$	0	0	0	0	0	0	0
7	0	0	0	0	0	$S_{i\_real}(1 - r_6)$	0	0	0	0	0	0
8	0	0	0	0	0	0	$S_{i\_real}(1 - r_7)$	$S_{i\_real}(1 - r_8)$	0	0	0	0
Widow	0	0	0	0	T_{i_wid}	T_{i_wid}	T_{i_wid}	T_{i_wid}	T_{wid_wid}	T_{succ_wid}	T_{fail_wid}	T_{skip_wid}
Successful breeder	0	0	0	0	T_{i_succ}	T_{i_succ}	T_{i_succ}	T_{i_succ}	T_{wid_succ}	T_{succ_succ}	T_{fail_succ}	T_{skip_succ}
Failed breeder	0	0	0	0	T_{i_fail}	T_{i_fail}	T_{i_fail}	T_{i_fail}	T_{wid_fail}	T_{succ_fail}	T_{fail_fail}	T_{skip_fail}
Skipper	0	0	0	0	0	0	0	0	0	T_{succ_skip}	T_{fail_skip}	T_{skip_skip}

Breeder transition probabilities

$T_{i\_wid} = S_{a\_real}r_i(F(1 - S_{a\_real}^P) + (1 - F)(1 - S_{a\_real}^P))$

$T_{i\_succ} = S_{a\_real}r_iFS_{a\_real}^P$

$T_{i\_fail} = S_{a\_real}r_i(1 - F)S_{a\_real}^P$

$T_{wid\_wid} = S_{a\_real}(1 - b) + S_{a\_real}b(F(1 - S_{a\_real}^P) + (1 - F)(1 - S_{a\_real}^P))$

$T_{succ\_wid} = S_{a\_real}(1 - S_{a\_real}^{(1 - P)})(1 - a) + S_{a\_real}(1 - S_{a\_real}^{(1 - P)}) a(F(1 - S_{a\_real}^P) + (1 - F)(1 - S_{a\_real}^P)) + S_{a\_real} S_{a\_real}^{(1 - P)}B_{succ}(F(1 - S_{a\_real}^P) + (1 - F)(1 - S_{a\_real}^P))$

$T_{fail\_wid} = S_{a\_real}(1 - S_{a\_real}^{(1 - P)})(1 - a) + S_{a\_real}(1 - S_{a\_real}^{(1 - P)}) a(F(1 - S_{a\_real}^P) + (1 - F)(1 - S_{a\_real}^P)) + S_{a\_real}S_{a\_real}^{(1 - P)}B_{fail}(F(1 - S_{a\_real}^P) + (1 - F)(1 - S_{a\_real}^P))$

$T_{skip\_wid} = S_{a\_real}(1 - S_{a\_real}^{(1 - P)})(1 - a) + S_{a\_real}(1 - S_{a\_real}^{(1 - P)}) a(F(1 - S_{a\_real}^P) + (1 - F)(1 - S_{a\_real}^P)) + S_{a\_real}S_{a\_real}^{(1 - P)}B_{fail}(F(1 - S_{a\_real}^P) + (1 - F)(1 - S_{a\_real}^P))$

$T_{wid\_succ} = S_{a\_real}bFS_{a\_real}^P$

$T_{succ\_succ} = S_{a\_real}(1 - S_{a\_real}^{(1 - P)})aFS_{a\_real}^P + S_{a\_real}S_{a\_real}^{(1 - P)}B_{succ}FS_{a\_real}^P$

$T_{fail\_succ} = S_{a\_real}(1 - S_{a\_real}^{(1 - P)})aFS_{a\_real}^P + S_{a\_real}S_{a\_real}^{(1 - P)}B_{fail}FS_{a\_real}^P$

$T_{skip\_succ} = S_{a\_real}(1 - S_{a\_real}^{(1 - P)})aFS_{a\_real}^P + S_{a\_real}S_{a\_real}^{(1 - P)}B_{fail}FS_{a\_real}^P$

$T_{wid\_fail} = S_{a\_real}b(1 - F)S_{a\_real}^P$

$T_{succ\_fail} = S_{a\_real}(1 - S_{a\_real}^{(1 - P)})a(1 - F)S_{a\_real}^P + S_{a\_real}S_{a\_real}^{(1 - P)}B_{succ}(1 - F)S_{a\_real}^P$

$T_{fail\_fail} = S_{a\_real}(1 - S_{a\_real}^{(1 - P)})a(1 - F)S_{a\_real}^P + S_{a\_real}S_{a\_real}^{(1 - P)}B_{fail}(1 - F)S_{a\_real}^P$

$T_{skip\_fail} = S_{a\_real}(1 - S_{a\_real}^{(1 - P)})a(1 - F)S_{a\_real}^P + S_{a\_real}S_{a\_real}^{(1 - P)}B_{fail}(1 - F)S_{a\_real}^P$

$T_{succ\_skip} = S_{a\_real}S_{a\_real}^{(1 - P)}(1 - B_{succ})$

$T_{fail\_skip} = S_{a\_real}S_{a\_real}^{(1 - P)}(1 - B_{fail})$

$T_{skip\_skip} = S_{a\_real}S_{a\_real}^{(1 - P)}(1 - B_{fail})$

two parameter sets using this discounting procedure, one assuming the moderate bycatch levels at the time demographic data were collected and the other assuming the high bycatch level. We did not discount *Verbesina* effects from reproductive rates because reproduction was measured in study plots free of this shrub. We did not incorporate density-dependent effects on demographic rates in any of our simulations.

Stochasticity was included in post-hatch-year survival rates, egg-to-fledge probabilities, and breeding probabilities using estimates of process variance after discounting sampling variance in observed rates (Table 3). We incorporated parameter uncertainty by generating random parameter sets from beta distributions, with the exception of process variance estimates, which we drew from lognormal distributions. We assumed no correlation in these rates. Incorporating uncertainty in demographic rates via random sampling from their estimated distributions can occasionally result in parameter sets that predict biologically implausible population behavior. We assumed that in the absence of anthropogenic threats, overall mean growth rates from "natural" demographic rates must be stable or positive, and thus we excluded parameter sets in which mean population growth rates were less than one (Bakker et al., 2009), which amounted to only 0.12% of all parameter sets for LAAL and 3.0% for BFAL. Bycatch estimates were year-specific and based on studies of albatross mortality for multiple fisheries and by necessity broadly extrapolated from a few

Table 2
Black-footed albatross population matrix. See Table 3 for parameter definitions.

	1	2	3	4	5	6	7	8	Widow	Breeder
1	0	0	0	0	0	0	0	0	0	$RF_{real}BS_0$
2	S_{i_real}	0	0	0	0	0	0	0	0	0
3	0	S_{i_real}	0	0	0	0	0	0	0	0
4	0	0	S_{i_real}	0	0	0	0	0	0	0
5	0	0	0	S_{i_real}	0	0	0	0	0	0
6	0	0	0	0	$S_{a\_real}(1 - r_5)$	0	0	0	0	0
7	0	0	0	0	0	$S_{a\_real}(1 - r_6)$	0	0	0	0
8	0	0	0	0	0	0	$S_{a\_real}(1 - r_6)$	0	0	0
Widow	0	0	0	0	0	0	0	0	T_{wid_wid}	T_{breed_wid}
Breeder	0	0	0	0	T_{i_breed}	T_{i_breed}	T_{i_breed}	S_{a_real}	T_{wid_breed}	T_{breed_breed}

Breeder transition probabilities

$T_{wid\_wid} = S_{a\_real}(1 - b)$

$T_{wid\_breed} = S_{a\_real}b$

$T_{breed\_wid} = S_{a\_real}(1 - S_{a\_real})(1 - a)$

$T_{breed\_breed} = S_{a\_real}(1 - S_{a\_real})a + S_{a\_real}^2$

$T_{i\_breed} = S_{a\_real}r_i$

Table 3

Parameter estimates for demographic matrix population models for black-footed and Laysan albatross, including parameter uncertainty (i.e., standard errors). Process variance estimates are annual environmental stochasticity. Two values are given if assuming moderate vs. high bycatch mortality results in different estimates (moderate/high).

Parameter	BFAL		LAAL		Description	Source and notes
	Estimate	SE	Estimate	SE		
N_i	Varies	–	Varies	–	Number of individuals in age class i	Model is initiated at stable age distribution given bycatch rate at start year
B_i	Varies	–	Varies	–	Number of individuals in age class i killed as fisheries bycatch. Two scenarios considered: (1) moderate and (2) high estimates	Moderate and high bycatch estimates from Arata et al. (2009)
S_0	0.654	0.051	0.778	0.043	Annual survival of hatch year birds from fledging. Consistent with matrix structures, for BFAL, estimate applies to portion of year from fledging to age 1, and for LAAL, estimate applies from fledging to a full year.	BFAL: Lebreton and Véran (2013): Mark recapture of 13,854 chicks from Tern island, banded 1980–2004, resighted 1997–2004. LAAL: (VanderWerf and Young, 2016): Mark recapture of 477 chicks from Oahu, banded and resighted 2002–2015. Estimate is for individuals not affected by avian pox
S_p	0.965	0.020	0.961	0.016	Survival of prebreeders in age class i without bycatch mortality	BFAL: Assumed equal to S_a following Lebreton and Véran (2013). LAAL: Assumed equal to S_a
S_a	0.965	0.020	0.961	0.016	Survival of adults without bycatch mortality	BFAL: Lebreton and Véran (2013). See S_0 for data details. S_a estimates are corrected for estimated bycatch, including underestimate of bycatch. LAAL: Estimate of S_{a_real} of 0.960 for Kaena point, Hawaii, VanderWerf and Young (2011) for 2003–2010, corrected for bycatch effects as S_{a_real}/S_{a_by}. For comparison, S_{a_real} estimated as 0.946 for 1961–1972 (Fisher, 1975), which corrects to 0.959, assuming high bycatch mortality and accounting for military mortality.
S_{L_by}	Varies	–	Varies	–	Survival of fisheries bycatch for individuals in age class i	Bycatch converted to S_{L_by} as $1-((0.5\ B_i)/N_i,)$ where $N_i,$ was estimated as the 3-year average of female non-hatch-year population size, based on linear interpolation of available counts of breeding pairs (Table S1). Bycatch was assumed to include only after-hatch-year birds. S_{a_by} assumed equal to S_{p_by}.
S_{p_real}	Varies	–	Varies	–	Survival of prebreeders in age class i from all mortality sources including bycatch. Estimated as: $S_p S_{p\_by}$	See S_p and S_{p_by}
S_{a_real}	Varies	–	Varies	–	Survival of adults from all mortality sources including bycatch. Estimated as: S_a, S_{a_by}	BFAL: Véran et al. (2007) present estimates for S_{a_real} based on mark-resight data for Tern Island of 0.920 for 1997–2002. Geometric mean rates from our stochastic model runs for the same time periods was: 0.931. LAAL: See S_a and S_{a_by}
S_{a_var}	0.0011	–	0.00071	–	Process variance in S_a	BFAL: Lebreton and Véran (2013). LAAL: Estimated LAAL at Kaena point, Hawaii (VanderWerf and Young, 2011) for 2003–2010
S_{p_var}	0.0011	–	0.00071	–	Process variance in S_p	BFAL: Assumed equal to S_{a_var}. LAAL: Assumed equal to S_{a_var}
r_5	0.279	0.056	0.016	0.0006	Probability of recruiting at age 5	BFAL: Véran (2006). LAAL: Van Ryzin and Fisher (1976)
r_6	0.612	0.122	0.146	0.018	Probability of recruiting at age 6 or 7	BFAL: Véran (2006). LAAL: Van Ryzin and Fisher (1976)
r_7	–	–	0.332	0.025	Probability of recruiting at age 7	LAAL: Van Ryzin and Fisher (1976)
r_8	–	–	0.599	0.002	Probability of recruiting at age 8 or later	LAAL: Van Ryzin and Fisher (1976)
a	0.341	0.068	0	0	Probability of a widow repairing without missing a breeding season	BFAL: Véran (2006). LAAL: Fisher (1976)
b	0.623	0.125	0.541	0.037	Annual probability of a widow repairing after first missed season	BFAL: Véran (2006). LAAL: Fisher (1976)
R	0.5	0.0001	0.5	0.0001	Sex ratio	Assumed
P	0.564	0.113	0.589	0.118	Proportion of year both parents needed to ensure breeding success, based on length of mean incubation and nestling stages of 205 days	Rice and Kenyon (1962). Although there is some evidence that at a certain stage of development, chicks can live without both parents, we conservatively assumed both parents were needed for the whole season.
F_{real}	Varies	–	Varies	–	Egg to fledge rate including the effects of parental mortality.	Calculated as $F((S_{a\_by})P)^2$

Table 3 (*continued*)

Parameter	BFAL Estimate	SE	LAAL Estimate	SE	Description	Source and notes
F	0.746 0.765	0.019 0.019	0.640 0.641	0.023 0.023	Egg to fledge rate excluding effects of parental mortality to allow variable rate with changing bycatch	Calculated as $F_{by}/((S_{a,by}·F_{by}^2))$ based on observed annual F_{by}. BFAL: Tern (1980–2010), Midway (Sand 1987, 1992–1995; Eastern 2007, 2011–2013), Laysan (1992–1995, 2007). Rates for F_{real} over same time is 0.679 ± 0.016. LAAL: Tern (1980–2010), Midway (Sand 1994–1995, Eastern 2002–2013), Laysan (2007), averaged across islands by year, and corrected for estimated annual $S_{a,by}$. Rates for F_{real} over same time is 0.611 ± 0.022. All data from USFWS unpublished data, Cousins and Cooper, 2000; Ludwig et al., 1997.
F_{real_var}	Varies	–	Varies	–	Process variance in egg to fledge rate including bycatch effects	
F_{var}	0.009 0.011	0.003 0.003	0.007 0.007	0.003 0.003	Process variance in egg to fledge rate excluding effects of bycatch	Calculated based on F_{-var} using methods of White (2000).
B	0.813	0.049	–	–	Annual probability of breeding	BFAL: Surrogate data. Calculated from LAAL data from 1962 to 1971 (Fisher, 1976), corrected for sampling error based on methods of White (2000). Consistent with one year return rate of 0.8 in 2000 (Rohwer et al., 2011). LAAL: see B_{succ} and B_{fail}. Mean B for 1000 model runs of 1000 years using B_{succ} and B_{fail} was 0.820.
B_{var}	0.029	0.013	–	–	Variance in B	Calculated from same data used to estimate B based on methods of White (2000). Extrapolated as proportion of maximum possible (Morris and Doak, 2004).
B_{succ}			0.764	0.053	Annual probability of breeding the season after successfully fledging a chick	Data from Kaena point, Hawaii, VanderWerf and Young (2011) for 2003–2010. Rate is sum of breeder-skipper and breeder-unobserved skipper transition probabilities. A correlation of 0.9 assumed between B_{succ} and B_{fail}.
B_{fail}			0.857	0.039	Annual probability of breeding the season after failing to fledge a chick	Data from Kaena point, Hawaii, VanderWerf and Young (2011) for 2003–2010. Rate is sum of failed breeder-skipper and failed breeder-unobserved skipper transition probabilities.
B_{succ_var}			0.034	0.010	Annual process variance in B_{succ}	Calculated from same data used to estimate B and B_{var}. Extrapolated as proportion of maximum possible (Morris and Doak, 2004).
B_{fail_var}			0.023	0.005	Annual process variance in B_{fail}	Calculated from same data used to estimate B and B_{var}. Extrapolated as proportion of maximum possible (Morris and Doak, 2004).
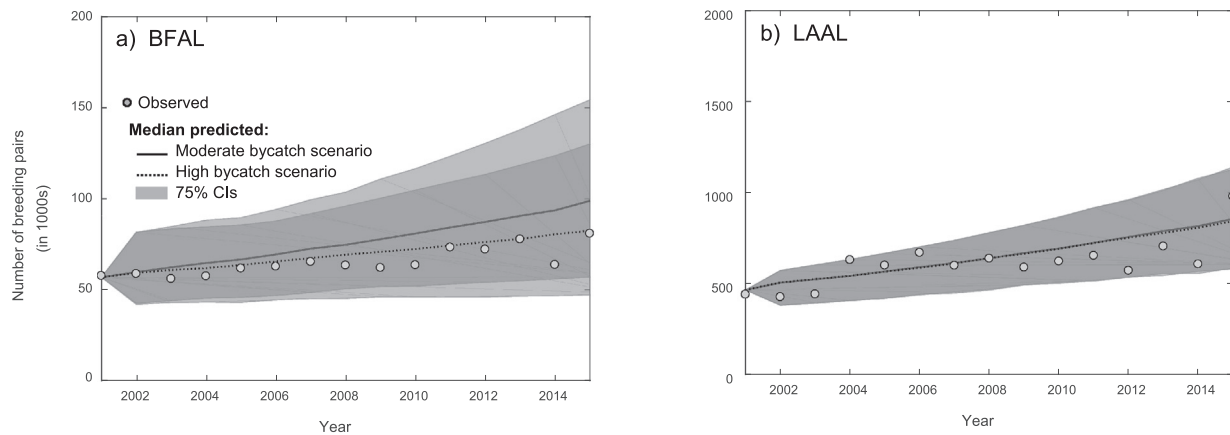
Fig. 1. Predicted numbers of breeding pairs based on stochastic demographic population model compared to observed numbers for (a) black-footed (BFAL) and (b) Laysan (LAAL) albatross. Model was parameterized with best available data (Table 1) and estimated *Verbesina* effects and historical bycatch mortality, using the moderate and high bycatch estimates of Arata et al. (2009) as well as military-related mortality (see text for additional details and Table S2). Median and 75% confidence intervals (shaded areas) are shown for 5000 replicate population trajectories from 2001 to 2015. Simulations were initiated at 3-year average of breeding pair counts and assuming stable age distribution.

studies (Arata et al., 2009). Likewise, mortality caused by military activities was based on reported mortality rates (Table S2), although data from the 1940s are sparse or lacking. In summarizing simulation output, we refer to long-term stochastic λ, estimated over 10,000 years (Morris and Doak, 2002) as λ_s and refer to short-term realized stochastic λ as λ_t where t represents the number of years over which the growth rate is summarized (i.e., $(N_t/N_0)^{1/t}$). Finally, the average of λ_t values across multiple simulations was calculated as $e^{\text{mean}[\log(\lambda_t)]}$.

2.3. Apparent density dependence

Two sampling processes can create nest count data sets that appear to show NDD when none exists. First, simple sampling error can create negative correlations between annual population growth and starting number over each time interval and otherwise complicate tests for NDD (Dennis et al., 2006; Eberhardt, 1970; Freckleton et al., 2006; Lebreton and Gimenez, 2013). Second, and more powerfully, if the observable population fraction is negatively auto-correlated across years, this too will generate the appearance of NDD. This latter effect is likely important for BFAL and LAAL, which have a higher probability of skipping breeding the year after successfully reproducing (Fisher, 1976; VanderWerf and Young, 2011; Young and VanderWerf, 2014); thus if annual variance in oceanographic conditions change the population-wide average nesting success rates (Cubaynes et al., 2011), the entire population will tend to have high and low breeding fractions in alternate years. This second process has received less attention than the first, and we derived an analytical approximation for how these two effects will influence tests for NDD.

To complement our more general analytical analysis for the particular life histories of our study species, we conducted simulation tests of the potential for state-dependent rebreeding rates to produce apparent NDD like that found for LAAL by Arata et al. (2009), even when it does not exist. For these tests, we used our demographic matrix model (Table 1), which does not include any density-dependent processes, to simulate 5000 replicate stochastic population trajectories from 1992 to 2005 on Laysan Island, to allow direct comparison to Arata et al. (2009). These models have no assumed auto-correlation in breeding probability, but the differential probability of breeding following a failed or successful breeding attempt combined with annual variation in breeding success, generates negative autocorrelation in the fraction of breeding adults. We assumed current conditions for *Verbesina* control and storms and imposed the high bycatch scenario (see methods below). For each trajectory, we saved the number of breeding pairs and regressed log λ (i.e., $\log(N_t/N_{t-1})$) against N_{t-1} where N is the number of breeding pairs and evaluated whether the regression slope was

significantly negative, comparable to the methods of Arata et al. (2009). We performed these simulations both with and without the addition of observation error in counts of breeding pairs, using a coefficient of variation of 0.25 to simulate observation error.

2.4. Historical population dynamics and model performance

We simulated historical population dynamics using our model and compared predicted trajectories to observed nest counts. Surveys of BFAL and LAAL nests have been conducted intermittently though time and across space, employing varying methods and having differing levels of uncertainty. Early colony size estimates may be quite rough and based on counts of just one or a few days of effort. However, beginning in 1992, more frequent estimates are available for Midway and Laysan Islands using standardized sampling methods (Table S1). Worldwide population estimates from concurrent surveys of all or most breeding colonies are available for four time periods for BFAL and three time periods for LAAL (Table S1). Thus, we tested our model by simulating the dynamics of the estimated worldwide population from three starting points when all the major colonies were censused: 1923, 1961, and 2001. Other worldwide population size estimates were made based on extrapolation from surveys on Midway and Laysan islands, or, in cases where surveys from these colonies were missing, from linear interpolation between available estimates (Table S1). Together Midway and Laysan islands have represented ~69–92% of the total BFAL population and ~75–92% of the LAAL population.

2.5. Simulating bycatch and military-related effects

We converted the estimated numbers of birds killed in fisheries to annual mortality rates for use in our models based on estimated population sizes. We assumed bycatch affected only after-hatch-year birds and was distributed among age classes according to their relative abundance. Bycatch mortality for both species subsequent to 2005 was assumed equal to 2005 bycatch mortality rates (Arata et al., 2009, Table S2). We similarly estimated rates of military-based mortality, obtaining numbers killed from Arata et al. (2009) and supplemental sources (Table S2). To assess the impact of bycatch on future population viability, we simulated population trajectories from 2001 through 2040, modifying bycatch mortality by a factor of 0.75 to 3.0 times the estimated 2005 rate. Because bycatch mortality rates are uncertain and independent studies suggest bycatch estimates are biased low (Brothers et al., 2010; Lebreton and Véran, 2013) we tested historical trajectories against both the moderate and high bycatch scenarios estimated by Arata et al. (2009). Although disproportionate bycatch mortality risk

has been documented for female wandering albatross in southern hemisphere fisheries (Jiménez et al., 2016), we did not have sufficient information to assess sex-related bycatch effects on LAAL and BFAL and thus assumed that males and females had equal bycatch mortality.

2.6. Potential Biological Removal (PBR)

We estimated species-specific PBR and compared it to historical and current bycatch rates. PBR is an estimate of the amount of human-caused mortality a population can withstand while recovering towards or maintaining an optimal sustainable population. PBR is mandated for stock assessments under the Marine Mammal Protection Act, and has been employed to assess bycatch mortality for seabirds (Žydelis et al., 2009), including albatrosses (Dillingham and Fletcher, 2011; Jimenez et al., 2012). The PBR approach is based on the assumption that human-caused mortality should not remove more individuals than are needed for the population to sustain half its carrying capacity (Taylor et al., 2000) and defined as:

$$PBR_{trad} = N_{min} \frac{1}{2} R_{max} F_r.$$

N_{min} is the minimum population estimate and generally assumed to be an estimate of the number of individuals subject to human-caused (e.g., bycatch) mortality. R_{max} is the maximum low-density per capita net growth rate (estimated as $\lambda_{max} - 1$) in the absence of human-caused mortality: $1/2 R_{max}$ is then the expected per capita growth at $1/2 K$ for logistic growth, so that PBR is estimating the maximum number of individuals that can be removed from the population while still ensuring positive population growth when N is at or below the maximum net productivity level. Because current numbers of both species are likely well below carrying capacity due to significant population declines from feather and egg hunting at the turn of the 20th century, we estimated λ_{max} as λ from our deterministic matrices using demographic rates that discount bycatch mortality and *Verbesina* effects, but acknowledge that for any species unbiased estimates of R_{max} or λ_{max} are impossible without comprehensive knowledge of demographic rates including the form and strength of density dependence (Niel and Lebreton, 2005; Wade, 1998). F_r is a recovery factor intended to account for biases due to underestimating incidental mortality or over-estimating demographic rates or population sizes, or to allow more rapid recovery of depleted populations (Taylor et al., 2000; Wade, 1998). Wade (1998) recommended a default value of 0.5 for F_r, and lower values if populations are severely depleted. Several authors have used IUCN threat status to guide F_r values; for example, Dillingham and Fletcher (2011) recommend use of 0.1 for endangered and critically endangered species, 0.3 for vulnerable and near-threatened species, and 0.5 for other species.

Further, Dillingham and Fletcher (2011) have proposed an albatross-specific PBR:

$$PBR_{alb} = \tau \hat{B} F_r.$$

Here, N_{min} is replaced with $\hat{B}$, the count of breeding pairs and $1/2 R_{max}$ is replaced with τ, a guild-specific coefficient that accounts for both the maximum growth rate and a multiplier on $\hat{B}$ to best approximate N_{min}. Dillingham and Fletcher (2011) used simulation studies to estimate τ values that accounted for the uncertainty inherent to population size estimates based on breeding bird censuses for each of three Procellariform guilds – biennially breeding albatrosses, annually breeding albatrosses, and petrels. They derived a τ value of 0.1 (when $\lambda \approx 1$ and $CV_B \approx 0.5$) for annual breeders such as BFAL and LAAL.

2.7. Detecting population change using count data

We assessed the probability that the observed annual counts of BFAL nests could arise as a stochastic result with a limited data set given a wide range of possible long-term population growth rates. We focused on the recent time period of clearly consistent data collection, 2001 to ~2015, and considered scenarios in which the actual bycatch mortality was the best estimate for the same time period, again using the high bycatch scenario, times a multiplier that ranged from 0.75 to 3.0. We ran 5000 replicate simulations for each bycatch mortality rate, with parameter and stochastic uncertainty, and recorded the predicted number of breeding birds observed assuming annual censuses with no sampling error. We calculated the proportion of model runs for which the realized stochastic λ, λ_t, of breeding BFAL counts equaled or exceeded the λ_t of observed counts from 2001 through 2014 and 2015, the last two years for which we have data. We considered the match with data through either 2014 or 2015 because these were years of relatively low and high returns, respectively, and thus inclusion of 2015 could have substantial impacts on the comparison. We estimated population growth for the time periods 2001–2014 (λ_{13}) and 2001–2015 (λ_{14}) and summarized results for a range of long-term λ, λ_s, values estimated for each parameter set and bycatch increase scenario. We also used our model to assess the likelihood of detecting future BFAL population declines using nest counts when the population was actually declining. To do so, we considered the scenarios described above in which the estimated high bycatch rate was increased by 1.5 to 3 times, but simulating over the time period from 2001 to 2040. At each time step, we recorded the predicted number of observed breeding BFAL (i.e., assuming annual census without sampling error) and total BFAL. We retained only runs in which total numbers of BFAL were declining at a given time step (i.e., $\lambda_t < 1.0$), and we assessed our power to detect declines by regressing the natural log of the number of breeders versus time (Eberhardt and Simmons, 1992) and calculating the proportion of simulated runs in which the upper confidence interval on the slope parameter was < 1.0.

## 2.8. Bycatch versus on-island threats

2.8.1. Storm surge effects

Periodic large storms are known to cause substantial reductions to BFAL reproductive success (Cousins and Cooper, 2000). We assumed that storms currently occur at an annual probability of 0.05 and that their spatial extent is 0.15 of the breeding range causing 15% of nests to fail in storm years. We applied these probabilities and extents to all scenarios, except for a subset of scenarios designed to investigate the population impact of increasing storm effects, projected under some climate change scenarios (Reynolds et al., 2015). For these, we conducted model runs in which storm probability increased to 0.5, storm extent increased to 0.5, or both (Murakami et al., 2013).

2.8.2. Verbesina effects (see also Appendix 2)

We simulated benefits to LAAL and BFAL populations from eradicating the invasive plant *Verbesina* on Midway and Kure atolls, where significant efforts between 2005 and 2015 resulted in the removal of *Verbesina*, yet this threat still remains at these and other breeding locations. Although Kure Atoll only hosts ~3% of the global LAAL population and ~5% of the global BFAL population, we included Kure in our simulations as this island was substantially impacted by *Verbesina* (VanderWerf, 2013). We estimated the proportion of LAAL and BFAL nesting in *Verbesina* habitat by calculating the proportion of LAAL and BFAL breeding pairs occupying each count sector and the proportion of each count sector affected by *Verbesina* (Table S3). For Midway, we used GIS habitat mapping from 2007 (Fig. S1), and assumed this approximately characterized the maximum extent of *Verbesina*. For Kure, we used the described vegetation types for each count sector. We included uncertainty in the proportion of breeders affected by drawing proportions from a uniform distribution within ± 10% of the estimated value (Table S3).

We estimated that reproductive success in *Verbesina* habitat was a fraction, 0.43 ± 0.14 SE, of success in all other habitats (USFWS unpublished data) and compared the population-level effects of four
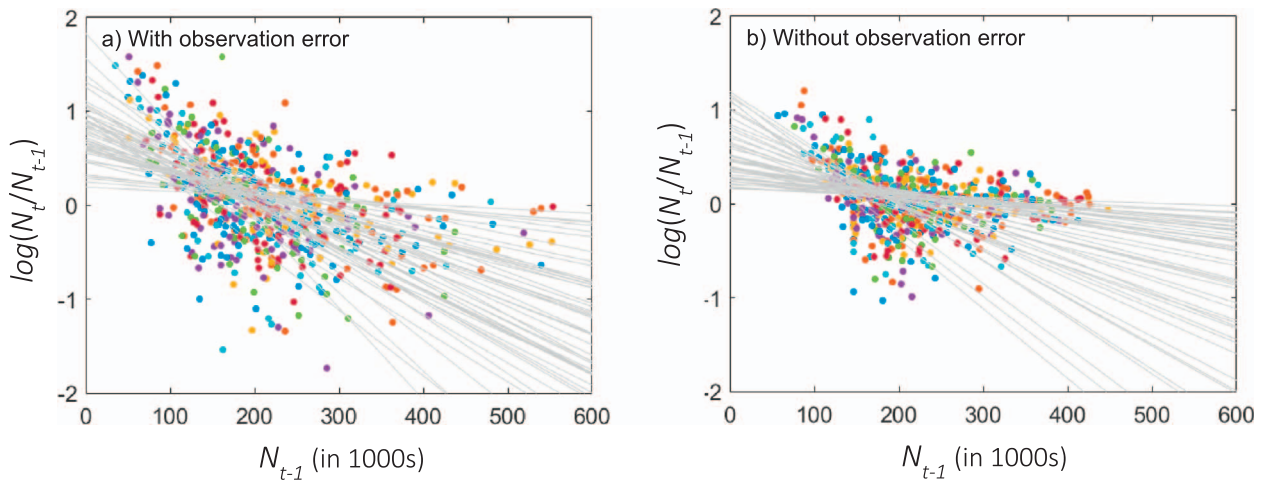
Fig. 2. The relationship between counts of LAAL breeding pairs in the previous year (N_{t-1}) and log λ for breeding pairs ($\log(N_t/N_{t-1})$) predicted using a stochastic demographic population model for the years 1992 to 2005 on Laysan Island. The generating process does not include negative density dependence but does include stochastic state-dependent breeding probabilities (Table 1), both (a) with and (b) without observation error in breeding bird counts equal to a coefficient of variation of 0.25. Lines indicate the best fit lines for $\log(N_t/N_{t-1})$ vs N_{t-1} for the first 50 (of 5000) replicate runs, with data points from each run plotted in a different shade.

Verbesina control scenarios running from 2001 through 2040. All scenarios assumed *Verbesina* was at its maximum extent at the start of simulations in 2001. The *no control* scenario assumed *Verbesina* remained at its pre-control spatial extent through the simulation interval. The *permanent control* scenario simulated a reduction in *Verbesina* starting in 2005 on Midway and 2009 on Kure and ending in 2013 on Midway and 2015 on Kure, which approximates the observed time table, with a linear decrease in the proportion of breeders in *Verbesina* habitat through that time period, and complete eradication persisting through the remainder of the simulation interval. While *Verbesina* control has continued to the present, *Verbesina* can return from the seed bank if control is halted. Thus, we evaluated the consequences of a *temporary control* scenario, which assumed *Verbesina* removal according to the permanent control time table, but with management ceasing in 2016, and *Verbesina* reaching its previous maximum extent over a five-year period, again assuming linear increases. Finally, we compared all these scenarios to a *no Verbesina* scenario in which no effect on reproduction from *Verbesina* was included.

2.8.3. Relative importance of bycatch vs. on-island threats

To evaluate the relative importance of conservation strategies that address on-island threats compared to bycatch reduction, we simulated 500 replicate population trajectories for the time period 2001–2040 for each breeding-island scenario (storm scenarios for BFAL and *Verbesina* scenarios for LAAL) and for a range of bycatch mortality rates (high bycatch scenario × 0, 0.5, 1.0, 1.5, 2, 2.5, 3), where 0 represents no bycatch and 1 represents the 2005 estimated rate. We then used multiple linear regression with bycatch increase and on-island threat scenarios as predictors of λ_t.

3. Results

3.1. Apparent density dependence

Despite the absence of any NDD process in the model, the majority (64.2%) of 5000 simulated trajectories for LAAL on Laysan Island from 1992 to 2005 showed significant first-order negative feedback ($P < 0.05$) between breeding pair log λ and the numbers of breeding pairs in the prior year when including observation error in breeding pair counts (Fig. 2a). In the absence of observation error, 29.1% of simulated trajectories still showed significant negative feedback (Fig. 2b). The median and upper and lower quartiles for the correlation between log λ and numbers of breeding pairs in the prior year was

−0.582 (−0.672, −0.488) with observation error and −0.445 (−0.553, −0.338) without observation error, compared to r = −0.593 found by Arata et al. (2009).

Using a Taylor expansion, we can show there is a strong likelihood of falsely finding apparent NDD for any species showing correlated breeding probabilities, when breeding birds are the segment of the population that is censused. If the observed numbers of birds each year is $N_{t,obs} = N_t E_t$, where E_t is the fraction of birds seen in a year, and observed population growth is measured as $\log(\lambda_{t,obs}) = \log(N_{t+1,obs}/N_{t,obs})$, then

$$corr\left(\log(\lambda_{t,obs}), N_t\right) \cong \frac{-[var(E) - cov(E_t, E_{t+1})]}{var(E)^{0.5} E'\left\{\frac{2}{E'^2}[var(E) - cov(E_t, E_{t+1})] + \frac{var(\lambda)}{\lambda'^2}\right\}^{0.5}}$$

where all E values have mean E' and var(E), while all λ have mean λ′ and var(λ). The easiest way to see the effects of sampling error, var(E), and correlation between this error across time, cov(E_t, E_{t+1}), is to set var(λ) = 0 and λ′ = 1. In this case:

$$corr\left(\log(\lambda_{t,obs}), N_{t,obs}\right) \cong \frac{-[var(E) - cov(E_t, E_{t+1})]^{0.5}}{stdev(E)^{0.5} 2^{0.5}}$$

$$\cong -[0.5(1 - corr(E_t, E_{t+1}))]^{0.5}$$

In the absence of any correlation between E_t and E_{t+1}, the correlation of population growth and starting numbers will be $-(2^{-0.5}) = -0.707$. In the extreme case with autocorrelation in E, if $corr(E_t, E_{t+1}) = -1$, $corr(\log(\lambda_{t,obs}), N_{t,obs}) \cong -1$. If $corr(E_t, E_{t+1}) = -0.5$, $corr(\log(\lambda_{t,obs}), N_{t,obs}) = -0.87$, showing how modest negative correlations in breeding probability (that is, observability) can drive substantial apparent NDD just as our simulations show in the particular case for LAAL (Fig. 2).

3.2. BFAL and LAAL model performance and population trajectories

BFAL and LAAL demographic models predicted recent count data (2001–2015) trajectories reasonably well with the median predicted number of breeding pairs similar to the observed number (Fig. 1). For BFAL in particular, population trajectories assuming the high bycatch scenario more closely approximated observed trends (Fig. 1a). The BFAL model predicted stochastic population growth rates, assuming the high bycatch scenario and the permanent control scenario for *Verbesina*, that were positive (mean λ_t for 2001 through 2015 = 1.027) while the deterministic λ for a population not experiencing any bycatch mortality, *Verbesina*, or storm-related effects on reproduction and thus
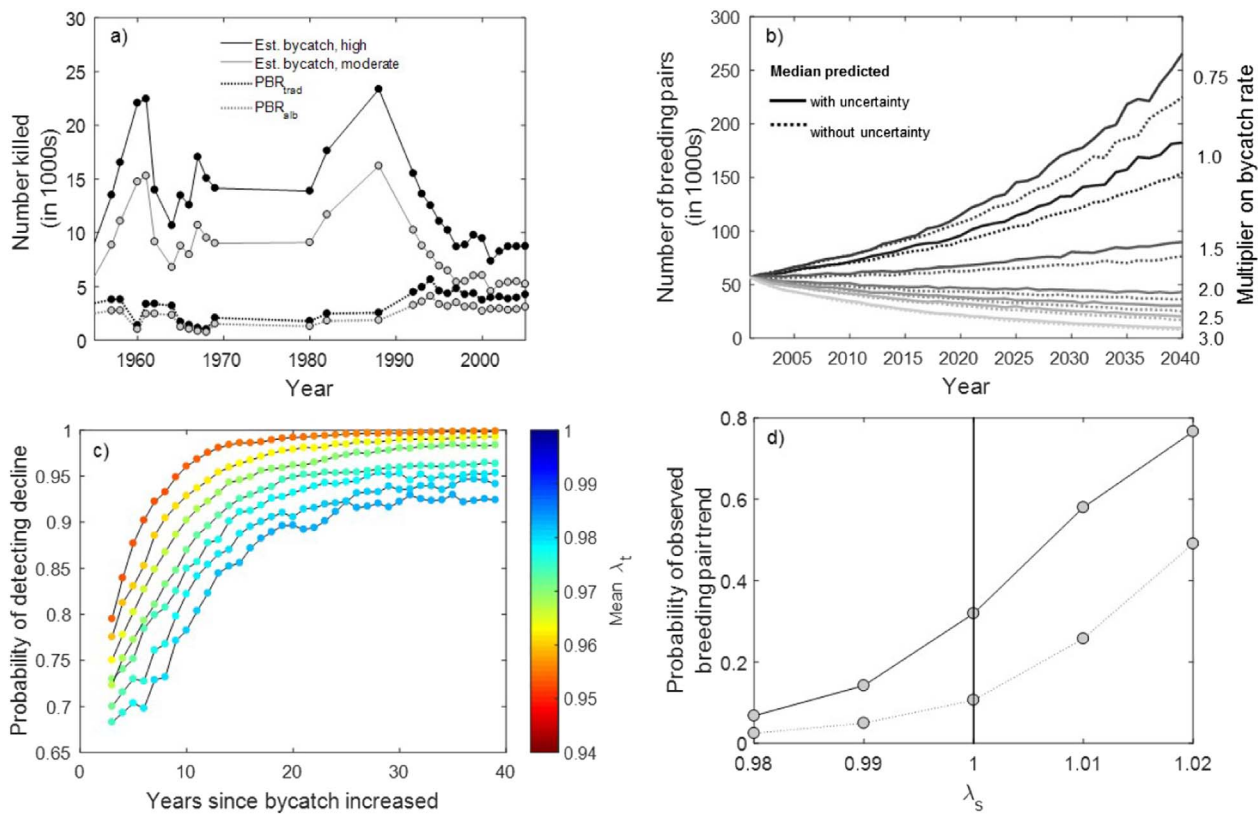
Fig. 3. The predicted effects of bycatch on black-footed albatross population dynamics. (a) Estimated bycatch (Arata et al., 2009) compared to the Potential Biological Removal rate based on the traditional formula, PBR$_{trad}$ (Wade, 1998), and an albatross-specific formula, PBR$_{alb}$ (Dillingham and Fletcher, 2011), (b) projected population trajectories from 2001 to 2040 with a proportional change in bycatch mortality, assuming the high bycatch scenario as baseline, from 0.75 to 3 times the estimated rate (1.0 indicates estimated current conditions), with and without uncertainty in parameter estimates for 5000 replicate runs for each scenario, (c) the number of years to detect a declining population trend, for population trajectories in which a decline was actually occurring ($\lambda_t < 1$), associated with increases in bycatch of ≥ 1.5 times the estimated rate for 2005; plot line labels indicate proportional increases in bycatch, and colors indicates mean λ_t for these bycatch levels, (d) the probability that λ_t of simulated breeding bird counts generated in 3b was equal to or greater than the λ_t of observed counts for 2001–2014 (solid line) or 2001–2015 (dotted line), summarized by simulated long-term stochastic λ, λ_s.

approaching its probable or realistic maximum population growth rate was 1.065. The LAAL population growth rate assuming high estimated bycatch levels and the permanent control scenario for *Verbesina* was also positive (mean λ_t for 2001 through 2015 = 1.045). The deterministic λ for a population not experiencing bycatch mortality or *Verbesina* effects on reproduction and thus approaching a realistic maximum population growth was 1.056. See Fig. S2 for histograms of λ values for parameter sets used in modeling each species, reflecting uncertainty. Applying our model to the historical time frame (1923–2001) (Fig. S3), when count data were not standardized (Table S1), the general trends predicted by the BFAL model approximated that of the count data (Fig. S3a–b). In contrast, the LAAL demographic model predictions initiated in 1961 significantly overestimated observed nest counts (Fig. S3d). Sensitivity analysis of the deterministic matrices confirm that adult survival is the most important demographic rate for both species (Tables S4a–f).

3.3. Potential Biological Removal

BFAL PBR$_{trad}$ ranged from ~3700 to 5600 ($F_r = 0.5$, $R_{max} = 0.065$) between 1992 and 2015, while the BFAL PBR$_{alb}$ ranged from ~2700 to 4100 ($\tau = 0.1$) (Fig. 3a). Estimated bycatch of BFAL exceeded PBR$_{alb}$ during this recent time period, under both moderate and high bycatch scenarios. Applying PBR$_{trad}$ to BFAL, the high bycatch scenario exceeded allowable removal while the moderate bycatch scenario was close to the allowable removal (Fig. 3a); however, projections with moderate bycatch were a poorer fit to the observed data compared to high bycatch (Fig. 1a). From 1960 to 1992, estimated bycatch of BFAL

substantially exceeded both PBR$_{alb}$ and PBR$_{trad}$. For LAAL, recently estimated bycatch was well below both PBR$_{trad}$ and PBR$_{alb}$ (Fig. S4, Table S2, Arata et al., 2009).

3.4. Detecting population change using count data

For BFAL, we found that a doubling or more of estimated bycatch mortality under the high bycatch scenario resulted in a declining population (Fig. 3b). We chose the high bycatch scenario because it produced trajectories that most closely matched the observed count data for the recent time interval (≥ 2001, Fig. 1a).

Using count data to evaluate trends in BFAL populations, we found that even a large reduction in short-term stochastic λ_t from ~1.029 to ~0.971 required 10 years of observed nest counts to ensure a 90% probability of detecting the decline (Fig. 3c). These λ_t values are the mean λ_{39} for the currently estimated high bycatch rate and for declining trajectories when the bycatch rate was increased 2.5-fold, an increase that resulted in declining population trajectories in 91% of simulated runs. Smaller increases in bycatch, such as an increase of 1.5-fold, resulted in declining populations 29% of the time; these declining populations had a mean λ_{39} of 0.983 and required 23 years to detect using nest count data (Fig. 3c).

We also assessed the likelihood of observing trends similar to the current increases in BFAL nest counts when the population was not growing, finding that if λ was 1, we would expect to see the observed 2001–2014 growth trend, λ_{13}, ~32% of the time, and the 2001–2015 growth trend, λ_{13}, 11% of the time (Fig. 3d).

3.5. Bycatch versus on-island threats

Increasing storm effects on reproduction had only modest effects on BFAL populations, with significant increases in both frequency and extent of storms required to produce large decreases in growth rates (Fig. 4a–b). An increase in storm frequency from 0.05 to 0.50 annually had a stronger population-level effect than an increase in storm extent (i.e., a greater proportion of habitat affected) from 0.15 to 0.50. In assessing bycatch effects on growth rate for each storm scenario, we found a small effect of storms relative to bycatch mortality (Fig. 4b). Indeed, increasing storm extent had an effect on growth rate equivalent to an increase in bycatch of only ~4%. Similarly, even large increases in both storm frequency and extent could be offset by a decrease in bycatch by about half (47%). Notably, we did not include permanent removal of nesting habitat in our simulations and because severe storms or sea level rise might destroy nesting habitat and reduce an island's carrying capacity, the long-term effects of storms may be underestimated in our model predictions.

We estimated for Midway and Kure atolls ~39–51% of LAAL nested in *Verbesina* habitat (Table S3) prior to effective control (initiated in 2005) and removal of *Verbesina* resulted in an estimated ~610,000 additional breeding pairs by 2040. However, if control activities were to cease and *Verbesina* returned, much of the potential gain was not achieved, with an estimated increase of only ~250,000 pairs. Over the course of the simulation (up through 2040), removing *Verbesina* on

Midway increased the global λ_t from 1.045 to 1.053. Comparing the benefits of alternate *Verbesina* control strategies to reductions in bycatch emphasized the small effect bycatch is currently estimated to have on LAAL population viability (Fig. 4c–d). Removal of *Verbesina* had an effect on growth rates far greater than halving currently estimated moderate or high bycatch mortality. While *Verbesina* removal has a substantial effect on LAAL population dynamics, these benefits are quickly reversed if *Verbesina* is not fully eradicated or if it is allowed to return to breeding islands (Fig. 4c-d). We also assessed the benefits of *Verbesina* removal to BFAL (Appendix 2) and found that permanent *Verbesina* removal increased BFAL population growth by ~0.4% (mean λ_t 1.030 compared to 1.026; Fig. S5).

4. Discussion

4.1. Apparent negative density dependence in counts can easily arise in the absence of NDD processes

Arata et al. (2009) reported negative density dependence in nest count data for LAAL. They found a recent decline in annual growth rates, with long-term nest count data best fit by a logistic function, and detected significant first-order negative feedback of observed growth rate with previous year's nest counts. However, due to ongoing and dramatic changes in the nature and strength of anthropogenic threats to survival and reproduction, slowing of population growth could arise
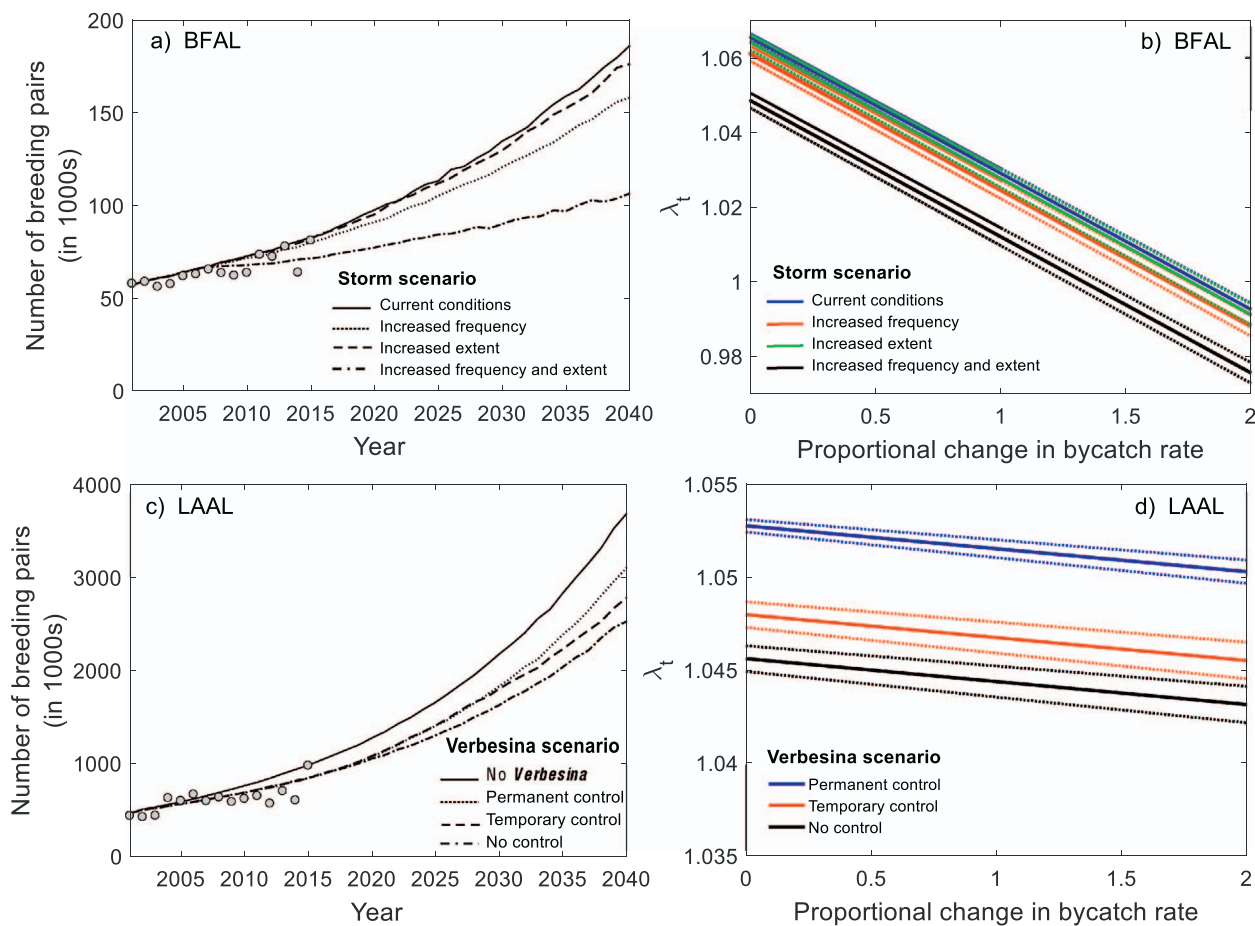

Fig. 4. The effects of threats to breeding colonies on the population dynamics of north Pacific albatrosses. Top panels show the effects on BFAL populations worldwide of (a) increased storm frequency and extent, and (b) the relative importance to population growth rate from 2001 to 2040, λ_{39}, of storm effects compared to changes in bycatch mortality. For (a), current conditions assume annual storm probability is 0.05 and extent of nests destroyed is 0.15, increased frequency assumes a storm probability of 0.5, and increased extent assumes proportion of nests destroyed is 0.5, with 5000 replicate runs for each scenario. Bottom panels show effects on LAAL populations worldwide of (c) *Verbesina* and alternative control strategies on Midway and Kure atolls and (d) the relative importance to population growth rate, λ_{39}, of *Verbesina* control compared to changes in bycatch. For both right side panels we used 500 replicate runs for each breeding-island scenarios and each of a range of bycatch mortality rates (high bycatch scenario × 0, 0.5, 1.0, 1.5, 2, 2.5, 3), where 0 represents no bycatch and 1 represents the 2005 estimated rate.

from changes unrelated to density. In addition, a pattern of apparent NDD is an expected outcome for any species in which individuals are counted with sampling error (Eberhardt, 1970; Freckleton et al., 2006; Kelly and Price, 2005), and our simulations of LAAL nest count data frequently suggested NDD even though our simulation process was density independent.

Less appreciated is the role of auto-correlation in sampling errors in enhancing apparent NDD. Apparent NDD is expected to be especially prominent in species in which adults are less likely to breed (and thus be observed) in years after successfully reproducing, because for these species, the fraction of individuals counted is temporally correlated. We illustrated how modest negative correlations in observability can drive substantial apparent NDD (Fig. 2) when none exists. Our findings are meaningful for assessing the population status and trends of albatrosses, which exhibit skipping behavior based on past reproductive performance, but also for other species such as yellow-bellied toads that will skip breeding based in part on breeding state during the prior breeding season (Cayuela et al., 2014). Incorrectly attributing fluctuations in count data to density dependence could substantially impact population model projections.

4.2. BFAL and LAAL model performance and population trajectories

Island-wide nest counts of BFAL on Midway Atoll and Laysan Island were initiated in 1992, while island-wide nest counts of LAAL were initiated in 2001 and 1992 respectively. Together these islands host the world's largest breeding colonies of both albatross species, so a better model fit with the recent census data (2001–2015, Fig. 1) is not surprising. Nonetheless, despite the sparse survey data and diverse and changing threats through time, the best estimates of demographic rates and bycatch and military mortality yield population trajectories that approximate observed BFAL population counts over the past century (Fig. S3a–b). The high bycatch scenario produced a better fit with BFAL recent trajectories (Fig. 1a), underscoring the importance of bycatch mortality to BFAL population growth rates. For both species, managers should prioritize long-term monitoring using standardized methods, including census counts to estimate breeding pairs and mark-recapture to update estimates of demographic rates, in particular adult survival given the sensitivity of BFAL and LAAL population growth to this vital rate (Table S4a–f).

4.3. PBR illustrates fisheries bycatch is limiting BFAL population growth

Similar to other studies (Lebreton and Véran, 2013; Lewison and Crowder, 2003; Véran et al., 2007) we conclude that fisheries bycatch is hindering growth of BFAL. This point is most clearly underscored by our PBR calculations, which indicate BFAL bycatch has continuously exceeded both the PBR_{trad} and PBR_{alb} estimates for this species for decades (Fig. 3a).

Surprisingly, our PBR_{trad} calculations for both BFAL and LAAL yielded estimates that were about half the PBR_{trad} reported in Arata et al. (2009). This discrepancy appears to result from the use by Arata et al. (2009) of a F_r value of 1.0, despite reporting the use of an F_r of 0.5. Similarly, the PBR_{trad} of Arata et al. (2009) uses N_t in 2003 rather than N_{min}, and appears to count all individuals, including chicks, although an implicit assumption of the PBR equation is that the removal of individuals will be done in proportion to the age and sex structure of the population used to define N_{min}. Wade (1998) recommends the 20th percentile of the abundance estimate be used for N_{min} while Richard and Abraham (2013) recommend N_{min} only include the proportion of the population subject to fisheries mortality (i.e., for seabirds, they exclude chicks) and propose an additional calibration factor of 0.17–0.43 for Procellariiformes to ensure a 95% probability that populations would exceed half carrying capacity in 200 years when accounting for environmental and demographic stochasticity.

We conclude that the PBR reported in the current USWFS Black-footed and Laysan Albatross Status Assessment (Arata et al., 2009) is overestimated by at least a factor of two, and thus underestimates the impact of fisheries bycatch for both species also by a factor of two. This overestimate is less critical for LAAL, whose estimated bycatch numbers are currently well below the PBRs calculated (Fig. S4), but could be significant for BFAL, whose bycatch numbers are estimated to be at or above the PBRs calculated (Fig. 3a).

4.4. Detecting population change using count data could take decades

Similar to Maxwell and Jennings (2005), we found that increased mortality that resulted in even a large reduction in λ_t (~6%) required 10 years to ensure a 90% chance of detecting the decline while a 5% decrease in λ_t required 20 years (Fig. 3c). Because species-specific data from USFWS were not available for our analyses, we used surrogate data from LAAL for the mean and variance in the breeding probability for BFAL (Table 3). If the variance in breeding probability for BFAL exceeds that of LAAL, detecting declines will require additional years to decades. The extended pelagic pre-breeder life stage of albatrosses also creates 'lost years' (Witham, 1980), which can further increase time lags for detecting changes in population trajectories.

Obtaining accurate fisheries bycatch estimates is inherently challenging (Brothers et al., 2010; Lewison and Crowder, 2003) with significant variation reported in the spatial and temporal risk of seabird capture (Gilman et al., 2016). Recent evidence suggests that for the Hawaiian longline fishery, BFAL and LAAL bycatch rates initially declined after the implementation of regulations in 2001, but over the past decade rates have significantly increased (Gilman et al., 2016). Thus, we recommend a cautionary approach to management as relatively small increases in bycatch mortality rates could change the future status of BFAL populations but not be detected for decades from observed breeding count data.

4.5. Relative importance of bycatch versus on-island threats is species-specific

Our models predict that for North Pacific albatrosses, the relative importance of on-island threats to reproduction versus at-sea threats to post-fledgling survival depends on the species and the threat intensity. For BFAL, bycatch levels are at or above the PBR and appear to be having a meaningful impact on population growth, while on-island threats such as storms are substantially less important. Given these findings, continued efforts to quantify and reduce bycatch mortality are critically important to assure BFAL population viability. Nonetheless, permanent *Verbesina* removal increased BFAL population growth rate by ~0.4% (Fig. S5) and thus could help to buffer the population against bycatch-related mortality. Estimated per capita bycatch mortality for LAAL is very low and is not predicted to be limiting growth, while on-island effects to reproduction such as the invasive shrub *Verbesina* exert a greater influence on population viability. Initial *Verbesina* removal has been completed for Midway and Kure atolls but we show that the reproductive gains on Midway and Kure are quickly reversed if *Verbesina* is allowed to return from the seed bank or re-introduced (Fig. 4c-d, Fig. S5). In addition, *Verbesina* remains an ongoing stressor for albatrosses breeding at Pearl and Hermes Atoll and a potential threat at all other albatross islands (Lisianski, Laysan, French Frigate Shoals) if it is accidentally introduced there (B. Flint pers. com.).

For long-lived, late-maturing species such as albatross, adult survival always has a strong influence on population growth rates, and significant adult mortality generally cannot be offset by increases in reproduction (Finkelstein et al., 2008). Nonetheless, as we have previously shown, when impacts to reproduction are relatively high, measures to increase reproductive success can be an effective management strategy (Finkelstein et al., 2010a). Likewise, the greater effect of combined increases in storm frequency and storm extent suggests that ensuring widely distributed breeding colonies could be an effective

strategy for enhancing population persistence in the event of climate-mediated changes in storm patterns. We note that changing conditions (bycatch, invasive species such as *Verbesina*) and unquantified threats to demographic rates such as plastic ingestion (Young et al., 2009b) or other unforeseen threats could impact BFAL and LAAL albatross populations in the future in ways not accounted for in our model projections. One clear example of a changing on-island condition is the first observations in 2015 that introduced house mice (*Mus musculus*), which have been present on Midway Atoll for over 75 years, have started biting incubating adult Laysan and black-footed albatross on that atoll, causing open wounds and stress, ultimately leading to numerous adult mortalities and nest abandonments (Duhr-Schultz et al., 2017).

5. Conclusion

Our work underscores the inherent difficulties in assessing population status and trends using annual nest count data for species such as albatrosses. Such nest count data quantify a varying fraction of the population, and this fraction tends to be negatively autocorrelated through time, giving the illusion of negative density dependence. We also illustrate that a conservative approach should be taken when setting management policy for BFAL and LAAL as detecting population declines from annual nest count data could take decades. Although nest count data will remain an important metric for tracking populations, our findings highlight their inherent limitations for detecting short-term trends and population processes, and we recommend complementary monitoring of adult survival, which is a key driver of population dynamics.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2017.08.022.

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