Too few data and not enough time: approaches to detecting Allee effects in threatened species

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Abstract

The detection of Allee effects is critical in assessing extinction risk, but is extremely difficult when sampling small, low-density populations. Failure to detect true Allee effects could lead to overoptimistic assessments of threat status, as well as the development of inappropriate species recovery plans. We outline a broadly applicable approach for evaluating Allee effect likelihood in analyses of sparse demographic data, explicitly acknowledging the uncertainties associated with detecting subtle Allee effects among the suite of factors that can influence demographic variability. Detailed information on the probability of Allee effects will empower conservation decision makers to balance extinction risks against the political and economic costs associated with management action. We use an illustrative case study involving demographic analyses of the endangered Cape Sable seaside sparrow, highlighting the value of information on Allee effect likelihood for the development of restoration measures within species recovery plans.

Introduction

Factors that cause declines in individual fitness with decreasing population density, termed Allee effects, are important determinants of extinction risk (Allee *et al*. 1949; Courchamp *et al*. 1999; Stephens & Sutherland 1999). Various lines of evidence hint that they may be widespread in nature (Leung *et al*. 2004; Lockwood *et al*. 2005), and they played deciding roles in the extinctions of various once-abundant species such as the passenger pigeon *Ectopistes migratorius* and Carolina parakeet *Conuropsis carolinensis* (Bucher 1992). However, they are difficult to detect and are seldom documented even among well-studied species (Courchamp *et al*. 2008; Kramer *et al*. 2009). The uncertainty surrounding Allee effects inhibits conservation prioritization, as it clouds our ability to accurately assess the immediacy of threats. In order to improve conservation prioritization, there is an urgent need

for more concerted efforts to assess Allee effects in threatened taxa. Here, we present a general framework for Allee effect assessment in the conditions of data paucity typically associated with rare or threatened species.

The principal reason Allee effects are seldom measured directly is a practical one: the difficulty of gathering data from small- or low-density populations (Courchamp *et al*. 2008). Sample size limitation is often seen as an insurmountable barrier, leaving conservationists with little choice but to make uninformed assumptions about extinction risk (Foin *et al*. 1998). For example, the IUCN conservation status criteria do not directly consider Allee effects (unless incorporated within a bespoke population viability analysis), but adopt blanket rules of thumb relating to population and range sizes, and rates of decline (IUCN 2001). This approach is sensible in the absence of detailed information on Allee effects, but inevitably runs the risk of underestimating extinction risk

in some taxa (Sanderson 2006; Mace *et al.* 2008). Uncertainty over Allee effects can inhibit the design of species recovery plans, as commonplace interventions such as habitat restoration may be ineffective for small populations where growth is directly impeded by intrinsic factors (Shirley & Lamberti 2009).

Positive relationships between population density and fitness can arise in various ways, for example, mate-finding, offspring-protection, and successful foraging may all be inhibited at low densities (Courchamp *et al.* 2008). Mechanisms operating on a single fitness parameter are typically referred to as "component" Allee effects (Stephens *et al.* 1999). In the absence of compensatory negative density dependence in other fitness parameters, these effects can suppress population growth, resulting in a "demographic" Allee effect (Stephens *et al.* 1999). We present a framework for assessing component effects via comparisons between spatially isolated subpopulations of varying size. Such fragmented populations are commonplace among threatened taxa, and effectively represent "natural experiments" on the effects of population density. We provide a set of analytical tools that can maximize the information extracted from sparse demographic samples, and illustrate their use with a case study involving the endangered Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*), a taxon subject to ongoing conservation recovery initiatives (Lockwood *et al.* 2003; Cassey *et al.* 2007). We also use simulations to illustrate the key challenges associated with the detection of component Allee effects from imperfect field data. We demonstrate that sample size limitation does not necessarily preclude meaningful analysis of demographic patterns at low densities, and that the information gained from analysis of sparse data on threatened taxa may be of high value for conservation practice.

Materials and methods

Motivating example: management of the Cape Sable seaside sparrow

The sparrow occurs in just six spatially isolated subpopulations of varying size within freshwater marl prairies in southern Florida (Figure 1; Lockwood *et al.* 2003). The smallest subpopulations (particularly subpopulation A) have shown limited recovery following significant declines in the 1990s, despite the imposition of direct management actions (Walters *et al.* 2000, Cassey *et al.* 2007). Possible reasons for the lack of recovery include: (1) management actions were ineffective, (2) other unmanaged environmental factors have prevented population recovery, or (3) the biology of the species limits population growth despite the alleviation of threats, that is, via Allee

effects. Plausible Allee effect mechanisms in this case include weakened nest defense (Soutullo *et al.* 2006) or decreased parental investment in small populations (Møller & Legendre 2001). To test for evidence of such an effect, we analyze nest survival data collected between 2002 and 2009 in three areas: a 1×2 km intensive-survey plot within the large and relatively stable subpopulation E, and plots covering two small subpopulations: A (6 km^2, 2009–2010) and C (9 km^2, 2006–2009). Territory mapping indicated that densities were an order of magnitude lower in the small subpopulations (1–4 males km^{-2} year^{-1}) than in the large subpopulation E (13–26 males km^{-2} year^{-1}; Table S1).

Framework for measuring Allee effects

Relationships between fitness parameters and population density are invariably difficult to detect (Freckleton *et al.* 2006), particularly when data collection is impaired at very low densities. Data sampled across a population density gradient will often display "availability bias," as there are invariably more individuals to sample at the high-density end of the spectrum. With such unbalanced data, the signal of an Allee effect can be drowned out by "noise" associated with sampling error, environmental stochasticity or other influential factors that drive variation in the parameter in question (Dinsmore *et al.* 2002).

We use a two-tier approach to test for Allee effects using demographic datasets of the kind exemplified by the sparrow case study. As a first step, we assess the strength of evidence for an Allee effect via information-theoretic model selection (Burnham & Anderson 2002). This widely used approach uses Akaike's Information Criterion (AIC), a penalized measure of model fit, to assess the power of statistical models in explaining the variation in a given dataset. The method is highly flexible and can be applied to many different study designs, including the analysis of data from mark-recapture survival studies, nest survival studies, or any dataset in which fitness parameters can be modeled statistically as a function of covariates. Demographic data are typically analyzed using generalized linear models (GLM), which employ a link function between the response variable (i.e., the fitness parameter in question) and the explanatory covariates of interest (Lebreton *et al.* 1992; Dinsmore *et al.* 2002). Analyses of nest survival, for example, typically utilize data in the form of discrete nest histories (Dinsmore *et al.* 2002) where the response variable (daily survival rate) is modeled as a logistic function of covariates measured at the scale of the individual nest site (Lebreton *et al.* 1992; White & Burnham 1999; Dinsmore *et al.* 2002). In order to minimize the risk of spurious inference, it is essential that the effects of "nuisance" variables (i.e.,
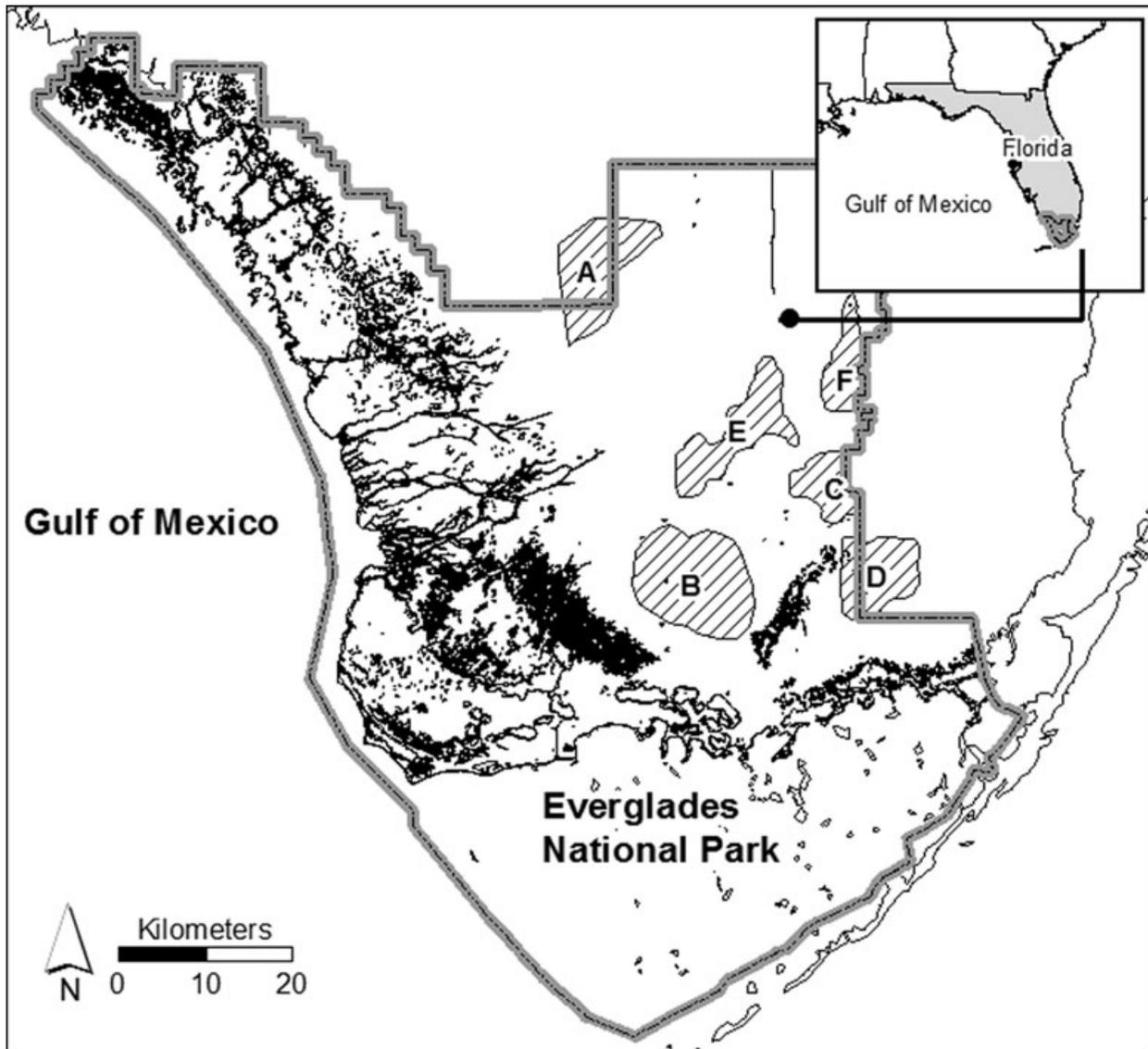
Figure 1 Map showing approximate extent of Cape Sable seaside sparrow subpopulations (A-F) in South Florida, USA, based on detections from range-wide helicopter surveys conducted since 2005.

influential factors that are not of immediate interest in analysis) are adequately controlled via the inclusion of appropriate covariates (e.g., measures of habitat quality). To test for an Allee effect, we assess the change in AIC when a covariate representing population size or density is added to a model that includes other "nuisance" covariates. AIC differences exceeding −2 are typically taken to indicate strong support for one model over another, while the relative importance of a covariate is indicated by the summed Akaike weight (ΣAIC_w) of all models including that covariate in a given set (Burnham & Anderson 2002). These methods are easily implemented for a wide variety of demographic data structures in the widely used Program MARK (White & Burnham 1999; Dinsmore *et al.* 2002).

As model selection can be sensitive to sample size and data imbalance across covariate levels (Burnham & Anderson 2002), we also use a bootstrap prediction interval method (Stine 1985) to examine the influence of sample size on effect detection. This method provides information on whether: (1) there are differences in the demographic parameter in question with respect to population size (i.e., patterns consistent with an Allee effect) and (2) whether these differences exceed the range of "null"

variation that might arise due to stochasticity in small samples in the absence of an Allee effect. Initially, we partition the dataset in question (e.g., a set of discrete nest histories) into separate samples from large and small subpopulations. We use the large subpopulation sample to generate a GLM linking the response variable in question (e.g., daily nest survival) to a set of relevant covariate effects (e.g., habitat features or other "nuisance" variables). Again, this can be easily achieved for a wide variety of demographic data structures and model families in Program MARK (White & Burnham 1999; Dinsmore *et al.* 2002). Next, we use this model to generate predicted survival rates for the small subpopulation sample(s), based on covariate data. These predictions are effectively "null" estimates of survival in small subpopulations under an assumption that factors driving variation in survival are the same in small and large subpopulations (i.e., Allee effects are absent). The difference between predicted and observed survival rates (the prediction error) can be used as a proxy measure of the magnitude of Allee effect, calculated thus

$$\text{Prediction error} = (\lambda - \phi)/\lambda \qquad (1)$$

where λ is the mean predicted survival rate for the low-density sample and ϕ is the observed mean survival rate for that sample.

In order to determine whether a given prediction error represents a meaningful difference, we use equivalently sized resamples drawn at random from the large subpopulation data to generate a set of "null" prediction errors. We use 1,000 bootstrap resamples (without replacement), each of the same size as the low-density sample in question, and use the same predictive model to calculate a prediction error for each sample, allowing a 95% interval of null errors to be generated. Observed prediction errors from small subpopulations that fall outside this interval are taken to indicate statistically meaningful effects (at an $\alpha = 0.05$ level).

To apply this method to the sparrow case study, we controlled for a suite of "nuisance" variables that are likely to influence nest survival. Previous studies have shown that sparrow nest survival is strongly dependent on hydrologic variability (Lockwood *et al.* 2001; Pimm & Bass 2002; Baiser *et al.* 2008), so we used model selection to evaluate the influence of six hydrological variables (Table 1) derived from the Everglades Depth Estimation Network database (Liu *et al.* 1999). Using MARK, we selected the best model from a candidate set including all combinations of these variables, together with a categorical term indicating membership to large high-density (E) or small low-density (A and C) subpopulations (Table 1). We then applied the bootstrap prediction method using

the best model fitted to data exclusively from the high-density subpopulation (E), calculating prediction errors using maximum likelihood nest survival estimates derived directly from each small subpopulation dataset (A and C).

Simulating the challenges associated with Allee effect detection

To provide a broader illustration of utility and limitations of the analytical methods presented above, we apply them to a set of simulated datasets incorporating a range of widely encountered data limitations (sample imbalance, nuisance parameter effects, and sampling error). Again, we use nest survival as a representative parameter, although the same principles apply to any fitness component that can be modeled as a function of covariate data. We simulate nest survival in subpopulations of varying size, where survival probability is influenced by an Allee effect alongside two "nuisance" parameters: seasonal variation (doubling the probability of nest failure in the second half of the breeding season) and variation associated with nest placement (25% lower failure probability for nests in a "high survival" group throughout the season). Sampling error is incorporated by simulating the stochastic observation process, whereby "observed" nest encounter histories are extracted from "true" nest survival histories in a manner analogous to standard field protocols (see Figure S1).

We examine a range of sample size and dataset imbalance scenarios (100 datasets in each scenario) by combining sets of nest histories from large and small subpopulations of varying size (large = 200 or 400 nests; small = 10 to 50 nests in increments of 10). To simulate an Allee effect, nest failure probability is increased by 30% in small subpopulations, resulting in datasets with survival rates ranging from 0.09 to 0.63 (mean 0.35) in the small subpopulation and 0.49 to 0.63 (mean 0.55) in the large subpopulation. To examine the risk of type I error (i.e., detecting a spurious effect) under each scenario, we also simulate datasets with no underlying Allee effect, where data heterogeneity arises purely from sampling error and "nuisance" parameters. In these datasets, realized nest survival rates ranged from 0.29 to 0.82 (mean 0.55) in small subpopulation samples, and from 0.49 to 0.63 (mean 0.55) in large subpopulation samples.

Results

Sparrow nest survival

Model selection results for the sparrow dataset showed no support for an effect of subpopulation membership

Table 1 Hydrologic variables used to model Cape Sable seaside sparrow nest survival, derived from the EDEN database (Liu *et al*. 2009).

Variable name	Scale of measurement (spatial[a], temporal[b])	Description
depth	Nest, nest monitoring period	Maximum water depth above ground
water cover	Region, nest monitoring period	Proportion of region with standing water
water days	Region, nest monitoring period	Number of days with standing water during nest period
flood	Region, nest monitoring period	Nest found before/after the onset of flooding (>90% standing water cover)
watertable	Region, season	Mean depth of regional water table
season flood	Region, season	Proportion of days with >50% standing water cover

[a]Nest = 0.5 km^2 grid square containing nest site; regional scale = 4 km^2 grid square containing nest site.
[b]Nest monitoring period = period from date found to assumed date of fledging or failure; season = maximum period of breeding activity, 31 March to 10 August.

Table 2 Results of model selection for nest survival models including data from two small subpopulations (A and C) and one large subpopulation (E), showing the 10 best performing models in explaining variability in daily survival rate.

Model	K[a]	AIC$_c$	$\triangle$AIC$_c$	AIC$_w$	Deviance
1. *season + flood + water days + watertable*	5	1,142.0	0.000	0.172	1,132.0
2. *season + flood + water days + watertable + water cover*	6	1,142.7	0.626	0.126	1,130.6
3. *season + flood + water days + watertable + depth*	6	1,143.7	1.665	0.075	1,131.7
4. *season + flood + water days + watertable + subpop*	6	1,143.9	1.855	0.068	1,131.9
5. *season + flood + water days + watertable + season flood*	6	1,144.0	1.964	0.064	1,132.0
6. *season + flood + watertable + water cover*	5	1,144.2	2.170	0.058	1,134.2
7. *season + flood + water days + watertable + water cover + subpop*	7	1,144.6	2.506	0.049	1,130.5
8. *season + flood + water days + watertable + water cover + season flood*	7	1,144.6	2.595	0.047	1,130.6
9. *season + flood + water days + watertable + water cover + depth*	7	1,144.7	2.606	0.047	1,130.6
10. *season + flood + water days + watertable + depth + season flood*	7	1,145.5	3.472	0.030	1,131.5
Null model (*season only*)	2	1,155.8	13.744	0.001	1,151.8

[a]Number of model parameters.

(ΣAIC$_w$ = 0.28), and hence no evidence for a component Allee effect (Table 2). Rather, variation in nest survival across all subpopulations was best explained by environmental variables (Table 3), principally seasonal water table depth (ΣAIC$_w$ = 0.98) and timing of nest activity relative to onset of flooding (ΣAIC$_w$ = 0.99), with weaker support for a positive effect of the number of days of flooding during the nest period (ΣAIC$_w$ = 0. 82). Prediction bootstrapping confirmed the underlying similarity of survival rates between high- and low-density subpopulations, as the best model for data from the large high-density subpopulation generated broadly accurate predictions when applied to the small subpopulations (Figure 2). The observed mean survival rate in small subpopulations (pooled across years, n = 72) was very close to the model prediction based on high-density data (prediction error 0.02), strongly suggesting that factors influencing nest survival were fundamentally similar across both large and small subpopulations (Figure 3). Annual nest survival rates in small subpopulations consistently fell within the 95% null interval generated by bootstrapping (Figure 3), indicating that observed rates of nest survival in low-density subpopulations were within the range of equivalently sized resamples from the high-

Table 3 Variable selection probabilities and parameter estimates (with standard errors and 95% CI) for each predictor variable included in model selection analyses for Cape Sable seaside sparrow nest survival data from two small subpopulations (A and C) and one large subpopulation (E). Parameter estimates are averaged across all models in the candidate set (Burnham & Anderson 2002).

Variable name	ΣAIC$_w$[a]	Estimate	S.E.	Lower CI	Upper CI
intercept	–	4.592	0.342	4.025	5.367
season	1.000	−0.023	0.004	−0.032	−0.017
depth	0.290	0.010	0.047	−0.075	0.109
water cover	0.492	0.192	0.546	−0.670	1.469
water days	0.823	0.049	0.030	−0.012	0.105
flood	0.992	−0.882	0.365	−1.702	−0.274
watertable	0.981	−0.016	0.007	−0.029	−0.002
season flood	0.314	−0.039	0.748	−1.803	1.129
subpopulation	0.278	0.008	0.189	−0.323	0.418

[a]ΣAIC$_w$ are selection probabilities derived by summing AIC$_w$ from all models including that variable (Whittingham *et al*. 2005).

density subpopulation. The only exception was the sample from subpopulation C in 2007, where the observed rate exceeded the upper limit of the 95% null interval (Figure 3).
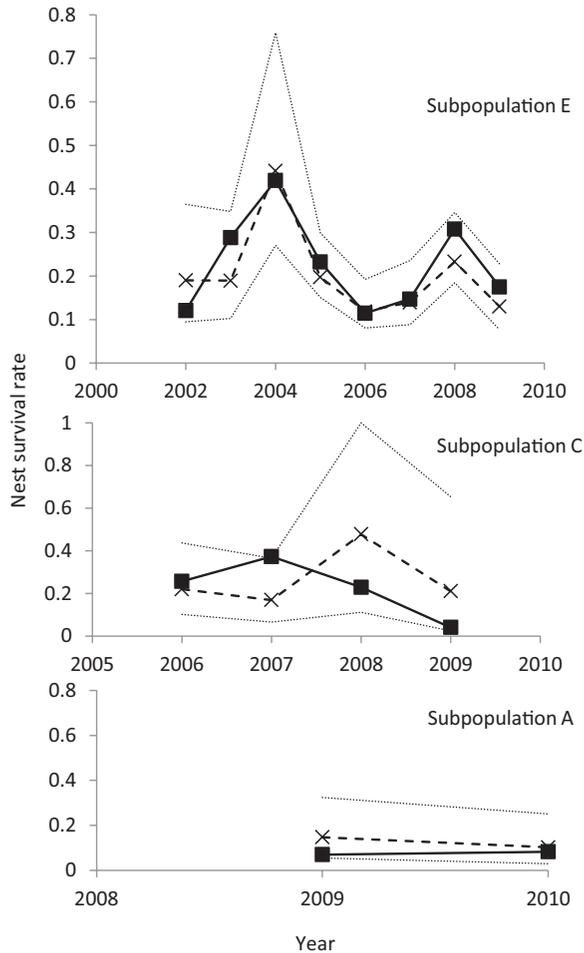
Figure 2 Comparisons between observed Cape Sable seaside sparrow nest survival rates (black squares joined by solid lines) and predicted values from a model built exclusively using data from the large subpopulation E (crosses joined by broken lines). Upper panel shows observations and predictions for the large subpopulation E, middle and lower panels show small subpopulations C and A, respectively. Dotted lines show limits of 95% null intervals generated by applying the model to bootstrap resamples of large subpopulation data (1,000 resamples of equivalent size for each datapoint).

Figure 3 Model prediction errors for nest survival rates in small subpopulations of the Cape Sable seaside sparrow, representing the proportionate difference between observed rates (ø) and predictions (λ) generated using a model built from large subpopulation data, together with the 95% null interval derived by prediction bootstrapping (dotted lines). Values >0 indicate samples where model predictions exceeded observed values. Black circles show samples for individual years in subpopulation C, open squares show individual years in subpopulation A, gray circle shows pooled data from all years in subpopulation C, gray square shows pooled data from all years in subpopulation A, black diamond shows pooled data from all years and both small subpopulations.

Inferential error rates with simulated data

Our simulated datasets displayed a high degree of variation in the magnitude of difference in nest survival rates between small and large subpopulation samples (Figure 4a & b), despite the underlying Allee effect being constant (30% increased failure rate). This variation arose due to process stochasticity, nuisance parameter effects and sampling error, all of which are compounded by sample size imbalance. Testing our framework against these simulated datasets indicated that the risk of overlooking a true Allee effect was highly sensitive to small subpopulation sample size (Figure 5), as expected given the in-
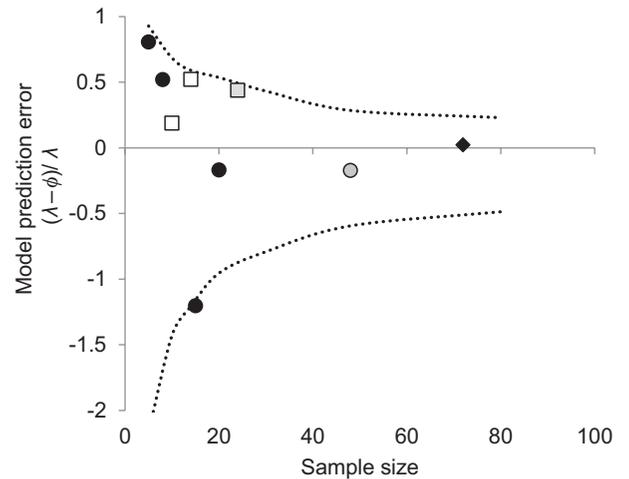
evitable reduction in statistical power when dealing with sparse data. At the smallest sample size considered (*n* = 10 nests from the small subpopulation), model selection techniques correctly detected Allee effects in 51% of simulated datasets, rising to 93% at the largest sample size considered (*n* = 50, Figure 5a). Prediction bootstrapping provided more conservative inferences, detecting true Allee effects in 33% of datasets at *n* = 10 and 86% at *n* = 50 (Figure 5c). This conservatism was reflected in the reduced rate of false positive error (i.e., the detection of spurious Allee effects in datasets where none were present) with prediction bootstrapping (Figure 5b & d). Doubling the sample size in the large subpopulation dataset (*n* = 400 nests) had little effect on inferential error rates, and did not change the relative performance of either model selection or bootstrap prediction techniques in detecting Allee effects (Figure S2).

Discussion

The difficulty of analyzing demographic variability at low densities presents a major barrier for the study of Allee effects in threatened species (Doak *et al.* 2005; Courchamp *et al.* 2008; Kramer *et al.* 2009). Our findings indicate that with appropriate analysis limited samples can indeed
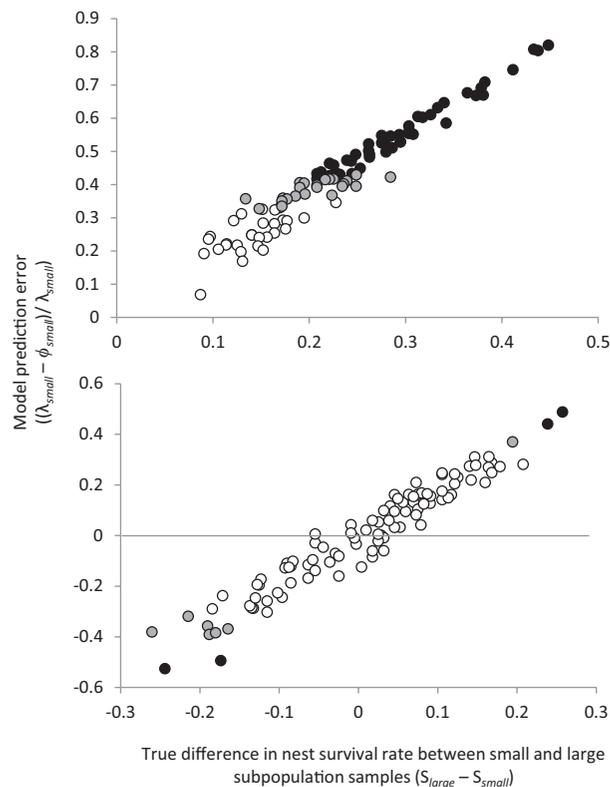
Figure 4 Differences in nest survival rate (*S*) between small and large subpopulation datasets generated by simulation, showing how the magnitude of difference influences the detection of component Allee effects. Each point represents a dataset consisting of unbalanced samples from large (*n* = 200) and small (*n* = 20) subpopulations. Model prediction errors are the proportionate difference between the true nest survival rate in the small population sample ($\varnothing_{small}$) and the rate predicted for that sample by a model based on large subpopulation data (λ_{small}). True differences between the small and large subpopulation samples are shown on the *x*-axis. The upper panel shows 100 simulations with a component Allee effect (nest failure probability 30% higher in the small subpopulation), while the lower panel shows 100 simulations without a true Allee effect (differences between subpopulation samples arise only from sampling error and process stochasticity). Points are labeled according to the outcome of analysis: black circles show cases where an Allee effect was inferred by both model selection and prediction bootstrapping; gray circles show cases where an effect was inferred only by model selection; open circles show cases where neither method inferred an Allee effect.

provide useful information on Allee effect likelihood. Our simulations highlight the complementary value of model selection and bootstrap prediction in balancing the risk of inferential errors in these analyses, with bootstrapping providing a direct measure of the uncertainty associated with data limitation. This framework can be applied to any fitness component that might vary in relation to population density, and could equally be used to evaluate demographic Allee effects in systems where population growth rate can be modeled directly as a function

of covariates. Our methods are easy to implement within freely available software packages, requiring only basic randomization routines (example Excel files are available on request from the authors).

In the sparrow case study, we hypothesized that diminished nest productivity at low densities might inhibit population growth. However, we found no clear evidence of an Allee effect on this fitness component after controlling for habitat and seasonal effects. Using prediction bootstrapping, we were able to estimate the magnitude of variation that might be expected between subpopulation samples in the absence of an Allee effect; at the maximum pooled sample size available for small sparrow subpopulations (*n* = 72), this variation extended to values 23% below the null model prediction based on large subpopulation data (95% null interval limit = 0.23 at *n* = 72; Figure 3). We therefore cannot exclude the possibility of a weak component Allee effect (<23%) being masked by unexplained variation within the data. Nevertheless, the close similarity between the observed nest survival rate in the small subpopulations and the null model prediction suggests that a pervasive Allee effect on this parameter is unlikely. We note that without further analyses on other fitness components that contribute to intrinsic population growth rate, we still cannot discount the possibility of a demographic Allee effect in the sparrow (Stephens *et al.* 1999).

Even allowing for uncertainties, the information provided under our approach is of significant value in selecting appropriate conservation interventions (Foin *et al.* 1998; Boersma *et al.* 2001). For example, our analyses for the sparrow suggest that in the absence of a strong Allee effect, habitat-based actions (e.g., sympathetic water flow management) should be effective in boosting nest productivity in small subpopulations. If a strong Allee effect had been uncovered, direct actions such as translocation or nest protection might have been required in order to boost population productivity in low-density areas (Shirley & Lamberti 2009). Further applications of our approach could facilitate the use of risk analysis to formally compare the use of different interventions, allowing a more rigorous evaluation of the costs and benefits of possible management strategies (Harwood 2000).

Our methods rely on the availability of data from small and large subpopulations (or low- and high-density conditions), which in some cases may be difficult to acquire. Moreover, the success of our method may be highly dependent on the quantity of data available from high-density conditions, as large samples may be essential in allowing "nuisance" variables to be detected and statistically controlled. The detection of Allee effects is likely to be highly sensitive to the influence of other
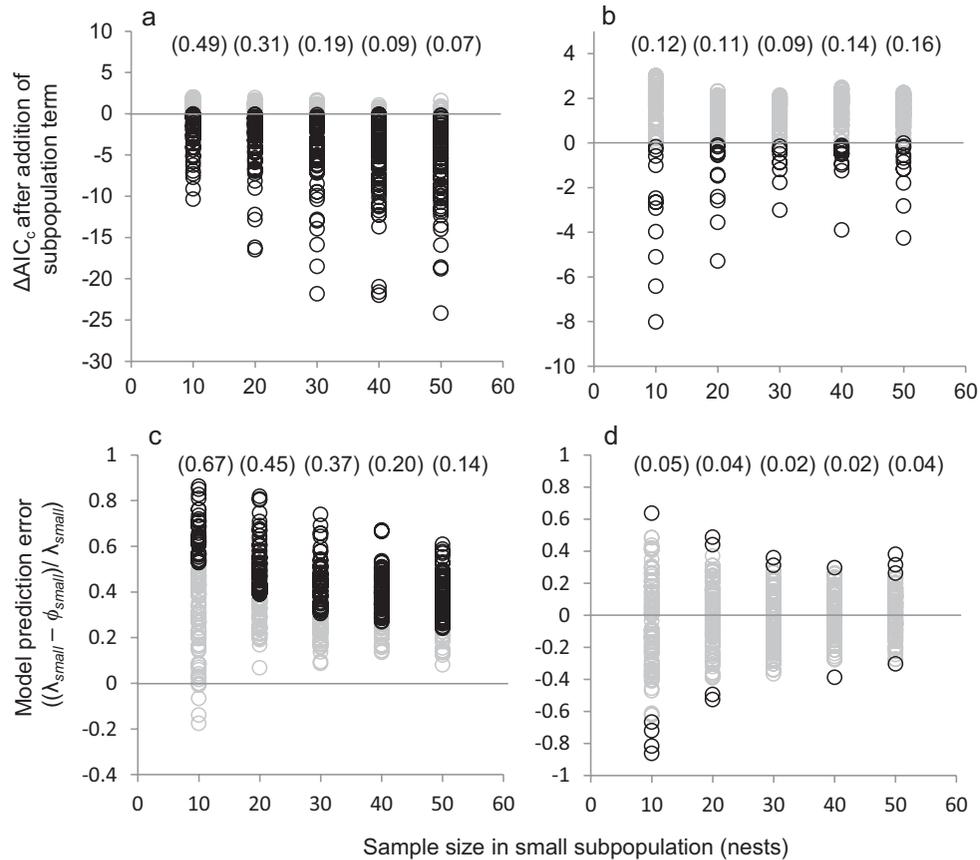
Figure 5 Effects of sample size on inferential error rates from model selection (a & b) and prediction bootstrapping (c & d) in detecting Allee effects, evaluated using simulated data. Left-hand panels (a & c) show simulated datasets with a genuine component Allee effect (nest failure probability 30% higher in the small subpopulation), while right-hand panels (b & d) show datasets without any Allee effect (failure probability similar between subpopulations). Symbol colour highlights whether a meaningful effect was inferred (black) or not (gray) for each dataset. For model selection, Allee effects are inferred if there is a negative change in AIC_c (ΔAIC_c) upon addition of a subpopulation term to the model. For bootstrap prediction, Allee effects are inferred if prediction errors from a model built from large subpopulation data fall outside a 95% null interval generated from 1,000 bootstrap resamples of large subpopulation data. Values in parentheses are rates of inferential error (type II in left-hand panels; type I in right-hand panels) across 100 datasets in each sample size category (large subpopulation sample = 200 nests in each case).

factors such as habitat quality on the fitness component in question, particularly if these factors are confounded within subpopulations (Lebreton *et al.* 1992; Rotella *et al.* 2007). While this problem is inevitably difficult to resolve, prediction bootstrapping at least provides a means of directly assessing the uncertainty arising from unexplained variation, improving the robustness of subsequent inferences.

Species-oriented approaches remain crucial for endangered species recovery (Shirley & Lamberti 2009), and they rely heavily on detailed knowledge of the biology of the species in question. For endangered taxa, information on demographic variability at low population density remains a major data gap (Kramer *et al.* 2009). We suggest that researchers make maximum use of the data available, acknowledging uncertainties associated with sample size and data heterogeneity, in order to evaluate Allee effects in taxa targeted by conservation action. Information of the kind provided under our framework will be extremely valuable in developing precautionary assessments of species vulnerability on a case by case basis.

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Supporting Information

Additional Supporting Information may be found in the online version of this article, including Supplementary Methods and References.

Table S1: Estimates of territory density (within study plots) in three Cape Sable seaside sparrow subpopulations (A, C, and E), derived from intensive surveys.

Figure S1: Schematic diagram showing the structure of a stochastic simulation model used to generate nest encounter history datasets typical of those observed in field studies.

Figure S2: Relative performance of model selection (a & b) and bootstrap prediction (c & d) methods in detecting differences in nest survival between small and large subpopulations from simulated data, where sample size in large subpopulation is increased to 400 nests.

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