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Modelling effects of nonbreeders on population growth estimates

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Summary

1. Adult individuals that do not breed in a given year occur in a wide range of natural populations. However, such nonbreeders are often ignored in theoretical and empirical population studies, limiting our knowledge of how nonbreeders affect realized and estimated population dynamics and potentially impeding projection of deterministic and stochastic population growth rates.

2. We present and analyse a general modelling framework for systems where breeders and nonbreeders differ in key demographic rates, incorporating different forms of nonbreeding, different life histories and frequency-dependent effects of nonbreeders on demographic rates of breeders.

3. Comparisons of estimates of deterministic population growth rate, λ, and demographic variance, σ_d^2, from models with and without distinct nonbreeder classes show that models that do not explicitly incorporate nonbreeders give upwardly biased estimates of σ_d^2, particularly when the equilibrium ratio of nonbreeders to breeders, N_{nb}^*/N_b^*, is high. Estimates of λ from empirical observations of breeders only are substantially inflated when individuals frequently re-enter the breeding population after periods of nonbreeding.

4. Sensitivity analyses of diverse parameterizations of our model framework, with and without negative frequency-dependent effects of nonbreeders on breeder demographic rates, show how changes in demographic rates of breeders vs. nonbreeders differentially affect λ. In particular, λ is most sensitive to nonbreeder parameters in long-lived species, when $N_{nb}^*/N_b^* > 0$, and when individuals are unlikely to breed at several consecutive time steps.

5. Our results demonstrate that failing to account for nonbreeders in population studies can obscure low population growth rates that should cause management concern. Quantifying the size and demography of the nonbreeding section of populations and modelling appropriate demographic structuring is therefore essential to evaluate nonbreeders' influence on deterministic and stochastic population dynamics.

Key-words: demographic stochasticity, floaters, intermittent breeding, matrix model, nonbreeding, population dynamics, reproductive skipping, sensitivity analysis

Introduction

Nonbreeders, here defined as sexually mature individuals that do not breed in a given breeding season, occur in numerous populations of diverse animal taxa, spanning reptiles (e.g., Olsson & Shine 1999), mammals (e.g., Beauplet *et al.* 2006), fish (e.g., Moore *et al.* 2013) and birds, in which they seem to be particularly common (e.g., Newton 1998; Cam *et al.* 1998; Renton 2004). Breeder and nonbreeder segments of a population might differ in demography (survival and future breeding), age structure, environmental stochasticity experienced and interactions with or effects on conspecifics, for example due to different habitat selection and space use (e.g., Sandercock *et al.* 2000; Renton 2004; Beauplet *et al.* 2006; Campioni *et al.* 2012). However, little is known about how the presence of nonbreeders might alter projections of future population growth and extinction risk. Can models that do not explicitly include demographic structure caused by

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nonbreeders provide accurate estimates of population growth? How biased are population growth rate estimates from studies of breeding segments of populations when populations also contain nonbreeders? How will populations respond to environmental changes that have different effects on breeders and nonbreeders?

Population growth consists of deterministic and stochastic elements. The deterministic growth rate, λ, quantifies expected population growth. The realized stochastic population growth rate is usually lower than λ, due to effects of environmental and demographic stochasticity (Lande, Engen & Sæther, 2003). Demographic stochasticity describes variation among individuals caused by chance realizations of survival and fecundity (May, 1973) and can be quite influential in small populations, where it tends to increase extinction risk (Lande, Engen & Sæther, 2003). Accurate estimates of stochastic population growth in small populations therefore require estimation of both λ and the demographic variance, σ^2_d.

Standard Leslie matrix models (Leslie 1945) explicitly account for age structure, but not other forms of demographic structure. In these commonly used models, nonbreeders are simply represented by zeros in the estimated distribution of offspring production (equal to failed breeders). Estimation of the demographic variance, σ^2_d, then requires knowledge of the distribution of offspring production in the population, as well as any covariance between survival and reproduction (Engen *et al.* 2009), such as that caused by consistent differences in survival between breeders and nonbreeders. Additionally, persistent differences among individuals in their propensity to breed create another source of covariation that cannot easily be accounted for within the basic Leslie matrix framework.

Alternatively, breeders and nonbreeders can be modelled in separate classes with distinct demographic rates. This is a straightforward way to account for demographic differences between breeders and nonbreeders and the resulting covariances, but it increases the number of parameters that need to be estimated from population data. Such models have been mostly restricted to studies of long-lived seabirds, parrots and plants (e.g. Werner & Caswell 1977; Jenouvrier *et al.* 2005; Beissinger *et al.* 2008; Gremer, Crone & Lesica 2012; Waugh *et al.* 2015). To reduce bias in projections of future population growth, we must determine when the more complex model structures should be used, by quantifying differences in estimates of λ and σ^2_d obtained from models with different structures.

Accurate predictions from population projection models also require accurate estimates of demographic rates. Nonbreeders are often harder to detect than breeders (Pardo *et al.* 2013), particularly because population studies tend to focus on breeders and the areas they occupy (Katzner *et al.* 2011b). For example, a common practice for studying breeding bird populations is to search for nests, colour-ring offspring and catch or resight adults at the nests without concurrent resighting of nonbreeders (e.g. Keyser 2004; Grüebler *et al.* 2008; Mounce *et al.* 2013). Fecundity estimates from the observed breeders are then combined with survival estimates from resighting data, implicitly assuming that surviving individuals breed at all time steps, even when not observed. An important step to avoid biased estimates of population growth is to test how this assumption affects the accuracy of population growth estimates when populations contain nonbreeders.

In addition to understanding how the presence of nonbreeders affects estimates of population growth and demographic variance, quantifying the role of nonbreeders in actual population dynamics can be crucial to projecting population responses to environmental change. Breeders and different types of nonbreeders might respond differently to changes, either because they utilize different areas and resources (Caro, Ontiveros & Pleguezuelos 2011; Campioni *et al.* 2012) or because conservation efforts are directed at one group more than the other. For example, conservation efforts that improve access to resources used by breeders might have no effect on nonbreeders, whereas habitat destruction in areas used by nonbreeders might have severe negative impacts on population dynamics without influencing breeders directly. Despite the prevalence of nonbreeders in natural populations, we currently lack a general framework for evaluating the potential impact of different types of nonbreeders on population dynamics and responses to change. Such a framework must incorporate population structure caused by different types of nonbreeders with different demographic rates, such as young individuals that have not yet entered the breeding population (sometimes referred to as prebreeders; e.g. Jenouvrier *et al.* 2008); nonbreeders that have bred previously but are currently skipping a year (experienced nonbreeders; e.g. Cubaynes *et al.* 2011); and old nonbreeders that are unlikely to acquire the resources needed for further breeding (senescent nonbreeders, e.g. Olesiuk, Bigg & Ellis 1990).

Population responses to environmental change might also depend on interactions between individuals. In addition to potential contributions to future breeding, nonbreeders can have negative or positive effects on current breeding through competition (Carrete, Donázar & Margalida, 2006), harassment and infanticide (Bonebrake & Beissinger 2010) or helping behaviour (Reyer 1990). Negative effects of nonbreeders can take two forms. By increasing the total population size, nonbreeders contribute to density dependence in much the same way that breeders do (Wauters & Lens 1995; Carrete, Donázar & Margalida, 2006). In addition, when nonbreeders interfere with breeding, for example by harassing breeders or forcing territory defence, frequency dependence can arise, in which breeder survival or fecundity is reduced when the ratio of nonbreeders to breeders becomes high (Wauters & Lens 1995; Newton & Rothery 2001). If such frequency dependence influences population dynamics, models projecting population responses to environmental change must also incorporate these effects.

We present a general framework of population projection models that explicitly incorporate various types of nonbreeders. We compare estimates of λ and σ_d^2 from these models to those from standard Leslie matrix models without distinct nonbreeder classes to determine whether differences in model structure are likely to bias estimates of population growth ('model structure analysis'). We then quantify the bias caused by estimating λ from observations of breeders only ('observation analysis'). Using a wide range of biologically realistic parameterizations within our model framework, we analyse the sensitivity of λ to changes in the demographic rates of breeders and nonbreeders in systems with different types of nonbreeders and test how frequency-dependent effects of nonbreeders on breeder survival and fecundity alter the responses of λ to demographic changes ('sensitivity analysis'). Thus, we establish how the often disregarded nonbreeders affect both population growth itself and our estimates of such growth.

Materials and methods

CLASSIFICATION AND MODELLING OF NONBREEDER SYSTEMS

Nonbreeding individuals have been referred to as floaters (Brown 1969; Lenda, Maciusik & Skorka 2012), intermittent breeders (Calladine & Harris 1997), nonbreeders (Cam *et al.* 1998) and non-nesters (Moynahan, Lindberg & Thomas 2006), with different connotations. Here, we define nonbreeders as individuals that are sexually mature but do not initiate breeding in a given breeding season.

We classify systems with nonbreeders by five characteristics: types of distinct nonbreeder classes (Fig. 1a,b); age structure (Fig. 1c); presence of senescent individuals (Fig. 1d); effect on breeding probability of recent breeding history (Fig. 1e); and age at maturity (Fig. 1f). Figure 1 demonstrates how each of these characteristics can be described by life cycle graphs that translate into single-sex matrix models. Combining subsets of these life cycles according to the characteristics of individual systems provides the flexibility to build appropriate matrix models for a wide range of populations.

In contrast to standard Leslie matrix models (Leslie 1945) in which individuals are separated only into age classes, our models distinguish nonbreeders from breeders (Fig. 1a). In some cases, nonbreeders can be further separated into distinct classes that differ in their probabilities of surviving or of becoming breeders. For brevity, we only analyse the common case where inexperienced nonbreeders (i.e. individuals that are sexually mature but have not yet bred) have a lower probability of surviving and of breeding at the next time step than experienced nonbreeders that have bred previously (Fig. 1b), as in kittiwakes (*Rissa tridactyla*; Cam *et al.* 1998; Desprez *et al.* 2011). Systems with other configurations of survival and breeding probability can be analysed in the same way using the R code (R Core Team 2014) provided in the Dryad Digital Repository (Lee, Reid & Beissinger 2016).

Age is an important factor in determining breeding probability and survival in many species and can have different effects in breeders and nonbreeders (e.g. in subantarctic fur seals (*Arctocephalus tropicalis*), Beauplet *et al.* 2006). Age-structured models with nonbreeders are then appropriate (Fig. 1c). One specific type of age structure is caused by senescent individuals that are too old to breed but are still alive (Fig. 1d). For example, in killer whales (*Orcinus orca*) females stop reproducing around age 40, but have a mean life expectancy of 50 years (max. 90 years; Olesiuk, Bigg & Ellis 1990; Brent *et al.* 2015). Such a postreproductive class does not contribute directly to population growth, but can still have indirect effects through (positive or negative) frequency or density dependence.

Finally, the probability of an individual breeding at a given time step can be influenced by its recent reproductive history (Fig. 1e). For example, if breeding is costly, breeding probability might decrease directly after a breeding event (or after several successive breeding events), whereas individuals that have not bred for a year or two gain a higher breeding probability. For example, female southern snow skinks (*Niveoscincus microlepidotus*) never breed two years in a row, and often skip two seasons before reproducing a second time (Olsson & Shine 1999).

Age at maturity, a_m, is the first age at which individuals are physiologically mature and could breed. For example, small primates, such as galagos (Galagidae), can usually breed at age one, whereas chimpanzees (*Pan troglodytes*) do not reach maturity until age ten (Harvey & Clutton-Brock 1985). In all our models, the parameter a_m determines the number of immature age classes present in the life cycle (Fig. 1f, Fig. 1a–e are shown with $a_m = 2$).

The life cycles shown in Fig. 1 are special cases of a broad spectrum of systems and are not mutually exclusive. For example, immatures, different types of nonbreeders and various forms of age structure can co-occur. The life cycles in Fig. 1 can be rearranged and used as building blocks to model most nonbreeder systems. Matrices for each life cycle can be constructed assuming either prebreeding or postbreeding census. With postbreeding census, there is an additional class of newborns in each case. Appendix S1 (Supporting Information) provides prebreeding census matrices for each life cycle in Fig. 1, with examples of how to construct corresponding postbreeding census matrices. R code (R Core Team 2014) for constructing matrices of either type and analysing them is available from the Dryad Digital Repository (Lee, Reid & Beissinger 2016).

All our analyses utilize parameterizations of the life cycles in Fig. 1, selected to represent a range of biologically representative systems with different types of nonbreeder structure (Table S1). Survival probabilities and age at maturity are chosen to represent long-lived, 'slow' species (high survival, medium age at maturity) and short-lived, 'fast' species (low survival, low age at maturity). In most systems analysed, nonbreeders are assumed to have lower probabilities of surviving and of breeding at the next time step than breeders, but we also consider systems where nonbreeders and breeders have the same demographic rates, or where breeders have lower survival and future breeding probabilities than nonbreeders. The latter case might represent situations where breeding is costly. Table S1 gives an overview of which systems are used in each analysis. All parameters are reported in Tables S2 and S3.

MODEL STRUCTURE ANALYSIS

For a range of systems with nonbreeders, estimates of stochastic population growth parameters λ and σ_d^2 from our prebreeding census population projection models with separate breeder and nonbreeder classes were compared to estimates from Leslie

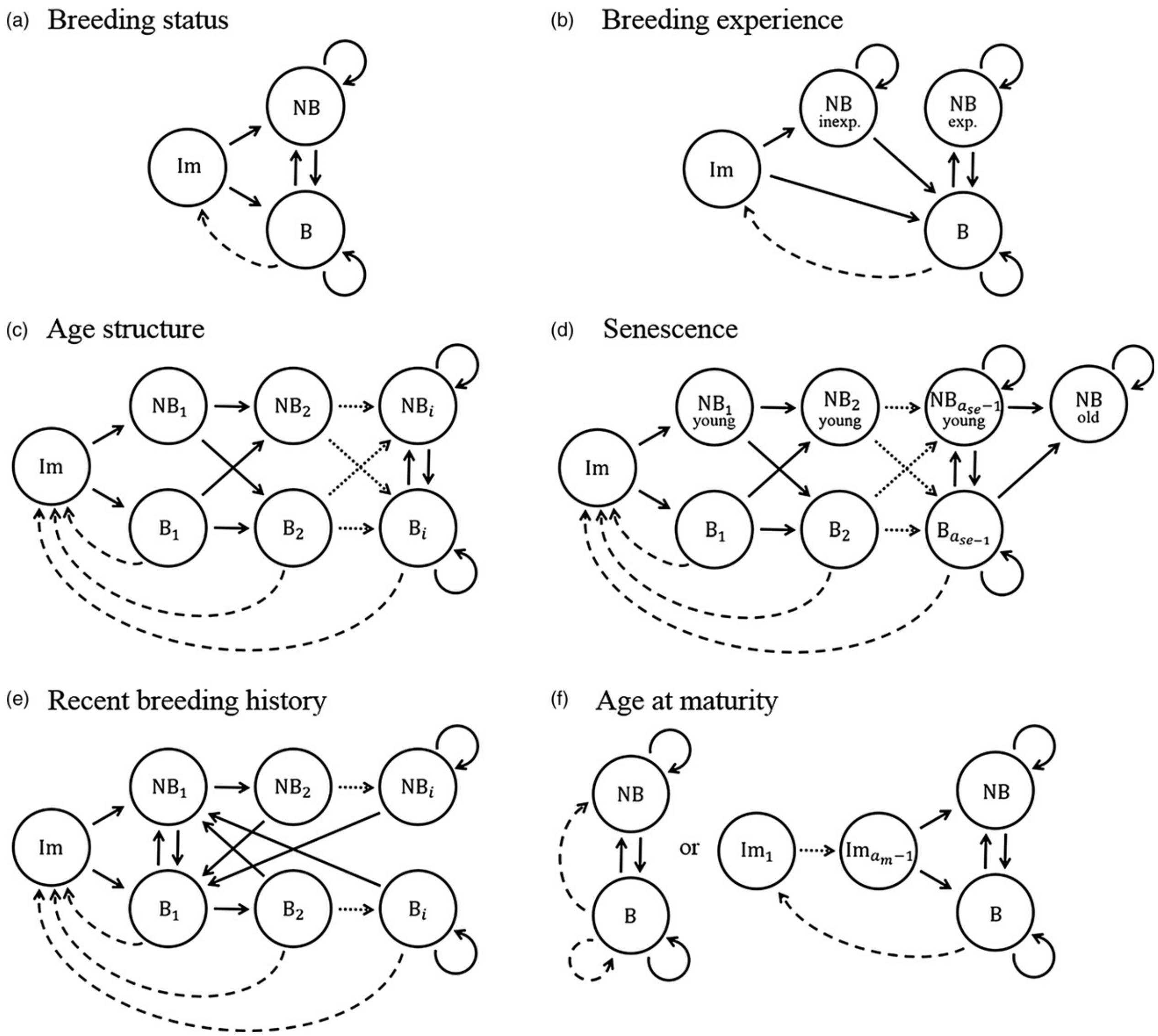

Fig. 1. Life cycle graphs with different types of nonbreeders and population organizations, assuming a prebreeding census. (a) System with two classes distinguished by breeding status (breeders, B, and nonbreeders, NB). Im is a class of immature individuals that have not yet reached the age of maturity, a_{m}. (b) System with two types of nonbreeders; inexperienced (have not yet bred) and experienced (have bred previously). (c) Age-structured system in which probability of becoming a breeder (or other parameters) change with age. (d) System with senescence. After age $a_{\mathrm{se}} - 1$, individuals have a probability, p_{se}, of becoming old nonbreeders that never re-enter the breeding population. (e) System in which probability of becoming a breeder (or other parameters) depends on the time an individual has had a particular breeding status. (f) When age at maturity, a_{m}, is one, offspring move directly into the breeder or nonbreeder class. When $a_{\mathrm{m}} > 1$ there are classes of immature individuals, Im. After age $a_{\mathrm{m}} - 1$, individuals move into the adult B or NB class. Models in panels a-e are shown with $a_{\mathrm{m}} = 2$. With a postbreeding census, life cycle graphs have an additional class of newborns.

matrix models of the same systems without separate nonbreeder classes. Systems representing several different types of nonbreeder structure and life-history 'speed' were considered (Tables S1–S3). Fecundity (defined as the number of female offspring produced per female that survive to age 1) was set so that $\lambda = 1 \pm 0{\cdot}00005$. Most analysed parameter sets resulted in populations with fewer nonbreeders than breeders at equilibrium ($N^*_{\mathrm{nb}} < N^*_{\mathrm{b}}$; Tables S2 and S3). To evaluate the importance of the $N^*_{\mathrm{nb}}/N^*_{\mathrm{b}}$ ratio, we also analysed 'breeding status' systems (Fig. 1a) with more nonbreeders than breeders at equilibrium ($N^*_{\mathrm{nb}}/N^*_{\mathrm{b}} > 1$) and with equal numbers ($N^*_{\mathrm{nb}}/N^*_{\mathrm{b}} = 1$). In the latter case, nonbreeder survival probability was set either equal to or greater than breeder survival probability (Table S2). Leslie matrices were parameterized by calculating demographic parameters for each age as the average of breeder and nonbreeder parameters, weighted by stable stage structure. This equates to classifying nonbreeders as failed breeders. In 'breeding experience' (Fig. 1b) and 'recent breeding history' (Fig. 1e) systems, where age is not part of the nonbreeding structure, parameterization of Leslie matrices entailed first analysing an expanded matrix with both breeding status and age structure, to find appropriate weights. The number of age classes in the Leslie model was set equal to the sum of breeder and nonbreeder classes in the non-age-structured models. For comparison, we also analysed a Leslie matrix with only one adult age class. The demographic variance was calculated from the matrices using the method described in

Engen *et al.* (2009), and covariances between survival and fecundity were accounted for in calculations from Leslie matrices (Engen *et al.* 2009).

OBSERVATION ANALYSIS

To quantify bias caused by the common practice of estimating λ based on observations of breeding segments of populations only, estimates of λ from 'age structure' models (Fig. 1c) parameterized with full data on both nonbreeders and breeders vs. data on only the breeding population were compared. For simplicity, the breeders only case assumed that all breeders and offspring were observed and marked, whereas nonbreeders were not observed. Thus, all individuals that bred at a given age affected survival estimates for all preceding ages (whether they bred previously or not), while fecundity estimates were based only on breeders. As complete detection of offspring in a system with unobserved nonbreeders is most likely when the population is censused directly after breeding, postbreeding census matrices were used for this analysis. The assumption that all offspring were observed allowed estimated survival probabilities to be calculated directly from the model parameters. For each age class, *a*, the probability of an individual being alive and breeding at this or future ages was calculated. This was achieved by calculating probabilities of each path through the life cycle, adding the probabilities for all paths leading to breeding at age *a*, and all paths in which individuals were nonbreeders at age *a* but breeders at a later age. This gave estimated survival up to the focal age *a*. Dividing this probability by the estimated survival probability found for age $a-1$ yielded the survival probability from age $a-1$ to *a*. We set a maximum life span, making the analysed system a variant of Fig. 1c, without self-loops for the last age classes. Underlying probabilities of survival and breeding were set equal for all age classes. We quantified how the difference between estimates of λ from the full model vs. the model that ignored nonbreeders was influenced by nonbreeder survival, transition probabilities from nonbreeder to breeder and maximum life span.

SENSITIVITY ANALYSES

Sensitivity analyses were used to quantify how changes in the demographic rates of breeders and nonbreeders are expected to affect λ in systems with different types of nonbreeders. Each life cycle presented in Fig. 1 was analysed, with parameters covering the same range of biologically representative systems as for the model structure analysis (Tables S2 and S3). Fecundity was again set such that $\lambda = 1 \pm 0{\cdot}00005$. For each prebreeding census system, we performed numerical sensitivity analysis using a finite difference approximation with $\delta = 0{\cdot}005$ and scaled the result to a unit change in each parameter. This is equivalent to a standard sensitivity analysis focused on lower level parameters (Caswell 2001) but is easier to implement in frequency-dependent systems. R code is provided in the Dryad Digital Repository (Lee, Reid & Beissinger 2016), including code for performing standard lower level sensitivity analysis for comparison.

Effects of negative frequency dependence were quantified by letting breeder survival or fecundity depend on the ratio of nonbreeders to breeders. In the former case, realized breeder survival was calculated as $s_\mathrm{b}/(1+\frac{N_\mathrm{nb}}{N_\mathrm{b}})$, where s_b is the breeder survival in the absence of nonbreeders, and N_nb and N_b are the numbers of nonbreeders and breeders in the population at a given time step. Similarly, when fecundity was frequency-dependent, realized fecundity was $f/(1+\frac{N_\mathrm{nb}}{N_\mathrm{b}})$, where f is fecundity in the absence of nonbreeders. The sensitivity analysis performed on the frequency-independent systems was repeated for each of the frequency-dependent systems. The deterministic growth rate, λ, was calculated by projecting each model over time until an equilibrium proportional population structure, $\hat{n}$, was reached, satisfying $\hat{n} = A[\theta,\hat{n}]\hat{n}/||A[\theta,\hat{n}]\hat{n}||$, where A is the population projection matrix, θ represents the matrix parameters, and $||A[\theta,\hat{n}]\hat{n}||$ is the one-norm of $A[\theta,\hat{n}]\hat{n}$ (i.e. the sum of the absolute values of its components, Caswell, 2001, 2008). At this equilibrium, populations grow exponentially at a rate λ given by the dominant eigenvalue of $A[\theta,\hat{n}]$. All systems analysed reached such an equilibrium.

Results

MODEL STRUCTURE ANALYSIS

Leslie matrix models without separate nonbreeder classes, that implicitly classify nonbreeders as failed breeders, gave identical estimates of λ as models with separate nonbreeder classes. However, models without separate nonbreeder classes gave higher estimates of σ_d^2 (Table 1). The greatest proportional differences occurred in the 'breeding status' system when the equilibrium ratio of nonbreeders to breeders ($N_\mathrm{nb}^*/N_\mathrm{b}^*$) exceeded one, followed by systems where $N_\mathrm{nb}^*/N_\mathrm{b}^* = 1$. When $N_\mathrm{nb}^*/N_\mathrm{b}^* < 1$, the 'recent breeding history' and the 'breeding experience system' without adult age structure had the greatest proportional differences in estimated σ_d^2. In the 'recent breeding history' system, adding adult age structure to the model without separate nonbreeder classes increased the difference in σ_d^2 (Table 1). 'Breeding status' systems with $N_\mathrm{nb}^*/N_\mathrm{b}^* < 1$ and slow life histories showed very small differences in estimated σ_d^2.

OBSERVATION ANALYSIS

As expected, using demographic estimates from observations of only the breeding population caused λ to be overestimated (Fig. 2). The bias in λ was large in many cases and increased with increasing nonbreeder survival probability, with increasing maximum life span and with increasing transition probability from nonbreeder to breeder.

SENSITIVITY ANALYSIS

In frequency-independent systems, the sensitivity of λ to survival probabilities depended on $N_\mathrm{nb}^*/N_\mathrm{b}^*$. When $N_\mathrm{nb}^*/N_\mathrm{b}^* < 1$, λ was typically more sensitive to small changes in breeder survival probability, s_b, than to small changes in survival probabilities of nonbreeders, s_nb, or immatures, s_im, or to small changes in breeding probabilities (i.e. probabilities of transitioning to or staying in the breeder class; b_am, b_nb, b_b) (Figs 3 and 4,

Table 1. Effects on estimates of demographic variance (σ^2_d) of pooling breeders and nonbreeders and calculating demographic parameter values from weighted averages ($\sigma^2_\text{d\_est}$), compared to estimates from models with separate nonbreeder classes ($\sigma^2_\text{d\_nb}$). s_b, b_b, s_nb and b_nb are survival probabilities (*s*) and probabilities of staying in or moving to a breeding class (*b*), of breeders and nonbreeders (subscripts *b* and *nb*, respectively). a_m is age at maturity. $N^*_\text{nb}/N^*_\text{b}$ is the equilibrium ratio of nonbreeders to breeders. Parameters are set equal to those used in systems in Figs 3 and 4. Variance in fecundity is 0·5 in all systems

System	Figures	a_m	Survival	Nonbreeder 'quality'	$N^*_\text{nb}/N^*_\text{b}$	$\sigma^2_\text{d\_nb}$	$\Delta\sigma^2_\text{d\_est}$
Breeding status	3a	4	High	$s_\text{nb}, b_\text{nb} < s_\text{b}, b_\text{b}$	<1	0·266	+0·003
Breeding status	3b	4	High	$s_\text{nb}, b_\text{nb} = s_\text{b}, b_\text{b}$	<1	0·194	+0·005
Breeding status	3c	4	High	$s_\text{nb}, b_\text{nb} > s_\text{b}, b_\text{b}$	<1	0·183	+0·003
Breeding status	3d	1	Low	$s_\text{nb}, b_\text{nb} < s_\text{b}, b_\text{b}$	<1	0·835	+0·012
Breeding status	3e	1	Low	$s_\text{nb}, b_\text{nb} = s_\text{b}, b_\text{b}$	<1	0·708	+0·028
Breeding status	3f	1	Low	$s_\text{nb}, b_\text{nb} > s_\text{b}, b_\text{b}$	<1	0·632	+0·026
Breeding status	5a	1	Low	$s_\text{nb} = s_\text{b}$	>1	0·750	+0·799
Breeding status	5b	1	Low	$s_\text{nb} = s_\text{b}$	1	0·750	+0·250
Breeding status	5c	1	Low	$s_\text{nb} > s_\text{b}$	1	0·531	+0·141
Breeding experience, 1 age class	4a	2	–	$s_\text{nb}, b_\text{nb} < s_\text{b}, b_\text{b}$	<1	0·314	+0·042
Breeding experience, 3 age classes	4a	2	–	$s_\text{nb}, b_\text{nb} < s_\text{b}, b_\text{b}$	<1	0·314	+0·001
Age structure	4b	2	–	$s_\text{nb}, b_\text{nb} < s_\text{b}, b_\text{b}$	>1	0·423	+0·043
Recent breeding history, 1 age class	4d	2	–	$s_\text{nb}, b_\text{nb} < s_\text{b}, b_\text{b}$	<1	0·324	+0·041
Recent breeding history, 6 age classes	4d	2	–	$s_\text{nb}, b_\text{nb} < s_\text{b}, b_\text{b}$	<1	0·324	+0·064

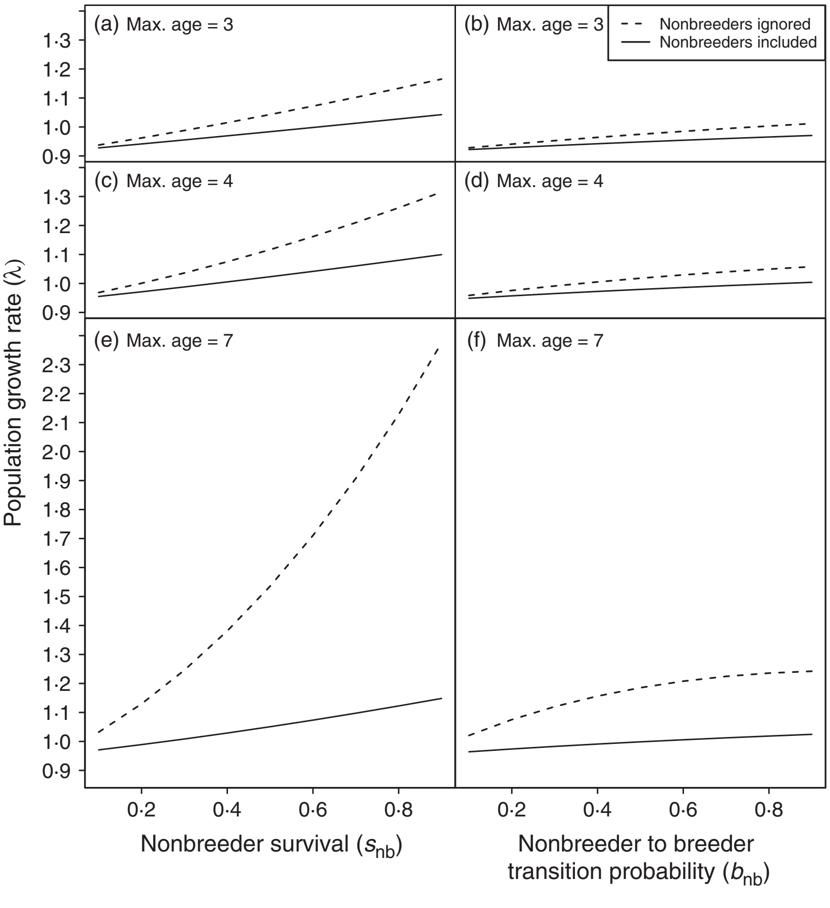

Fig. 2. Population growth rate estimates from full population model (solid lines) and observations of breeders only (dashed lines) in a postbreeding census model. All individuals are assumed to die after age 3 (panels a, b), 4 (c, d) or 7 (e, f). Age at maturity is $a_\text{m} = 1$, fecundity $f_\text{post} = 1{\cdot}5454$ and newborn survival $s_\text{o} = 0{\cdot}5$. This is equivalent to a fecundity of $f = 0{\cdot}7727$ in the prebreeding census model (Fig. 3f) where fecundity includes survival to age 1. All other parameters are set equal to those in Fig. 3f (see Table S2). In panels a, c and e, nonbreeder survival probability is adjusted from 0·1 to 0·9. In b, d and f, the transition probability b_nb is adjusted from 0·1 to 0·9.

grey bar to left of dashed line). Conversely, when $N^*_\text{nb}/N^*_\text{b} > 1$, λ was more sensitive to s_nb than to any other parameter (Fig. 5a, black bar to left of dashed line). Finally, when $N^*_\text{nb}/N^*_\text{b} = 1$, λ was equally sensitive to s_nb and s_b (Fig. 5b,c, grey and black bars to left of dashed line).

In general, the relative sensitivity of λ to breeding probabilities vs. survival probabilities was higher in systems representing short-lived species than in systems representing long-lived species (Fig. 3, compare bars on each side of dashed line). The relative sensitivity to breeding probabilities compared to survival probabilities was also highest

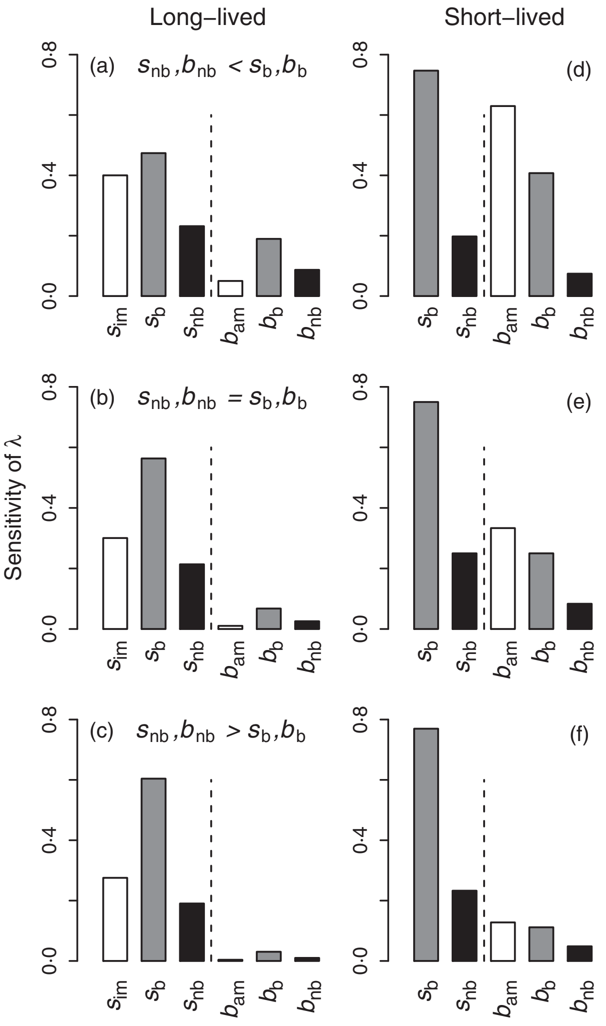

Fig. 3. Sensitivity of the deterministic population growth rate, λ, to survival probabilities (*s*, bars to the left of dashed lines) and probabilities of becoming or remaining breeders (*b*, bars to the right of dashed lines). Bar colours indicate breeding status; immature (im, white), breeder (b, grey) and nonbreeder (nb, black). Note that b_{am} is the probability of breeding at first maturity. Breeding probability for younger immatures is zero. All systems follow the 'breeding status' and 'age at maturity' life cycle (Fig. 1a,f) with high survival and medium age at maturity ('long-lived', panels a–c) or low survival and low age at maturity ('short-lived' d–f). Nonbreeder survival and breeding probabilities (s_{nb}, b_{nb}) are either lower (panels a, d), equal (panels b, e) or higher (panels c, f) than survival and breeding probabilities of breeders (s_b, b_b). Exact parameter values are in Table S2.

in systems where nonbreeders had lower demographic rates than breeders (s_{nb}, $b_{nb} < s_b$, b_b), and lowest in systems where breeding was 'costly' ($s_{nb}, b_{nb} > s_b, b_b$) (Fig. 3, top and bottom panels). The sensitivity of λ to s_{im} depended on fecundity rates, with higher sensitivity in systems with higher fecundity (e.g. Figs 3a and 4c, white bar to left of dashed line).

Overall, in long-lived species, s_{nb} was one of the demographic parameters to which λ was the most sensitive, even when $N^*_{nb}/N^*_b < 1$ (Fig. 3, left column of panels, black bar to left of dashed line). The absolute sensitivity to s_{nb} was

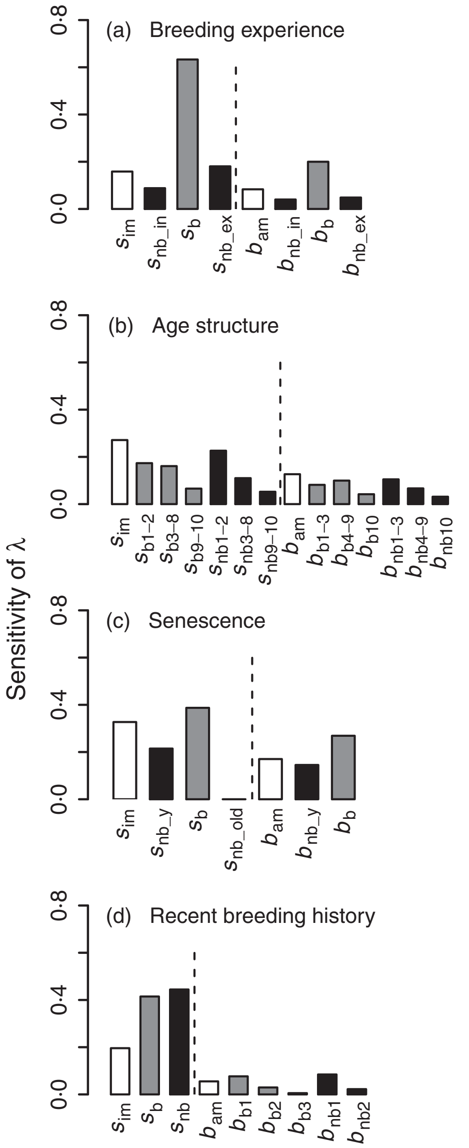

Fig. 4. Sensitivity of the deterministic population growth rate, λ, to survival probabilities (*s*, bars to the left of dashed lines) and probabilities of becoming or remaining breeders (*b*, bars to the right of dashed lines). Bar colours indicate breeding status; immature (im, white), breeder (b, grey) and nonbreeder (nb, black). Additional subscripts distinguish different types of nonbreeder (or breeder) classes; inexperienced (in), experienced (ex), young (y), age (numeric subscripts, panel b), consecutive year breeding/not breeding (numeric subscripts, panel d). (a) 'Breeding experience' system (Fig. 1b) where $s_{nb\_in}, b_{nb\_in} < s_{nb\_ex}, b_{nb\_ex} < s_b, b_b$; (b) 'Age structure' system (Fig. 1c) where survival and probability of becoming (or remaining) a breeder increases and then decreases again with age and $s_{nb}, b_{nb} < s_b, b_b$ at all ages; (c) 'Senescence' system (Fig. 1d) where individuals have a 0·6 probability of entering the senescent age class at age 5 and above; (d) 'recent breeding history' system (Fig. 1e) where the probability of remaining a breeder decreases with time spent in the breeding class and individuals are very unlikely to breed more than three times consecutively. Nonbreeders are slightly more likely to become breeders after two (or more) time steps not breeding. Exact parameter values are in Table S3.

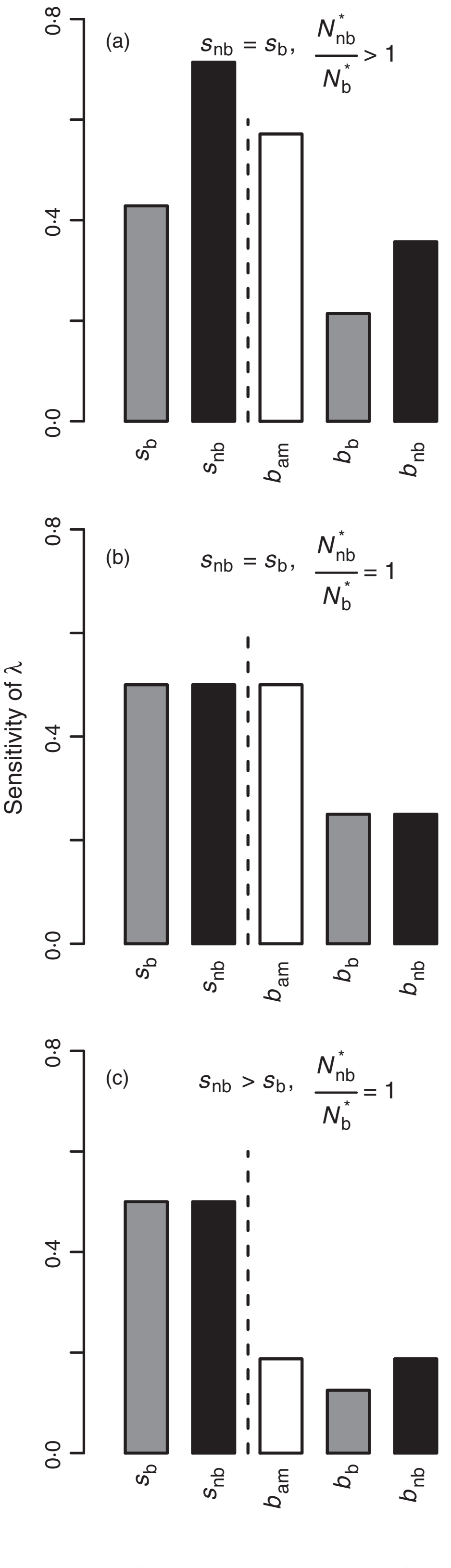

Fig. 5. Sensitivity of the deterministic population growth rate, λ, to survival probabilities (*s*, bars to the left of dashed lines) and probabilities of becoming or remaining breeders (*b*, bars to the right of dashed lines). Bar colours indicate breeding status; immature (im, white), breeder (b, grey) and nonbreeder (nb, black). b_{am} is the probability of breeding at first maturity. All systems follow the 'breeding status' and 'age at maturity' life cycles (Fig. 1a,f) with low survival and low age at maturity. Survival and breeding probabilities are set such that the equilibrium ratio of nonbreeders to breeders, N^*_{nb}/N^*_b, is (a) greater than one, or (b,c) equal to one. In (b,c) $b_{am} = b_{nb} = b_b = 0 \cdot 5$. Nonbreeder survival ($s_{nb}$), is (a, b) equal to breeder survival (s_b), or (c) higher than breeder survival (s_b). Exact parameter values are in Table S2.

similar in short-lived and long-lived species, but λ was more sensitive to breeding probabilities in short-lived species. This caused s_{nb} to be one of the demographic parameters to which λ was the least sensitive in short-lived species when $N^*_{nb}/N^*_b < 1$ (Fig. 3, right column of panels, black bar to left of dashed line). The exception was the system with 'costly' breeding, where λ was less sensitive to breeding probabilities than to s_{nb} even in the short-lived species (Fig. 3, right bottom panel, black bar to left of dashed line). In the 'recent breeding history' system, λ was slightly more sensitive to s_{nb} than to s_b (Fig. 4d).

The sensitivity of λ to breeding probabilities of newly mature individuals or breeders (b_{am}, b_b) was generally quite high in short-lived species (Fig. 3, right column; Fig. 5, white and grey bar to right of dashed line), particularly when nonbreeders had lower survival and breeding probability than breeders (Fig. 3d). The sensitivity of λ to breeding probability of nonbreeders, b_{nb} was low in all frequency-independent systems with $N^*_{nb}/N^*_b < 1$ (Figs 3 and 4, black bars to right of dashed line). However, when $N^*_{nb}/N^*_b > 1$, λ was more sensitive to b_{nb} than to b_b. When $N^*_{nb}/N^*_b = 1$, the sensitivity of λ to b_{nb} and b_b was determined by the survival probabilities. Thus, when $s_{nb} = s_b$, λ was equally sensitive to b_{nb} and b_b (Fig. 5b, grey and black bars to right of dashed line), whereas $s_{nb} > s_b$ caused λ to be more sensitive to b_{nb} than to b_b (Fig. 5c, grey and black bars to right of dashed line).

With frequency dependence in the form of a negative effect of nonbreeders on breeder survival, λ generally became less sensitive to s_b, and more sensitive to b_{am} and b_{nb} (compare top row of Fig. 6 to Figs 3a,d and 4a,c). In the 'breeding experience' system (Fig. 1b), frequency dependence in survival increased the sensitivity of λ to the demographic parameters of inexperienced breeders (Fig. 6e, black bars). When fecundity was frequency-dependent, λ became slightly more sensitive to breeding probabilities (particularly in short-lived species), but sensitivity to survival probabilities changed little (compare bottom row of Fig. 6 to Figs 3a,d and 4a,c). Both types of frequency dependence caused the sensitivity of λ to the survival probability of senescent nonbreeders to become negative (i.e. an increase in survival of senescent nonbreeders caused a decrease in λ; hatched bars in Fig. 6g,h).

Discussion

Nonbreeders of various forms are common in nature and could substantially impact population demography, dynamics and responses to environmental change, thus playing a crucial role in determining the stability and viability of animal populations. However, nonbreeders are surprisingly often ignored in both theoretical and empirical studies of population dynamics. Here, we defined a conceptual framework for modelling systems with different types of nonbreeders and quantifying their effects on population growth. Parameterizations for diverse representative life histories demonstrate the potential major effects of failing to account for nonbreeders when estimating current and future population growth, and demonstrate the influence of model structure on estimates of stochastic population dynamics.

MODEL STRUCTURE ANALYSIS

The observation that matrix models with distinct nonbreeder classes give identical estimates of λ as a simpler Leslie matrix model with breeders and nonbreeders combined in the same class(es) is expected, as λ is estimated from mean survival and fecundity rates, which do not differ between the two models. However, Leslie matrix models tended to give higher estimates of σ^2_{d} than models with separate nonbreeder classes (Table 1). This is because Leslie matrix models treat systematic or structured variation in demographic rates among same-aged breeders and nonbreeders as random variation among average individuals, whereas such structured variation actually decreases the demographic variance compared to that found in a homogeneous population ('variance reduction effect', Fox & Kendall 2002). This effect was most marked when there was a high proportion of nonbreeders in the equilibrium population ($N^*_{\mathrm{nb}}/N^*_{\mathrm{b}} \geq 1$) which exaggerates the 'zero inflation' of the offspring production distribution caused by nonbreeder population structure. In systems with lower equilibrium proportions of nonbreeders, the differences in estimates of σ^2_{d} between the two models were quite small (Table 1). Thus, censusing the nonbreeding segments of populations is crucial for evaluating the impact of model structure on estimates of σ^2_{d} in wild populations. Unfortunately, nonbreeder censusing is rarely considered in current monitoring programs (Citta, Reynolds & Seavy 2007; Rönkä *et al.* 2011; Baasch, Hefley & Cahis, 2015).

When survival probability differs among breeders and nonbreeders, some of the systematic demographic variation caused by the presence of nonbreeders appears as a covariance between survival and reproduction. This covariance can be accounted for in the model without separate nonbreeder classes, thus decreasing the

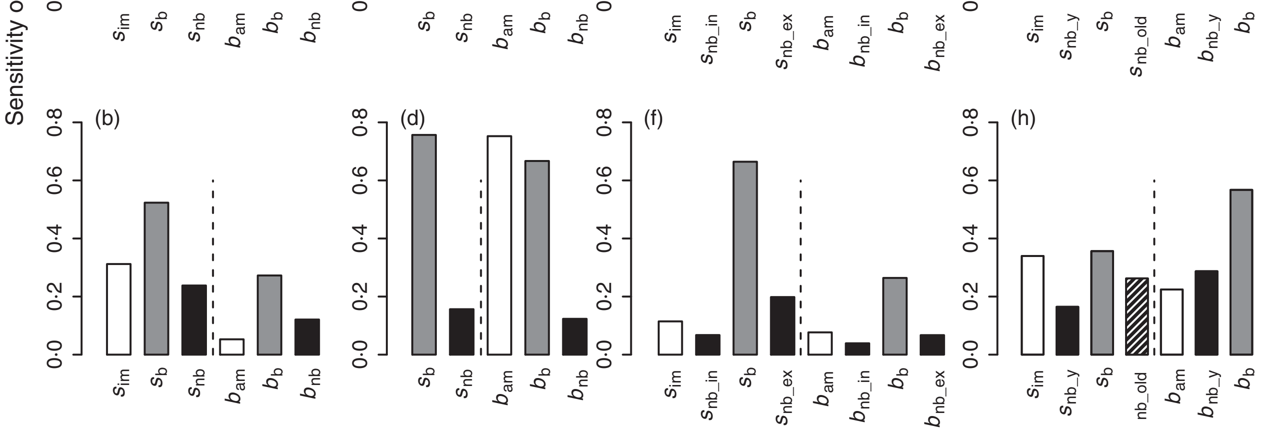

Fig. 6. Sensitivity of the deterministic population growth rate, λ, to survival probabilities (*s*, bars to the left of dashed lines) and probabilities of becoming or remaining breeders (*b*, bars to the right of dashed lines) in systems with frequency-dependent effects of nonbreeders on breeder survival (panels a, c, e, g) or fecundity (panels b, d, f, h). Bar colours indicate breeding status; immature (im, white), breeder (b, grey) and nonbreeder (nb, black). Hatched bars indicate negative sensitivities (i.e. an increase in the parameter decreases λ). Additional subscripts distinguish among different types of nonbreeder (or breeder) classes; inexperienced (in), experienced (ex), young (y). Systems are equivalent to those shown in Fig. 3a ('long-lived'; panels a,b), Fig. 3d ('short-lived'; c,d), Fig. 4a ('breeding experience'; e,f) and Fig. 4c ('senescence'; g,h). λ is 0·85, 0·96, 0·90, 0·84, 0·81, 0·96, 0·83, 0·82 in panels a–h, respectively. All systems reached equilibrium within 200 time steps.

discrepancy between estimates of σ_{d}^2 in the two models (e.g. compare lines 8 and 9 of 'breeding status' models in Table 1). When nonbreeding is correlated with age, as in the 'breeding experience' system, much of the demographic structure is captured by purely age-structured models ('breeding experience' system with 3 adult age classes, Table 1). When all adults are placed in a single age class, this demographic structure is no longer directly accounted for, causing higher estimates of σ_{d}^2 ('breeding experience' system with 1 adult age class, Table 1). Conversely, the structure in the 'recent breeding history' system is not closely correlated with age. Therefore, in this system, adding adult age structure caused the estimated σ_{d}^2 to deviate more from that estimated in the model with separate nonbreeder classes ($\sigma_{\mathrm{d\_nb}}^2$) ('recent breeding history' system with 6 age classes compared to with 1 age class, Table 1). Thus, it is not model structure per se that is important, but how well the structure accounts for demographic heterogeneity.

Modern mark–recapture methods facilitate identification of population structures other than age that explain heterogeneity in demographic rates (e.g. Pradel, Choquet & Béchet 2012). In nature, nonbreeders are often harder to detect than breeders (e.g. Sandercock *et al.* 2000; Katzner *et al.* 2011a; Pardo *et al.* 2013). Using mark–recapture models that account for such differences in detection probability is essential to avoid bias in estimates of demographic rates, and a natural next step is to test whether the demographic rates of breeders and nonbreeders differ. If they do, the life cycles shown in Fig. 1 might be more appropriate representations of the systems than pure age structure.

OBSERVATION ANALYSIS

Accounting for demographic differences between breeders and nonbreeders is clearly important for estimating population growth rates, but what happens if the presence of nonbreeders is unknown or ignored? The common practice of estimating demographic parameters and growth rates based solely on the breeding population (Grüebler *et al.* 2008; Katzner *et al.* 2011b; Chastant *et al.* 2014) results in potentially large overestimates of λ when the population contains nonbreeders (Fig. 2). This is because estimating fecundity from only breeders invokes an implicit assumption that all surviving individuals breed at all time steps. As individuals observed as breeders after a period of nonbreeding contribute to survival estimates, estimates of λ are inflated. This situation can easily arise when survival and fecundity are estimated separately, for example when survival estimates from published mark–recapture studies are paired with fecundity estimates from breeders (as in Mounce *et al.* 2013). The same type of overestimation of λ has been demonstrated when unproductive females are excluded from estimated maternity rates in large carnivores (Chapron, Wielgus & Lambert 2013).

Such overestimation of λ arose in all systems studied, but to varying degrees. The most extreme bias was found when nonbreeder survival probability was high, when maximum life span was high and when nonbreeders had a high probability of becoming breeders at a future time step (Fig. 2). This is because all these factors increase the proportion of nonbreeders that survive and later (re-)enter the breeding population. When only breeding individuals are observed, only nonbreeders that (re-)enter the breeding population contribute to the overestimation of λ. In fact, if nonbreeding were permanent, λ could be accurately estimated from the breeding population. This overestimation of λ can be partially rectified using mark–recapture methods that estimate the probability of an individual being a first-time breeder (Pradel 1996). However, this method only considers inexperienced nonbreeders, not individuals that skip a year after having bred previously. Nonbreeders that *are* observed during the breeding season can help improve estimates of λ if they are included in the fecundity estimates. We suggest that the best way to avoid biased estimates of λ when the presence of nonbreeders is unknown is to report estimates of λ as a range of values with the lower limit calculated under the assumption that all undetected individuals are nonbreeders, and the upper limit under the assumption that they are all breeders.

SENSITIVITY ANALYSIS

Accurately predicting population responses to changes in various demographic rates can be crucial for population management, yet sensitivities of λ to nonbreeder parameters are rarely considered. Our analyses of systems incorporating different types of nonbreeders showed that the relative sensitivity of λ to survival and breeding probability of breeders and nonbreeders depended on several factors. The equilibrium ratio between nonbreeders and breeders, $N_{\mathrm{nb}}^*/N_{\mathrm{b}}^*$, was central. λ was most sensitive to change in the survival probability of nonbreeders, s_{nb}, when there was a high proportion of nonbreeders in the population (Fig. 5), and indeed was more sensitive to s_{nb} than to any other parameter in such systems (Fig. 5). Conversely, when there were more breeders than nonbreeders in the population at equilibrium, λ was more sensitive to breeder survival than to any other parameter. This further highlights the need to collect sufficient data on the nonbreeding segments of populations to evaluate the ratio, $N_{\mathrm{nb}}^*/N_{\mathrm{b}}^*$. However, showing that there are more breeders than nonbreeders in a population does not mean that nonbreeders can safely be ignored. In long-lived species with $N_{\mathrm{nb}}^*/N_{\mathrm{b}}^* < 1$, nonbreeder survival was still one of the parameters to which population growth rate was the most sensitive. In such species, protecting nonbreeders could therefore be expected to increase population growth more than facilitating higher breeding probabilities. Conversely, in short-lived species, improving conditions for early recruitment into the breeding population and repeat breeding across time steps would be expected to increase λ more than improving nonbreeder survival (except when breeding is 'costly'). But as the absolute sensitivity of λ to s_{nb} is similar in short- and long-lived species, changes that decrease nonbreeder survival would cause similar changes in λ in both systems. If only breeders are monitored, changes in mortality rates of nonbreeders might initially go undetected, potentially preventing appropriate conservation actions from being implemented (Kenward *et al.* 2000; Penteriani *et al.* 2005).

Population growth rate was also particularly sensitive to changes in nonbreeder survival probability when individuals were unlikely to breed in many consecutive time steps, but rather tended to take years off between breeding events ('recent breeding history' system, Fig. 4d). In such systems, which are quite common in nature (Shaw & Levin 2013), a high proportion of individuals will be nonbreeders at some point in their life before potentially re-entering the breeding population, explaining why λ would be sensitive to changes in nonbreeder survival.

Our analysis indicates that the transition probability from nonbreeder to breeder has little effect on λ in frequency-independent systems when $N^*_{\mathrm{nb}}/N^*_{\mathrm{b}} < 1$. This is particularly evident in systems with high survival, where nonbreeders are likely to have multiple opportunities to become breeders. In such systems, increasing the rate at which nonbreeders become breeders will have only a minor effect on the total number of breeders in the population. Conversely, in systems with $N^*_{\mathrm{nb}}/N^*_{\mathrm{b}} \geq 1$, changes in the transition probability from nonbreeder to breeder can be expected to have a substantial impact on λ, as the total number of breeders is more sensitive to this transition rate.

The complexity of the patterns of sensitivity with life-history, system and $N^*_{\mathrm{nb}}/N^*_{\mathrm{b}}$ ratio evident in Figs 3–5 demonstrate the need to undertake an appropriate sensitivity analysis for any system of interest, rather than simply relying on general patterns. We provide R code for running such analyses for a wide range of systems with different types of nonbreeders and any combination of parameters (Lee, Reid & Beissinger 2016).

Negative effects of nonbreeders on breeder survival or reproduction have been found in several studies (Wauters & Lens 1995; Carrete, Donázar & Margalida, 2006). This can happen when nonbreeders spend time at breeding areas and attempt to oust breeders from their territories or breeding sites (Bretagnolle, Mougeot & Thibault 2008; Bonebrake & Beissinger 2010), and when they share foraging areas away from the breeding grounds (Carrete, Donázar & Margalida, 2006). Frequency dependence, in which breeder survival or fecundity is reduced when the ratio of nonbreeders to breeders is high, can then emerge. Our analyses show that such frequency-dependent effects of nonbreeders on breeder survival changed the relative influence of demographic parameters on λ. Specifically, λ became less sensitive to changes in breeder survival, as frequency dependence caused realized s_{b} to be lower than the baseline s_{b}. Sensitivity to transition probabilities from juvenile or nonbreeder to breeder became higher, as any increase in these rates helped to decrease the negative frequency-dependent effects (e.g. if individuals that breed are less likely to harass other breeders). Frequency dependence in fecundity had little effect on sensitivities, except that sensitivity to the probability of remaining in the breeding class increased.

These results highlight the need to consider social interactions within populations when selecting an appropriate focus for conservation efforts. However, they also demonstrate that, in the absence of information about social interactions, decisions based on frequency-independent systems and models are unlikely to be highly inappropriate in frequency-dependent systems. Our models and code can be used to evaluate the potential influence of unknown frequency dependence in specific systems by running models with different levels of suspected interactions and comparing them to models without such effects.

FURTHER NONBREEDER SYSTEMS

Nonbreeders can also occur in and affect population dynamics of systems quite different from the ones we have modelled. One type of nonbreeder that has been the focus of much research is helpers in species with cooperative breeding (e.g. Koenig & Dickinson, 2004; Lukas & Clutton-Brock 2012; Paquet *et al.* 2015). In contrast to the negative frequency-dependent effects of nonbreeders in our models, helpers have positive effects on breeding. Cooperative breeding and helping behaviour is often closely linked with family structure and kinship, prompting different types of models and questions than ours (Hatchwell 2009; McLeod & Wild 2013).

When the presence of nonbreeders is directly determined by a limited number of territories or breeding sites, population dynamics are expected to differ from those studied here (Kokko & Sutherland 1998; Durell & Clarke 2004). One potentially important role of nonbreeders in this type of system is to buffer populations against extinction from sudden environmental events (Penteriani *et al.* 2005). If nonbreeders experience different environmental conditions from those affecting the breeding component of a population, they can function as a pool of individuals ready to move in and replace lost breeders (Penteriani *et al.* 2005), thus buffering the population against sudden loss. This means that the nonbreeder to breeder transition probability varies with the number of breeders present in the population. Penteriani, Otalora & Ferrer (2008) showed that increased nonbreeder mortality in such systems can cause an Allee effect.

In some systems, mate limitation is the primary reason for the presence of nonbreeders. The single-sex matrix models used here model an individual's breeding status at a given time as the outcome of a (generalized) Bernoulli trial, and the probability of moving from nonbreeder to breeder can be influenced by several factors, including mate availability. However, when mate limitation is the main cause of nonbreeding, two-sex models are more appropriate. Analysing two-sex models in a similar framework as that presented here would be an interesting future step.

Populations that are large relative to their carrying capacity are often subject to density-dependent effects as resources become limiting or negative effects of crowding come into effect. Nonbreeders can contribute to these effects when they compete with breeders for resources (Carrete, Donázar & Margalida, 2006). Modelling the influence of nonbreeders on density-dependent dynamics is another interesting next step. For example, the carrying capacity of a population might be influenced by the way in which breeders and nonbreeders interact. The ratio of nonbreeders to breeders, which has been suggested as a proxy for population health and stability (Hunt 1998), is also likely to be affected.

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Data accessibility

R code available from the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.t56cn (Lee, Reid & Beissinger 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Overview of focal systems and analysis structure.

Table S2. Demographic parameters used and $N^*_{\mathrm{nb}}/N^*_{\mathrm{b}}$ obtained in Figs 3 and 5.

Table S3. Demographic parameters used and $N^*_{\mathrm{nb}}/N^*_{\mathrm{b}}$ ratio obtained in Fig. 4.

Appendix S1. Matrices for life cycles shown in Fig. 1.