Limited evidence for the demographic Allee effect from numerous species across taxa

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Abstract. Extensive theoretical work on demographic Allee effects has led to the latent assumption that they are ubiquitous in natural populations, yet current empirical support for this phenomenon is sparse. We extended previous single-taxon analyses to evaluate the empirical support for demographic Allee effects in the per capita population growth rate of 1198 natural populations spanning all major taxa. For each population, we quantified the empirical support for five population growth models: no growth (random walk); exponential growth, with and without an Allee effect; and logistic growth, with and without an Allee effect. We used two metrics to quantify empirical support, information-theoretic and Bayesian strength of evidence, and observed top-rank frequency. The Ricker logistic model was both the most supported and most frequently top-ranked model, followed by random walk. Allee models had a combined relative support of 12.0% but were top-ranked in only 1.1% of the time series. Accounting for local climate variation and measurement error caused the loss of top-ranked Allee models, although the latter also increased their relative support. The 13 time series exhibiting Allee models were shorter and less variable than other time series, although only three were non-trending. Time series containing observations at low abundance were not more likely and did not show higher support for Allee effect models. We conclude that there is relatively high potential for demographic Allee effects in these 1198 time series but comparatively few observed cases, perhaps due to the influences of climate and measurement error.

Key words: Akaike information criterion (AIC); Bayesian information criterion (BIC); demographic Allee effect; empirical support; evidence; exponential; population dynamics; random walk; Ricker.

Introduction

An Allee effect describes a positive relationship between fitness and population size (or density; Courchamp et al. 2008). It is further classified into either a component Allee effect, which modifies one or multiple surrogate measures of fitness (Berec et al. 2007), or a demographic Allee effect, which is a manifestation of a component Allee effect whereby the growth rate increases with population size (hereafter termed "positive density feedback"; Stephens et al. 1999). The Allee effect, named after zoologist W. C. Allee (Odum 1953), was first described as an improvement in fitness with increasing population size and discussed in terms of cooperation (Allee et al. 1949). Thirty years later, however, M. A. Soulé highlighted declines in animal and plant populations (Gibbons 1992), which prompted population biologists to view the Allee effect in terms of a reduction in fitness with decreasing population size

and issue warnings of its threat to population persistence (Lande 1988, Dennis 1989, Fowler and Baker 1991).

Following the focal shift from cooperation to conservation, theoretical and empirical studies of Allee effects proliferated (Kramer et al. 2009). Empirical support for Allee effects has now been provided for a wide range of species and mechanisms. For example, Davis et al. (2004) experimentally demonstrated that sparse invasive cordgrass (*Spartina alterniflora*) at the leading edge of an estuarine invasion were pollen limited compared to plants in established aggregations. Angulo et al. (2007) showed how the survival of adult Californian Channel Island foxes (*Urocyon littoralis*) increased when elevated predation risk was shared among more individuals. Almost without exception, however, empirical studies of Allee effects have focused on component Allee effects; studies of demographic Allee effects remain largely in the theoretical domain and predict their widespread existence in natural (Liermann and Hilborn 1997) and invasive (Taylor and Hastings 2005) populations. Given the abundant empirical support for component Allee effects (Kramer et al. 2009) and their predicted dynamical consequences (Berryman 2003), the latent assumption held by many

population biologists is that demographic Allee effects must be widespread (Courchamp et al. 2008).

Notwithstanding some noteworthy examples, there are few studies demonstrating empirical evidence of demographic Allee effects. Johnson et al. (2006) used a rigorous empirical approach to reveal the existence of a demographic Allee effect at the leading edge of the Eurasian Gypsy moth (*Lymantria dispar*) invasion in the northeastern United States. Davis et al. (2004) showed that the pollen-limited cordgrass also suffered a demographic Allee effect. Interestingly, both examples may be driven by a mate-finding component Allee effect (Tcheslavskaia et al. 2002, Davis et al. 2004; see Gascoigne et al. 2009 for a review). Angulo et al. (2007) revealed a demographic Allee effect in island fox populations, together with component Allee effects in their adult survival and reproduction. In this case, the demographic Allee effect was weak because it did not cause the population growth rate to become negative (the condition that defines a strong demographic Allee effect; Wang and Kot 2001). Rather, it appeared that the release from competition in small fox populations favored larger litters and higher juvenile survival, which compensated for reduced adult survival and reproduction (Angulo et al. 2007).

As illustrated by Angulo et al. (2007), a demographic Allee effect is an unstable population state emerging from the interplay between density-dependent fitness-regulating mechanisms. Central to its theory is the assumption that a strong demographic Allee effect acts around an unstable threshold population size known as the "Allee threshold." Above the Allee threshold, the net effect of the underlying mechanisms is increased fitness and the population grows, but below this threshold the net effect is decreased fitness, causing the population to decline (Courchamp et al. 1999). Such instability in populations within the range of population sizes affected by demographic Allee effects will, paradoxically, render them difficult to detect (Stephens et al. 1999). Further, if demographic Allee effects modify dynamics of small populations as predicted (Courchamp et al. 1999), then detecting demographic Allee effects might be complicated by increased temporal variance in abundance at small population sizes. For example, Lande et al. (2003) showed how demographic stochasticity in small populations could produce population dynamics mirroring those driven by Allee effects. Finally, environmental stochasticity plays an important regulatory role in the population dynamics of animals, from butterflies (Nowicki et al. 2009) to ungulates (Forchhammer et al. 1998), and can affect population growth rate directly (Rothery et al. 1997) or indirectly though its influence on vegetation quality and abundance (e.g., Månsson and Lundberg 2006). While its influence can act independently of population size (Lande et al. 2003), extreme climatic variability or catastrophes that have high impact but low frequency can have a disproportional effect on small and declining populations (Lande 1993).

Beyond its particular effects on small and declining populations, climatic variability in population growth rate, unless explicitly investigated, might be misinterpreted as process variability, which in turn, can lead to overestimation of the role of density feedback in population regulation (Rothery et al. 1997).

Besides the aforementioned issues, there is a large literature devoted to factors inhibiting the statistical detection of density feedback (negative or positive) in time series (recall that demographic Allee effects are observable in population dynamics as positive density feedback). The existence of deterministic trends (Turchin 2003) accompanied by unbounded variance (Lande et al. 2003), which are both more likely in shorter time series (Solow and Steele 1990), will confound any density feedback signal. Furthermore, Shenk et al. (1998), and later Freckleton et al. (2006), demonstrated how density feedback could be masked or spuriously emerge if the populations monitored were not closed. Importantly, Freckleton et al. (2006) also showed how measurement error in population observations could lead to a spurious negative correlation between population growth rate and population size even for density-independent time series. In addition to factors affecting both positive and negative density feedback, sparse observations at low population sizes might further inhibit detection of positive density feedback (Fowler and Baker 1991, Myers et al. 1995, Sæther et al. 1996, Shelton and Healey 1999).

Here we examine the latent assumption of abundant demographic Allee effects given by the widespread empirical support for component Allee effects. We test the hypothesis that demographic Allee effects are abundant using multi-model, information-theoretic, and Bayesian inferential approaches to provide measures of empirical support for five population growth models (including Allee effect models) in population time series of 1198 species across a wide range of taxa (Brook and Bradshaw 2006). This approach reduces the problem of model misspecification inherent in hypothesis testing (Zeng et al. 1998). We use two measures of empirical support: (1) relative strength of evidence (Brook and Bradshaw 2006), which measures the likelihood of observing each model fit in the population growth rate given the data, and (2) top-ranked frequency (Zeng et al. 1998), which measures the frequency with which each model is the most parsimonious descriptor of population growth rate. In addition, we evaluate the effects of local climate variation, measurement error, and time series attributes (length, variation, trend, and skew) on our results. We predict that these factors will quantitatively but not qualitatively change the spread of empirical support between population growth dynamics, but will generally diminish detection of positive density feedback due to their potentially disproportional effects on small population observations. We consider a strong positive density feedback signal as suggestive of a demographic Allee

effect; however, we defer asserting the existence of a demographic Allee effect until further study reveals the existence of an underlying component Allee effect mechanism in each case.

METHODS

Population time series

We used a database of 1198 population time series, which differed from other databases previously examined for positive density feedback in two major aspects. First, it comprised nearly twice as many species as other examined databases (1198 species vs. 674 species in Sibly et al. [2005]). Second, it incorporated representatives from several major taxonomic groups and biomes (compared to Myers et al. [1995], Sæther et al. [1996], Liermann and Hilborn [1997], Barrowman et al. [2003], and Reed [2005], who all examined single-taxon databases). The time series were drawn primarily from the Global Population Dynamics Database (GPDD; NERC Centre for Population Biology 1999) but also from the peer-reviewed literature, gray literature, and online sources (Brook et al. 2006). Specifically, time series were only included if they possessed: (1) a minimum of eight year-to-year census transitions and (2) a minimum of four different census values to ensure sufficient variation for analysis. Where the GPDD held more than one time series for a single species, only the highest quality time series was selected to avoid biasing our findings toward a few well-studied species (Brook and Bradshaw 2006). We also collated geographical and temporal metadata for all 1198 time series, which were used in the climate analysis. All analyses were done using R (R Development Core Team 2008).

Some time series contained missing values. To maximize the number of suitable time series for analysis (i.e., with eight year-to-year transitions), we treated missing values as follows. Single missing values were substituted with the mean of their two neighboring points. This assumed that a single missing value was a failure to census and its value was best predicted as a linear function of local observations. The first missing value in a string of missing values was substituted for the lowest value in the time series. This assumed that a string of values was a failure to record individuals at low abundance or population extirpation, and there was a negligible effect of the lowest value substitution. In practice, 175 and 216 time series were treated for single and strings of missing values, respectively. We investigated the possible effect of applying these treatments by repeating our main analysis without them. Missing values falling outside of these categories were removed.

Modeling population growth dynamics

We modeled per capita population growth rate ($r = \log_e(N_{t+1}/N_t)$) using a set of five nested models, representing a set of working hypotheses, to examine the 1198 population time series for empirical support for positive density feedback. The five models of population growth rate were: a no growth model (random walk), two density-independent growth models (with and without an Allee effect), and two negative density feedback growth models (with and without an Allee effect). The decision was reached to assess support for strong demographic Allee effects so density-independent and negative density feedback models could be nested within the Allee effect models. In addition, the chosen Allee effect term enabled the Allee effect to be characterized by a single parameter, thereby minimizing the penalty imposed on Allee fits by the empirical model evaluation measures. The final model set represented population growth dynamics increasing incrementally in complexity from a null model of no growth to a model including both negative and positive density feedback in r and was used by Berryman (2003) in his development of a general theory of population growth.

Specifically, the models were: (1) the random walk model, which assumes $r = 0$ and all variation in r is due to random fluctuations in population size (N) over t time units and is modeled as $r = 0 + \sigma$, where σ is a stochastic Gaussian variable with mean 0 and variance σ^2 that encapsulates the process error (and measurement error); (2) the exponential growth model, which assumes constant r independent of population size and is modeled as $r = r + \sigma$; (3) the exponential Allee growth model, which assumes constant r independent of population size unless a critical lower Allee threshold (A) exists, above which r may be depressed and below which r becomes negative and is modeled as $r = r_m((N_t - A)/N_t) + \sigma$, where r_m is the maximum intrinsic growth rate; (4) the Ricker logistic negative density feedback model, which assumes a linear decline in r with increasing population size and is modeled as $r = r_m(1 - (N_t/K)) + \sigma$, where K is the carrying capacity; and (5) the Ricker Allee positive density feedback model that describes the negative influence of N on r modified by the relative distance from A and K. It is modeled as $r = r_m(1 - (N_t/K))((N_t - A)/N_t) + \sigma$. We collectively refer to models with and without the Allee term as "Allee models" and "non-Allee models," respectively.

Least-squares model fits were estimated using a sequential quadratic programming algorithm (donlp2; Spellucci 1998) subject to box constraints $0 \leq r_m$, $0 \leq K$, and $0 \leq A$ and an additional linear constraint $A < K$ for the Ricker Allee model. We used the free parameter σ to calculate Akaike's information criterion (adjusted for small sample sizes; AIC_c) and Bayesian information criterion (BIC) to measure the strength of evidence for each candidate model (Brook and Bradshaw 2006). Although we primarily report AIC_c throughout this work, we present BIC in the empirical support summary tables because AIC_c tends to favor higher dimensional fits (in this case from the Allee effect models) with tapering parameter coefficients (Burnham and Anderson 2002). The BIC, on the other hand, will favor lower dimensional fits with nonzero parameter coefficients, i.e., should provide the least support for spurious Allee

model fits. We used discrete-time models for all species because the majority of populations were located in the temperate Northern Hemisphere where breeding/reproduction is usually discrete. We compared models using the difference in AIC_c between the top-ranked and current model (ΔAIC_c) and calculated the empirical support for each model as its AIC_c weight ($AIC_c\ w$). We compared specific models using the evidence ratio (ER), calculated as the ratio of model weights (Burnham and Anderson 2002). The top-ranked model in a model set was selected using $AIC_c\ w$. Deviance explained (using the random walk as the null model fit) was used as a measure of a model's structural goodness of fit.

Our model set excluded weak Allee effect models that depress r above A without requiring $0 \leq A$ (Wang and Kot 2001). We did not include weak Allee models primarily because they require an additional parameter to admit the exponential and Ricker logistic models as special cases and we wanted to characterize the Allee effect using a single parameter in a set of nested models. Nevertheless, weak Allee effect models would represent an additional step of complexity in our hypothesis set, and their exclusion will bias our findings. To investigate the degree of bias, we repeated our main model-fitting exercise including a weak Ricker Allee effect model and present summary background and results of this modified model set in Appendix A.

Including climate variation

We investigated whether interannual climate variation affected the support for the population growth models by directly incorporating climate variables into model fits as covariates (Rothery et al. 1997). Climate variables were drawn from the Climate Research Unit's 2.1 time series database (CRU TS 2.1; *available online*),[5] which includes nine climate variables measured (or extrapolated) at a 0.5° scale for every month from 1901 to 2002 (Mitchell and Jones 2005). This database provided us with fine-scale climate variables for most time series. We calculated the mean annual temperature (in degrees Celsius), mean annual precipitation (in millimeters), annual frost-day frequency (in days), and annual wet-day frequency (in days) for each year.

For each time series falling between 1901 and 2002, we used census dates and geographical coordinates to extract the corresponding climate variables and incorporated these into the model fits as variables representing mean climate (mc; an orthogonal regression of mean annual temperature and mean annual precipitation) and extreme climate (xc; an orthogonal regression of annual frost-day frequency and annual wet-day frequency). We used orthogonal combinations of climate variables derived using principal components analysis to encapsulate the principal variation in and interactions between the underlying variables (Hallett et al. 2004) while

minimizing the number of parameters added to each model. We defined mean and extreme climate combinations because they might influence population dynamics differently, via, for example, differences in mortality (e.g., Frederiksen et al. 2008), and might affect populations differently depending on their size (Lande 1993). For this analysis, our model set included all models both with and without all possible combinations of climate parameters (a total of $5 \times 4 = 20$ models).

Measurement error and data attributes

We assumed that populations were censused without measurement error and σ represented only process error or random fluctuations in population size. In fact, it is likely that σ encapsulates both process and measurement error (Brook and Bradshaw 2006). Although without empirically estimating measurement error it is difficult to calculate its relative contribution to σ, we attempted to understand the effect of assuming no measurement error by repeating our analyses on time series with randomized measurement error. For a time series U with observations $i = 1, 2, \ldots, j$, we resampled i with replacement j times to create a bootstrap time series U^* and calculated its mean $\bar{U}^*$. This was repeated 1000 times to create a bootstrap distribution of 1000 $\bar{U}^*$ from which we calculated the bootstrap standard error of U (SE_U). This assumed that any signal in the original time series could have been produced spuriously by measurement error. We parameterized a Gaussian distribution for each time series observation U_i with mean $= i$ and variance $= SE_U$ from which we randomly drew a population estimate. We repeated this for all U_i to construct a new time series of length j with randomized measurement error. We did this for all 1198 species and subjected the resulting time series to the analyses described in *Modeling population growth dynamics*. We repeated this entire procedure 200 times and estimated the support for each population growth model given randomized measurement error.

Previous studies have stressed how the probability of detecting phenomenological density feedback depends, to some extent, on whether the time series is trending (Turchin 2003). To determine whether our results were sensitive to the inclusion of trending time series, we examined each time series for a linear trend between N_t and t (compared to a no-trend null model using AIC_c; Kölzsch et al. 2007) and investigated how support for non-Allee and Allee models was affected. Likewise, detection probability depends on the length of monitoring period (Solow and Steele 1990) and variation in the time series (Brook and Bradshaw 2006). We examined the relationships between support for non-Allee and Allee models, length of monitoring period, and variation in time series for all 1198 time series. Finally, detection of positive density feedback might require that a time series include population censuses lower than some threshold proportion of the maximum population census. For example, Fowler and Baker (1991) only
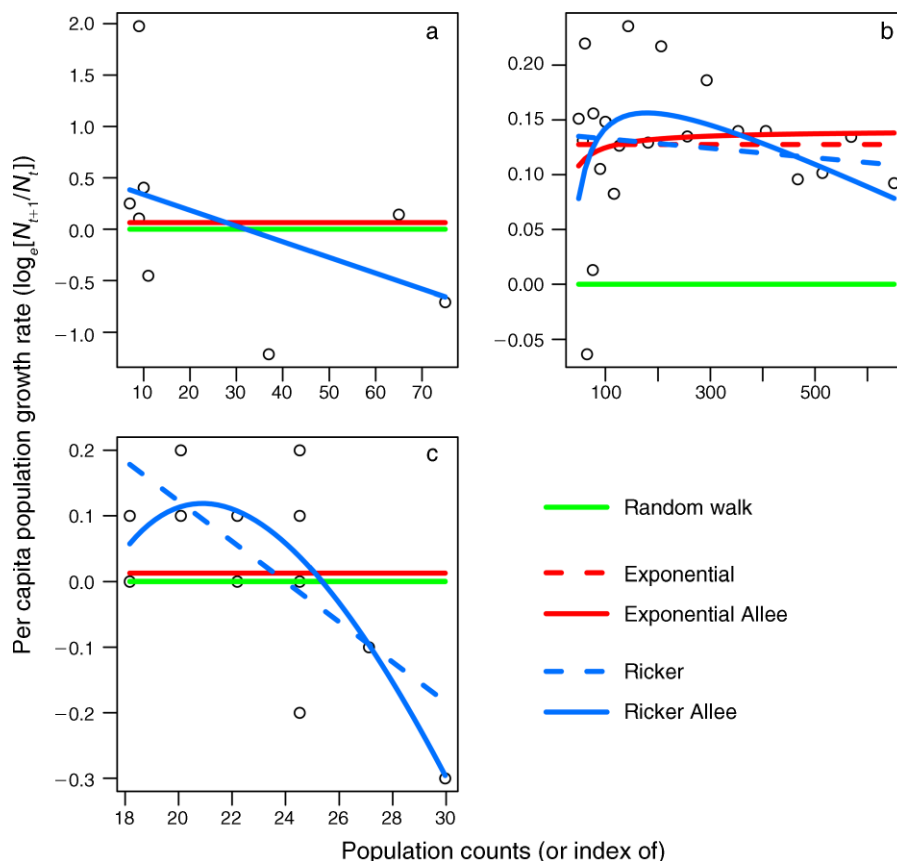
FIG. 1. Three example data sets showing fits of the five population growth dynamic models measured in this study. (a) Data for the small blue butterfly (*Cupido minimus*) for which the random walk (RW) is the best model. The exponential (EX) and exponential Allee (EA) growth models achieve the same fit, as do the Ricker (RL) and Ricker Allee (RA) logistic growth models. (b) Data for the muskox (*Ovibos moschatus*), for which EX is the top-ranked model but both Allee models acquire good support. (c) Data for the lilac beauty moth (*Apeira syringaria*), for which the RA is the top-ranked model and EX and EA achieve the same fit.

used time series for which the minimum N was ≤10% of the maximum N, while Sæther et al. (1996) set the threshold at 15%. We calculated the minimum N of each of our 1198 time series as a proportion of the maximum N and examined how the support for non-Allee and Allee models was related to minimum N.

RESULTS

Support for population growth models

Our model-fitting procedure achieved model fits satisfying parameter constraints for 99.4% of the 1198 time series using the Ricker logistic model, 98.2% using the exponential Allee model, 97.9% using the Ricker Allee model, and 100% using each of the remaining models, confirming that the procedure was robust and adequate to compare model fits among time series (see examples in Fig. 1).

Overall AIC_c w support was highest for the Ricker logistic (45.3%) and random walk (32.2%) models (Table 1). Support for the Allee models was low (exponential Allee, 2.2%; Ricker Allee, 9.8%), being highest for birds and mammals (Table 1) and excep-

tionally high for 61 time series (open circles in Fig. 2a), including 3.3% and 2.7% of the mammal (MAM) and bird (BIR) time series, respectively. The Ricker logistic and exponential growth models had higher AIC_c w support than their Allee counterparts despite their similar overall goodness of fit, as did the random walk model despite, as the null model, explaining zero deviance (Fig. 2b).

The spread of AIC_c w support was similar for each taxonomic group (Table 1) and was reflected in the numbers of top-ranked models (Fig. 2a). Interestingly, Allee models were only the top-ranked models in 13 (1.1%) of the 1198 time series, and none of these was due to the exponential Allee model. The BIC support was generally lower than the AIC support for the Ricker logistic model and higher for the Ricker Allee model, particularly among those taxonomic groups with fewest representative time series (Table 1).

Including a weak Allee effect model did not qualitatively change these findings (Appendix A: Table A1). In summary, the weak Ricker Allee effect model had similar support to the strong Ricker Allee effect model

TABLE 1. Overall and major taxonomic group support (corrected Akaike information criterion weights, AIC_c w) for population growth models and overall AIC_c w and Bayesian information criteron (BIC) support for non-Allee (nAE) and Allee (AE) models as a percentage of all support.

Group	n	Model AIC_c w					AIC (%)		BIC (%)	
		RW	EX	EA	RL	RA	nAE	AE	nAE	AE
Overall	1198	0.322	0.106	0.022	0.453	0.098	55.9	12.0	52.8	20.9
INS	603	0.304	0.089	0.018	0.488	0.101	57.8	11.9	54.9	14.3
BIR	225	0.287	0.113	0.025	0.457	0.118	57.0	14.3	52.7	12.2
MAM	152	0.337	0.119	0.027	0.413	0.104	53.3	13.1	48.7	12.3
FIS	115	0.449	0.114	0.020	0.368	0.049	48.2	6.9	50.3	14.0
RAM	37	0.363	0.146	0.026	0.386	0.078	53.2	10.5	50.1	12.6
AQI	36	0.470	0.146	0.028	0.304	0.053	45.0	8.0	43.9	13.4
PLA	30	0.431	0.120	0.017	0.396	0.036	51.6	5.4	53.4	13.9

Notes: Taxonomic abbreviations are: INS, insects; BIR, birds; MAM, mammals; FIS, fish; RAM, reptiles and amphibians; AQI, aquatic invertebrates; PLA, plants. Model abbreviations are: RW, random walk; EX, exponential growth; EA, exponential Allee; RL, Ricker logistic; RA, Ricker Allee logistic. Sample size (n) is the number of time series.

and took most AIC_c w support from the Ricker logistic model. On the other hand, the weak Allee model increased the number of top-ranked Allee models from 13 to 22, despite reducing the number of top-ranked strong Allee models to nine (Appendix A).

Finally, our missing-value treatment resulted in qualitatively identical results, and slightly higher support for the Ricker logistic model over the exponential and random walk models (Appendix B).

Influence of climate variation

Local climate variables were obtained for the full temporal duration of 1015 time series, including 11 that exhibited a top-ranked Allee model in the population growth analysis. In most cases, the addition of local climate variables improved model fits but when the information-theoretic bias correction was applied for the additional parameters, the general effect was to reduce the model's AIC_c w. Reduction in AIC_c w was largest for the Ricker logistic model, and within model types was largest for models including both mean and extreme composite climate variables (Fig. 3).

The frequency with which the addition of climate variables improved the non-climate model fit was higher among those 11 time series with a top-ranked Allee model (45.5% of cases) compared to the remaining 1004 time series (28.2% of cases). Of the former time series, 27.3% supported a random walk or non-Allee model with climate variable(s) and only 1.2% of the latter time series supported an Allee model with climate variable(s). Six time series with top-ranked Allee models showed improved support with inclusion of both mean and extreme climate variables compared to one time series for each climate variable separately.

Influence of measurement error and data attributes

Repeating our population growth analysis using time series with randomized measurement error revealed a qualitatively similar spread of AIC_c w support to that obtained under the assumption of negligible measurement error (Appendix C). However, randomized measurement error shifted AIC_c w support toward the Allee

models from the random walk and non-Allee models (Appendix C). In addition, the top-ranking model changed more frequently among the 13 time series originally exhibiting a top-ranked Ricker Allee model (median = 51.0% of cases, 25–75% interquartile range based on 200 replicate treatments [IQR_r] = 44.5–68.5) compared to time series originally exhibiting either a top-ranked Ricker logistic (median = 9.5% of cases, IQR_r = 1.5–35.5) or random walk model (median = 2.0% of cases, IQR_r = 0.0–16.0).

Median AIC_c w support for non-Allee and Allee models was higher in non-trending time series ($n = 732$; non-Allee median = 0.541, 25–75% interquartile range based on 1000 bootstrap resamples [IQR_b] = 0.521–0.549; Allee median = 0.095, IQR_b = 0.092–0.099) compared to trending time series ($n = 466$; non-Allee median = 0.277, IQR_b = 0.272–0.301; Allee median = 0.058, IQR_b = 0.054–0.063). Only a few of the 13 time series with top-ranked Allee models were, however, non-trending and provided less support for positive density feedback ($n = 3$; median = 0.534) than the trending time series ($n = 10$; median = 0.553). The opposite pattern was observed among the time series with top-ranked non-Allee models (non-trending $n = 452$, median = 0.729; trending $n = 184$, median = 0.623). No pattern in the direction of trends was evident among the 10 trending time series with top-ranked Allee models (six increasing vs. four decreasing trends).

Median AIC_c w support for non-Allee and Allee models increased in longer time series, but decreased in more variable time series (measured by the coefficient of variation), despite a weak increase in time series variation with time series length (evidence ratio [ER] = 4449, $R^2 = 1.6\%$; Fig. 4). Indeed, a model including both time series length and variation was ranked above competing models considering each factor separately (although their interaction term could not be disregarded; Table 2). While time series with a top-ranked non-Allee model supported this pattern, time series with a top-ranked Allee model were shorter and less variable (median length = 17, median CV = 0.314) compared to
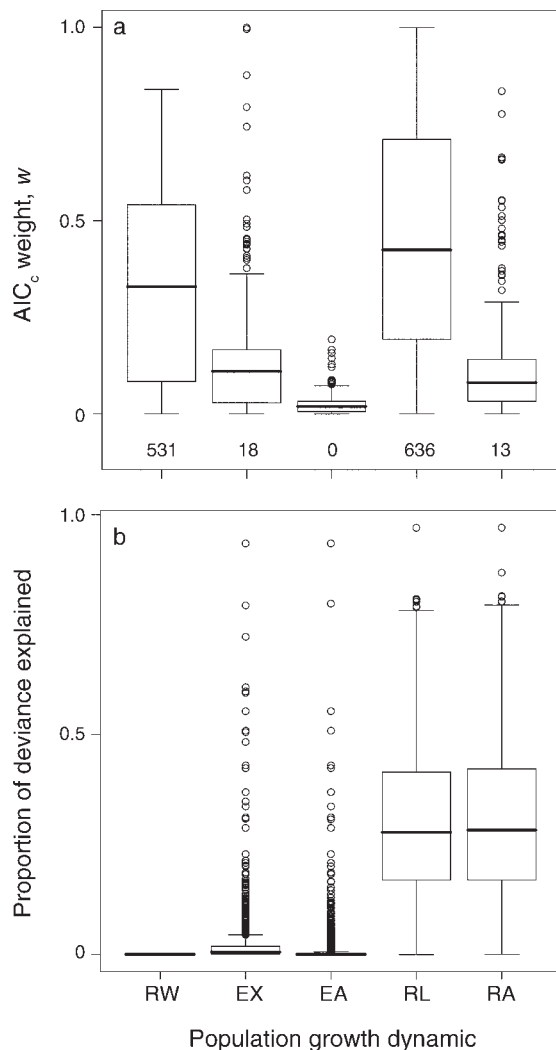
FIG. 2. (a) Support for each population growth model as indicated by Akaike weight, AIC_c w. Values below lower whiskers represent the top-ranked frequency. The Ricker logistic model (RL) received highest empirical support in these data followed by random walk (RW) and exponential growth (EX) models. Ricker Allee (RA) and exponential Allee (EA) models received the least support. (b) Boxplot showing the deviance explained for each population growth model, where the random walk (RW) model is taken to be the null model (zero deviance explained). Exponential growth (EX) generally explained more deviance than the exponential Allee (EA) growth model, whereas the Ricker (RL) and Ricker Allee (RA) logistic growth models explained similar deviance. Boxes delimit the 25–75% interquartile range (IQR), the bar represents the median, whiskers delimit the $1.5 \times$ IQR range, and open circles represent extreme values $\geq 1.5 \times$ IQR.

the remaining time series (median length = 19, median CV = 0.518).

Both non-Allee and Allee AIC_c w support increased with increasing minimum N when compared to a null mean model (non-Allee $\Delta AIC = 12.56$; Allee $\Delta AIC = 5.38$; Fig. 5). Median AIC_c w support for time series with a minimum N of $\leq 10\%$ ($n = 533$) was 0.373 for

non-Allee models ($IQR_b = 0.359–0.383$) and 0.067 for Allee models ($IQR_b = 0.064–0.069$). Measures of support were higher for those time series with a minimum N of $\leq 15\%$ ($n = 646$; non-Allee median = 0.390, $IQR_b = 0.382–0.406$; Allee median = 0.078, $IQR_b = 0.072–0.080$) and $\leq 50\%$ ($n = 107$; non-Allee median = 0.506, $IQR_b = 0.470–0.516$; Allee median = 0.086, $IQR_b = 0.081–0.092$). Median minimum N was larger for the 13 time series with a top-ranked Allee model (23.5%) than for the median of the other 1185 time series (12.7%).

DISCUSSION

We quantified the empirical support for positive density feedback (suggestive of a demographic Allee effect) in the per capita population growth rate of 1198 species and evaluated the factors hypothesized to influence its detection. Overall, we found 12.0% relative model support for positive density feedback compared to 55.9% relative support for the same models without an Allee effect term. Given that our results accord with the prevalence of negative density feedback reported in similar meta-analyses undertaken for insects (Woiwod and Hanski 1992) and vertebrates (Turchin and Taylor 1992), our result suggests that positive density feedback
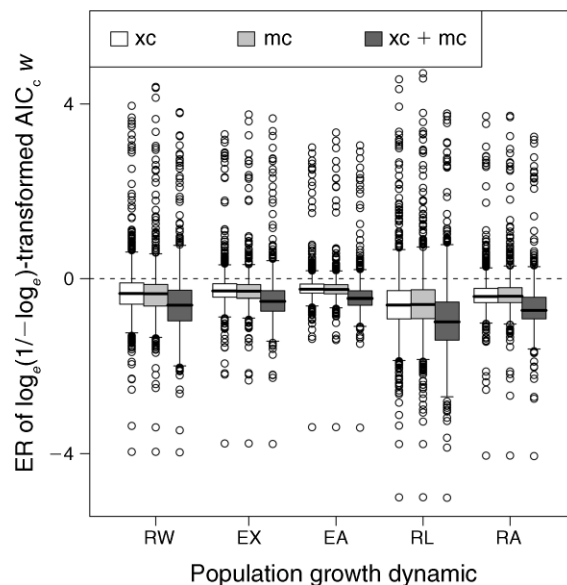

FIG. 3. Relative support for each population growth model combined with extreme (xc), mean (mc), or both climate variables compared to support for the population growth model without climate variables (using evidence ratio [ER] of $\log_e(1/-\log_e)$-transformed corrected Akaike information criterion weights, AIC_c w). The general effect of including climate variables in model fits was to decrease their AIC_c w, particularly for the Ricker logistic (RL) and random walk (RW) models. Other models were exponential growth (EX), exponential Allee growth (EA), and Ricker Allee logistic growth (RA). Boxes delimit the 25–75% interquartile range (IQR), the bar represents the median, whiskers delimit the $1.5 \times$ IQR range, and open circles represent extreme values $\geq 1.5 \times$ IQR.
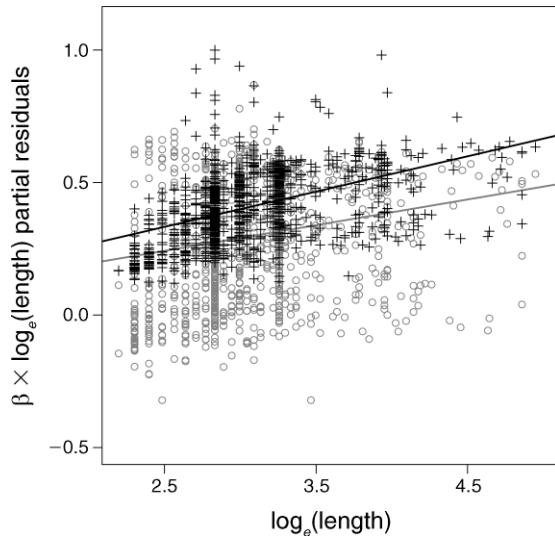
FIG. 4. Support for non-Allee (open circles) and Allee (plus signs) models as a function of time series length while holding for the effect of time series variation (measured as the coefficient of variation). Partial residuals plotted on the y-axis are calculated as $\text{residuals}_l \approx \text{residuals}_{lv} + \beta \times \log_e(\text{length})$ where β is the regression coefficient estimate relating $\log_e(\text{length})$ to AIC_c w in the full model (i.e., the top-ranked models in Table 2) and residuals_{lv} are the full model residuals.

might influence the growth rate of over one in 10 natural populations. Indeed, we detected strong positive density feedback in populations of 13 species not previously observed to exhibit demographic Allee effects (Appendix D).

Those 13 populations exhibiting a top-ranked Allee model were, however, the only populations to do so and constituted only 1.1% of the 1198 population time series examined. This support for positive density feedback falls between the 2.3% of 128 fish stocks observed by Myers et al. (1995) and the 0.2% of 3269 time series, including insects, fish, birds, and mammals, observed by Sibly et al. (2005). Furthermore, our database included time series for species previously exhibiting either a demographic Allee effect, including gypsy moth (*Lymantria dispar*) and Atlantic cod (*Gadus morhua*), or a component Allee effect, including African wild dogs (*Lycaon pictus*) and coyotes (*Canis latrans*), but none of our population time series for these species supported a top-ranked Allee model.

The AIC support for positive density feedback was highest for birds and mammals (Table 1), and a relatively high proportion of their time series supported top-ranked Allee models (Fig. 2). Plants, reptiles and amphibians, and aquatic invertebrates, on the other hand, exhibited least support for positive density feedback. These findings are not completely consistent with those emerging from published studies of demographic Allee effects (Kramer et al. 2009), and the reason for this might be due to difficulties in experi-

menting on some taxa (Gascoigne et al. 2009). Based on the BIC criterion, which supports lower dimensional models whose parameter estimates are nonzero (Burnham and Anderson 2002), plants and aquatic invertebrates show considerably higher support for positive density feedback. Although BIC might support less realistic model fits than AIC (Burnham and Anderson 2002), the high BIC support in these taxa indicates the existence of nonnegligible Allee threshold parameter estimates, which, when considered with experimental evidence of component Allee effects in species of these taxa (see Courchamp et al. 2008), means we cannot dismiss the possibility they might exhibit demographic Allee effects.

Our results are based on five population growth models chosen to reflect a set of hypotheses from a null model and incrementally increasing in complexity to a saturated model of population growth including both negative and positive density feedback (see Berryman [2003] for a similar model set). However, our model set excluded weak Allee effect models and will be biased toward a dichotomous "strong Allee effect or no Allee effect" result. To investigate this bias while retaining our simple non-Allee/Allee model set, we repeated our model-fitting analysis using the same model set modified to include a weak Allee effect version of the Ricker logistic model (Appendix A). In summary, the weak Allee effect model usurped most AIC_c w support from the Ricker logistic model, as expected, and then from the random walk and Ricker Allee growth models. Its inclusion, however, did not qualitatively change the spread of support over the population growth dynamics. This suggests our measure of support for Allee effects was not highly sensitive to exclusion of weak Allee effects and is likely to be an underestimate. Similarly, although the number of time series with a top-ranking Allee model increased from 13 (1.1%) to 22 (1.8%) (i.e.,

TABLE 2. Comparison of models examining the influence of time-series duration (length) and variability (coefficient of variation, CV) on the relative empirical support (corrected Akaike information criterion weights, AIC_c w) for non-Allee and Allee models.

Model	AIC_c	ΔAIC	ER	R^2 (%)
Non-Allee effect models				
Length + CV	−257.6	⋯	⋯	7.1
Length + CV + $I(\text{length} \times \text{CV})$	−255.6	2.00	2.7	7.1
Length	−206.8	50.74	1.0×10^{11}	2.9
CV	−211.3	46.29	1.1×10^{10}	3.3
Allee effect models				
Length + CV	−1662.6	⋯	⋯	22.4
Length + CV + $I(\text{length} \times \text{CV})$	−1660.6	2.00	2.7	22.4
Length	−1603.8	58.77	5.8×10^{12}	18.3
CV	−1391.9	270.75	6.2×10^{58}	2.1

Note: Evidence ratios (ER) >2.72 (e^1) indicate increasingly implausible models compared to the top-ranked model.

a 69% increase), this increase would not change our finding that occurrence of Allee effects is low.

Given the high relative AIC_c w support for positive density feedback (a measure of its bias-corrected likelihood), one might ask why a higher number of these 1198 population time series did not exhibit a top-ranked Allee model. We investigated several major factors previously proposed to explain this discrepancy. Local climate variation can directly influence population growth rate and thus conclusions on the role of density feedback in population regulation (Rothery et al. 1997). We found inclusion of climate variables generally improved growth model fits but the improvement was usually offset by the AIC_c bias correction, so the non-climate growth models were generally most parsimonious. This contrasts with the growing evidence that climate, and more generally environmental stochasticity, can play an important role in population regulation (Turchin 2003). On the other hand, these results might be due to factors inherent in a meta-analytic approach such as, for example, whether the defined climate variables are equally appropriate for all (or any) of the species analyzed. Interestingly, almost half of the Allee model fits were improved by inclusion of climatic variability (compared to almost 30% of non-Allee model fits) and almost a third of time series with top-ranked Allee models switched to supporting a top-ranked non-Allee or random walk model (compared to just 1.2% of non-Allee models that switched to supporting a top-ranked Allee model). These findings suggest that detection of positive density feedback is sensitive to climatic variability, which should be incorporated in attempts to detect Allee effects. On the other hand, there was no discernable difference between mean and extreme climate influences, despite the higher theoretical influence of extreme climate on population dynamics of small populations (Lande 1993), hinting at ill-defined mean and extreme climate variables.

Measurement error can either generate or mask evidence for density feedback in population time series (Shenk et al. 1998, Freckleton et al. 2006). As such, we investigated the possible consequences of our negligible measurement error assumption. Although relaxing the assumption of negligible measurement error had no qualitative effect on our results (cf. Table 1 and Appendix C), it did cause (1) a shift in AIC_c w support from the random walk and Ricker logistic models to the Ricker Allee model and (2) 51% of the 13 time series exhibiting top-ranked Allee models to support a top-ranked random walk or non-Allee model. We conclude that empirical support for positive density feedback can arise spuriously from excessive measurement error and that detection of positive density feedback might be sensitive to extreme (and possibly erroneous) observations (Freckleton et al. 2006). Because positive density feedback acts around unstable thresholds (Courchamp et al. 1999), observations in the range of population sizes at which it acts should be rare. By definition, such rare
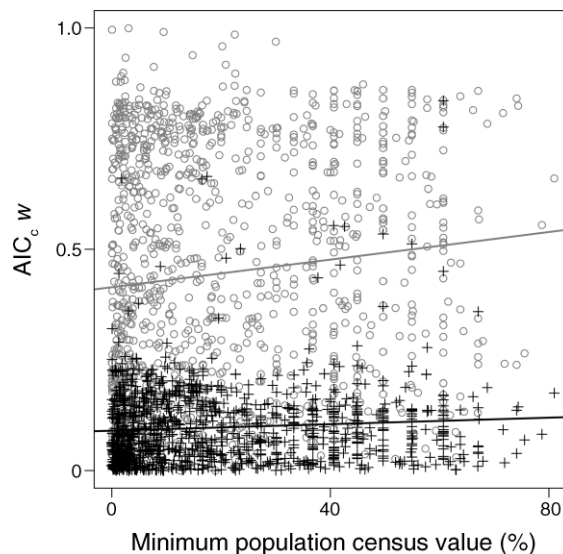

Fig. 5. Support for non-Allee (open circles) and Allee (plus signs) models, as indicated by Akaike weight, AIC_c w, increased with increasing minimum population census value (as a proportion of maximum population census value).

observations will be extreme compared to the general pattern in the time series (Chan et al. 2005). Therefore, determining whether observed positive density feedback is real will require careful monitoring and independent assessment of the various sources of measurement error.

The presence of extreme observations in time series exhibiting positive density feedback should be evident in measures of time series variation. However, we found lower variation in the 13 time series exhibiting top-ranked Allee models compared to the remaining time series. Although these 13 time series were shorter than the remaining time series and time series variation increases with time series length (Inchausti and Halley 2001), these results suggest that detection of positive density feedback in these time series was not necessarily due to extreme values. Rather, we found that empirical support for Allee models generally increased with increasing time series length and decreasing time series variation. This indicates that detection of density feedback (positive and negative) is more likely in non-trending time series (Inchausti and Halley 2001); however, only a quarter of the time series exhibiting positive density feedback here were non-trending (with no pattern among trend directions). This conundrum merits closer study because of the potential practical value in the ability to foresee a demographic Allee effect from time series characteristics, as is under investigation for regime shifts (e.g., Carpenter and Brock 2006).

Finally, we found limited support for the prevalent hypothesis that sparse observations at low population sizes might underpin the failure to observe more empirical support for positive density feedback (Myers et al. 1995, Sæther et al. 1996, Shelton and Healey 1999).

We found median support for both negative and positive density feedback increased with increasing minimum population census. Indeed, the minimum census value in the 13 time series exhibiting top-ranked Allee models was higher than that for the remaining time series. Furthermore, the opposite observed relationship to that hypothesized suggests this finding is unlikely to be changed by the inclusion of weak Allee effects. Rather, it seems this criterion has limited value as a requirement to detecting an Allee effect.

We emphasize that (1) our comparative approach ranks models in terms of their relative consistency with patterns in the time series, and thus a top-ranked model can still provide an inadequate structural representation of the underlying dynamical signal (Turchin 2003), and (2) our approach is necessarily general and makes several assumptions to analyze population growth dynamics of a range of species with different life histories and populations with different extrinsic pressures (e.g., Getz and Lloyd Smith 2006). Nevertheless, our ability to detect positive density feedback in some populations given an inherent bias to detect negative density feedback, exaggerated by measurement error (Freckleton et al. 2006) and model oversimplification (Festa Bianchet et al. 2003), could be taken as relatively strong evidence that they do indeed exhibit positive density feedback. Whether an observation of positive density feedback can be considered indicative of a demographic Allee effect will still require a combination of careful monitoring and replicated experimentation (Turchin 2003); however, the higher likelihood of positive density feedback compared to the number of observed cases suggests that there might be more cases present than observed (Stephens et al. 2007).

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APPENDIX A

Assessing the exclusion of weak Allee effect models (*Ecological Archives* E091-149-A1).

APPENDIX B

Missing-value treatment table: overall and major taxonomic group support (Akaike weights; AIC$_c$ *w*) for population growth models and overall AIC$_c$ *w* and Bayesian information criterion support for non-Allee and Allee models as a percentage of all support (*Ecological Archives* E091-149-A2).

APPENDIX C

Measurement error table: overall and major taxonomic group support for population growth models and overall AIC$_c$ *w* and Bayesian information criterion support for non-Allee and Allee models as a percentage of all support (*Ecological Archives* E091-149-A3).

APPENDIX D

Time series with Allee effects: measures of model support (Akaike weights; AIC$_c$ *w*) for the 13 time series with highest support for Allee models (*Ecological Archives* E091-149-A4).

Limited evidence for the demographic Allee effect from numerous species across taxa

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1 Appendices

Appendix A: Assessing the exclusion of weak Allee effect models.

Background

The choice of models to include in our model set was the most important decision we made in this analysis, and all results depend upon it. It is for this reason we selected our models carefully based on three main criteria:

1. **The models had to be published**: We chose only models we found in the population growth literature (and we consulted experts to locate these models). We compiled what we considered the optimum model set for our question and found it to be the same model set developed by Berryman (2003). Although the model set excludes weak Allee effect models, it represents a logical model set starting at the null model of no growth (random walk), working up systematically to the most complex model including negative and positive density feedback.

2. **The models should be nested**: We chose an elegant model set reflecting the major population growth dynamics incorporated in a stepwise fashion. Such an attempt was desirable to enable us to assess the additional support attributable to each model term added. Nevertheless, the model set excludes weak Allee effects by imposing the constraint $0 < A$ in all Allee model fits. Our reason for doing this was to two-fold: (1) it was a requirement to obtain a nested model set. Although several weak Allee models exist (and have been published), they do not admit the Ricker logistic or exponential growth models as special cases when there is no Allee

effect, at least not without an additional parameter (see Berryman 2003 and chapter 3 in Courchamp et al. 2008). Also, we do not know of an equivalent weak Allee exponential model. (2) our emphasis on strong Allee effects reflects our perceived importance of this dynamic over weak Allee effects, which do not cause negative growth rate (i.e., population decline).

3. **Numbers of parameters**: We opted to use an information-theoretic approach to model ranking that penalizes models for additional parameters. The number of odel parameters therefore became an important selection criterion when searching for Allee effect models. In the model set used in the main text, the Allee effect is incorporated using a single parameter A (constrained $0 < A$; see point 2 above). While the Allee effects can be incorporated using other formulations, these generally entail additional parameters, or do not admit the Ricker logistic or exponential growth as special cases. For example, one could characterize the Allee effect using two parameters, say A and C with $0 < C$, which would allow the model greater flexibility to find Allee effects (strong or weak) (see chapter 3 in Courchamp et al. 2008). Including additional parameters, however, will be penalized by $\mathrm{AIC_c}$.

Nevertheless, our model set biases our results and we wanted to investigate the extent of this bias. We therefore repeated our model-fitting analysis with an additional model; a 4-parameter weak Allee effect version of the Ricker Allee model (WA; Courchamp et al. 2008); $r = r_m(1-(N_t/K))((N_t-A)/K)$. The Allee term in the model is $(N_t-A)/K$, and equals 1 when N_t equals $(K+A)$; for all other N this term will weight the negative density feedback term preventing us from assessing the support due to the term in isolation. We fitted this model, along with the others, using the same methods outline in the main text.

Results

The WA model received similar support to the RA model both overall, and for each taxa considered separately (Table 1, Fig. 1a) but had higher support among the aquatic invertebrate and plant taxa. Furthermore, it was the top-ranked model in 13 cases (Fig. 1). Although at first sight these results are similar to those for the RA model used in the original model set (1) the WA is an additional model and therefore usurps empirical support from other models in the model set. Specifically, WA appears to take the support from RL, RW and RA, although this causes no overall change to the spread of empirical support across the population growth dynamics examined. (2) As an additional Allee model, the WA top-ranked model count is added to that of RA for a combined top-ranking Allee model count of 22. The RA top-ranked model count was only reduced by 4 (from 13 to 9) when including WA in the model set, and the increase in the top-ranked model count is not sufficiently large to change our findings using the model set excluding weak Allee effects. (3) Finally, the WA model frequently achieved the same fit as the RL and RA models, as indicated from the deviance explained (Fig. 1b), and the WA model was not the top-ranking mode for any species previously shown to exhibit component or demographic Allee effects (Table 2; cross reference main article).
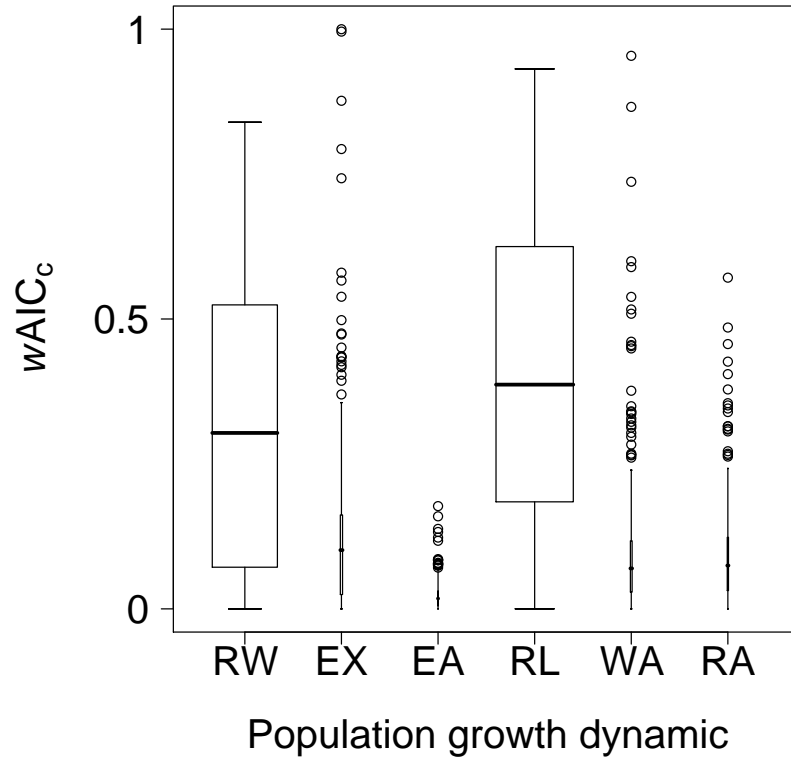
(a)

Figure 1: (a) Support for each population growth model where bar width represents the frequency the model was top-ranked. The Ricker logistic model (RL) received highest empirical support in these data followed by random walk (RW) and exponential growth (EX) models. Ricker Allee (RA) and Weak Allee (WA) models received similar support and both more than the exponential Allee (EA) model.
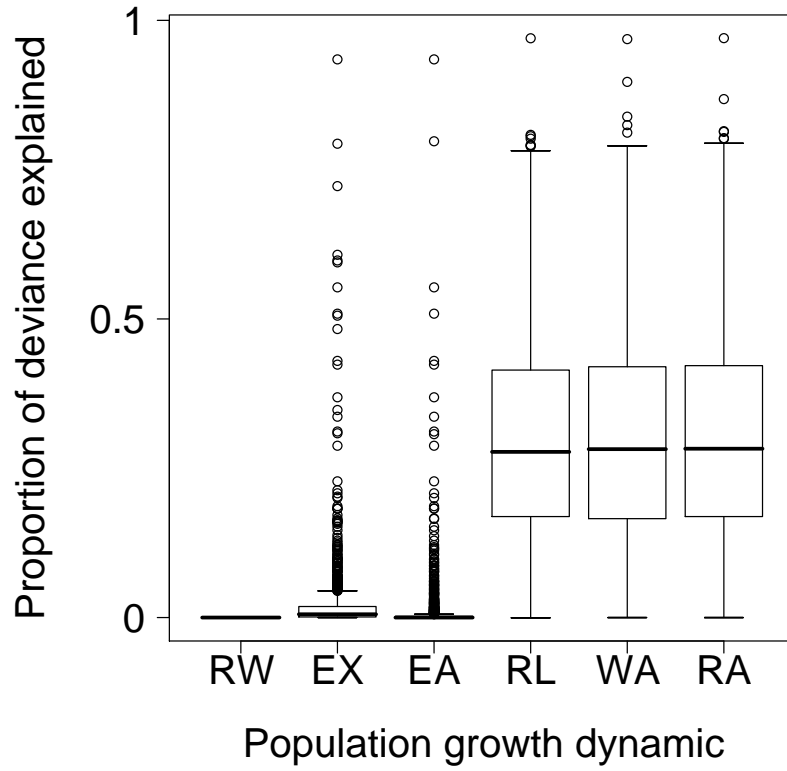
Figure 1: (b) Boxplot showing the deviance explained for each population growth model, where the random walk (RW) model is taken to be the null model (zero deviance explained). Exponential growth (EX) generally explained more deviance than the exponential Allee (EA) growth model, whereas the Ricker (RL), Weak Allee (WA) and Ricker Allee (RA) logistic growth models explained similar deviance. Boxes delimit the 25-75% interquartile range (IQR) and open circles (∘) represent extreme values ≥ 1.5 × IQR.

Table 1: Overall and major taxonomic group $w\mathrm{AIC_C}$ support for population growth models.

	n	Model $w\mathrm{AIC_C}$					
		RW	EX	EA	RL	WA	RA
overall	1198	0.307	0.100	0.020	0.404	0.084	0.085
INS	603	0.288	0.085	0.017	0.436	0.086	0.088
BIR	225	0.272	0.107	0.023	0.402	0.095	0.100
MAM	152	0.323	0.113	0.025	0.359	0.094	0.086
FIS	115	0.438	0.111	0.019	0.343	0.043	0.046
RAM	37	0.350	0.142	0.025	0.352	0.062	0.069
AQI	36	0.452	0.134	0.025	0.288	0.054	0.047
PLA	30	0.417	0.116	0.016	0.366	0.051	0.033

Taxonomic groups: INS, insects; BIR, birds; MAM, mammals; FIS, fish; RAM, reptiles and amphibians; AQI, aquatic invertebrates; PLA, plants. Model abbreviations: RW, random walk; EX, exponential growth; EA, exponential Allee; RL, Ricker logisitic; WA, weak Ricker Allee logistic; RA, strong Ricker Allee logistic.

Table 2: Population time series with greatest wAIC$_C$ support for either the weak or strong Ricker Allee model. ID, database identification number; TaxG, taxonomic group.

| | ID | TaxG | $\sum w$AIC$_C$ | | | | | |
			RW	EX	EA	RL	WA	RA
Four-spotted chaser	5	Ins	0.105	0.034	0.009	0.313	0.461	0.078
American crow	1181	Bir	0.000	0.000	0.000	0.250	0.265	0.485
Spanish sardine	1944	Fis	0.000	0.000	0.000	0.289	0.140	0.571
Chiff chaff	2770	Bir	0.002	0.001	0.000	0.335	0.323	0.340
Barred chestnut	6218	Ins	0.046	0.013	0.003	0.248	0.336	0.355
Least yellow underwing	6245	Ins	0.000	0.000	0.000	0.360	0.261	0.379
Clouded silver	6468	Ins	0.008	0.002	0.000	0.079	0.600	0.311
Lilac beauty	6484	Ins	0.011	0.003	0.001	0.075	0.453	0.457
Northern shrimp	6783	Aqi	0.066	0.226	0.043	0.109	0.376	0.179
Double dart	6875	Ins	0.214	0.195	0.016	0.144	0.084	0.346
Buff ermine	6986	Ins	0.028	0.013	0.002	0.416	0.449	0.092
White-bearded Wildebeest	7060	Mam	0.000	0.001	0.000	0.195	0.737	0.067
Laxmann's masked shrew	10018	Mam	0.005	0.001	0.000	0.458	0.509	0.027
European otter	10177	Mam	0.298	0.227	0.013	0.085	0.027	0.351
Roe deer	10331	Mam	0.048	0.017	0.005	0.261	0.590	0.079
Lord Howe Island woodhen	20030	Bir	0.022	0.022	0.004	0.281	0.266	0.405
Snail Kite	20063	Bir	0.006	0.002	0.001	0.007	0.954	0.030
Chillingham cattle	20114	Mam	0.011	0.010	0.003	0.046	0.866	0.064
Horse	20121	Mam	0.157	0.046	0.007	0.199	0.538	0.053
Feral Goat	20158	Mam	0.011	0.005	0.001	0.290	0.455	0.237
Blue Grama	20181	Pla	0.245	0.095	0.019	0.229	0.339	0.074
Lesser scaup	30106	Bir	0.049	0.019		0.148	0.516	0.268

Model abbreviations: RW, random walk; EX, exponential growth; EA, exponential Allee; RL, Ricker logisitic; WA, weak Ricker Allee logistic; RA, strong Ricker Allee logistic.

Appendix B: Missing data

Table 3: Overall and major taxonomic group support (Akaike weights; $w\text{AIC}_\text{C}$) for population growth models and overall $w\text{AIC}_\text{C}$ and Bayesian Information Criterion (BIC) support for non–Allee (nAE) and Allee (AE) models as a percentage of all support. Support based on time series without missing value treatment.

		Model $w\text{AIC}_\text{C}$					AIC (%)		BIC (%)	
	n	RW	EX	EA	RL	RA	nAE	AE	nAE	AE
overall	1198	0.319	0.104	0.021	0.457	0.098	56.1	11.9	53.4	13.9
INS	602	0.303	0.090	0.018	0.489	0.099	57.9	11.8	55.0	14.4
BIR	224	0.276	0.105	0.023	0.476	0.121	58.0	14.4	54.6	13.2
MAM	147	0.331	0.123	0.027	0.412	0.106	53.6	13.3	49.0	12.7
FIS	114	0.443	0.116	0.019	0.376	0.046	49.2	6.5	52.3	14.5
RAM	37	0.370	0.149	0.026	0.375	0.080	52.5	10.6	50.3	13.6
AQI	35	0.462	0.139	0.026	0.316	0.057	45.5	8.3	45.2	14.2
PLA	30	0.454	0.115	0.015	0.381	0.035	49.6	5.1	52.9	14.9

Appendix C: Measurement error

Table 4: Overall and major taxonomic group support (Akaike weights; $w\mathrm{AIC_C}$) for population growth models and overall $w\mathrm{AIC_C}$ and Bayesian Information Criterion (BIC) support for non–Allee (nAE) and Allee (AE) models as a percentage of all support. Support based on time series with randomized measurement error.

| | n | Model $w\mathrm{AIC_C}$ | | | | | AIC (%) | | BIC (%) | |
		RW	EX	EA	RL	RA	nAE	AE	nAE	AE
overall	1198	0.326	0.111	0.022	0.397	0.144	50.8	16.6	47.9	18.1
INS	603	0.309	0.091	0.019	0.432	0.148	52.3	16.7	49.3	19.7
BIR	225	0.280	0.114	0.024	0.390	0.192	50.4	21.7	46.6	19.2
MAM	152	0.342	0.125	0.026	0.364	0.142	48.9	16.8	45.1	15.6
FIS	115	0.369	0.174	0.028	0.353	0.077	52.6	10.5	49.9	12.3
RAM	37	0.479	0.133	0.022	0.319	0.047	45.2	6.9	47.3	13.5
AQI	36	0.443	0.144	0.028	0.267	0.118	41.1	14.6	41.1	17.4
PLA	30	0.442	0.126	0.019	0.311	0.101	43.7	12.0	47.0	18.8

Appendix D: Time series with Allee effects

Table 5: Population time series with greatest support for positive density feedback.

	ID	TaxG	$\sum w\mathrm{AIC_c}$ RW	EX	EA	RL	RA
American crow	1181	Bir	0.000	0.000	0.000	0.340	0.660
Spanish sardine	1944	Fis	0.000	0.000	0.000	0.336	0.664
Chiff chaff	2770	Bir	0.002	0.001	0.000	0.495	0.501
Barred chestnut	6218	Ins	0.069	0.020	0.004	0.373	0.534
Least yellow underwing	6245	Ins	0.001	0.000	0.000	0.487	0.512
Clouded silver	6468	Ins	0.019	0.005	0.001	0.198	0.776
Lilac beauty	6484	Ins	0.021	0.006	0.001	0.137	0.835
Double dart	6875	Ins	0.234	0.214	0.018	0.157	0.378
European otter	10177	Mam	0.306	0.233	0.013	0.087	0.361
Lord Howe Island woodhen	20030	Bir	0.029	0.030	0.006	0.383	0.552
Snail Kite	20063	Bir	0.127	0.046	0.011	0.158	0.658
Chillingham cattle	20114	Mam	0.082	0.072	0.021	0.345	0.480
Lesser scaup	30106	Bir	0.102	0.038		0.306	0.554

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