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

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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