STRENGTH OF EVIDENCE FOR DENSITY DEPENDENCE IN ABUNDANCE TIME SERIES OF 1198 SPECIES

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Abstract. Population limitation is a fundamental tenet of ecology, but the relative roles of exogenous and endogenous mechanisms remain unquantified for most species. Here we used multi-model inference (MMI), a form of model averaging, based on information theory (Akaike's Information Criterion) to evaluate the relative strength of evidence for density-dependent and density-independent population dynamical models in long-term abundance time series of 1198 species. We also compared the MMI results to more classic methods for detecting density dependence: Neyman-Pearson hypothesis-testing and best-model selection using the Bayesian Information Criterion or cross-validation. Using MMI on our large database, we show that density dependence is a pervasive feature of population dynamics (median MMI support for density dependence = 74.7–92.2%), and that this holds across widely different taxa. The weight of evidence for density dependence varied among species but increased consistently with the number of generations monitored. Best-model selection methods yielded similar results to MMI (a density-dependent model was favored in 66.2–93.9% of species time series), while the hypothesis-testing methods detected density dependence less frequently (32.6–49.8%). There were no obvious differences in the prevalence of density dependence across major taxonomic groups under any of the statistical methods used. These results underscore the value of using multiple modes of analysis to quantify the relative empirical support for a set of working hypotheses that encompass a range of realistic population dynamical behaviors.

Key words: Akaike information criterion; density dependence; endogenous population dynamics; multi-model inference; negative feedback; population regulation; strength of evidence; time series.

INTRODUCTION

If density dependence is to be a cornerstone of ecological theory, a certain burden of proof needs to be satisfied.

—den Boer (1991)

Most biologists accept that density-dependent demographic processes (or more generally, negative feedback mechanisms; Berryman 2002) work to regulate natural populations (Turchin 1999, Lande et al. 2002), at least under some circumstances (Hixon and Carr 1997). That said, statistical detection of regulation using population abundance indices (as opposed to demographic data) can be problematic. For instance, exogenous (density-independent) factors may overwhelm endogenous (density-dependent) processes (Andrewartha and Birch 1954), small sample sizes (i.e., few time steps of observation relative to the generation length of the organism being studied) reduce statistical power (Solow and Steele 1990), and sampling error can affect both Type I and Type II error rates (Shenk et al. 1998). The most biologically intuitive means of quantifying regulation (and determining critical mechanistic detail) is by

direct examination of the relationship between density, realized demographic rates, and environmental covariates (Osenberg et al. 2002). However, a broad-scale evaluation of the nature and prevalence of population regulation across many species requires a different approach, such as meta-analysis of abundance time series.

Although considerable effort has been given to developing statistical approaches to detect density dependence in time series data, no single, superior test has emerged (Fox and Ridsdillsmith 1995). Classic tests that fall under the Neyman-Pearson hypothesis testing (NPHT) framework (e.g., Bulmer 1974, Pollard et al. 1987, Dennis and Taper 1994) determine the probability that a null (density-independent) model generated the observed or more extreme data (Johnson 1999), with density independence rejected if this probability is small (typically <5%). Alternative approaches have typically involved selecting a best model from an a priori set of candidate density-independent and density-dependent models, using either the Bayesian Information Criterion (BIC; e.g., Zeng et al. 1998, Dennis and Otten 2000) or jackknifed cross-validation (C-V; e.g., Turchin 2003).

In recent years, statistical approaches that attempt to provide strengths of evidence for multiple working hypotheses have found favor (Hilborn and Mangel 1997, Burnham and Anderson 2002), based on ideas

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TABLE 1. Seven example species representing major taxa with long-term (≥14 years) time series abundance data.

Common name	Scientific name	Taxon	q	AIC$_c$ model weight					wt DD (%)
				RW	EX	RL	GL	TL	
Whooping Crane	*Grus americana*	BIR	57	0.213	**0.430**	0.146	0.163	0.049	35.8
Grizzly bear	*Ursus arctos*	MAM	38	**0.524**	0.262	0.092	0.095	0.027	21.4
Snapping turtle	*Chelydra serpentina*	REP	14	**0.451**	0.124	0.166	0.230	0.029	42.4
Atlantic salmon	*Salmo salar*	FIS	110	0.017	0.006	0.367	**0.459**	0.150	97.6
Desert locust	*Schistocerca gregaria*	INS	104	0.002	0.001	0.005	**0.964**	0.028	99.7
Spiny lobster	*Panulirus interruptus*	MIN	62	0.096	0.035	0.121	**0.607**	0.141	86.9
Blue grama	*Bouteloua gracilis*	PLA	22	0.096	0.037	0.090	0.047	**0.729**	86.7

Notes: Abbreviations for taxa are: birds, BIR; mammals, MAM; reptiles, REP; fish, FIS; insects, INS; marine invertebrates, MIN; and plants, PLA; q is the median number of yearly transitions. Shown are relative strengths of evidence for five a priori population dynamics models (Akaike's Information Criterion [AIC$_c$] weight) under density-independent (random walk [RW], exponential [EX]) and density-dependent (Ricker-logistic [RL], Gompertz-logistic [GL], and θ-logistic [TL]) growth. The sum of AIC$_c$ weights for the density-dependent models represents the combined percentage weight for those models (wt DD). The binary outcomes (yes [Y] or no [N]) for the selection of density dependence using AIC$_c$, Bayesian Information Criterion (BIC), cross-validation (C-V; Turchin 2003), R (Bul; Bulmer 1974), randomization (Ran; Pollard et al. 1987), and parametric bootstrap likelihood ratio test (PBLR; Dennis and Taper 1994) are shown, as is whether a lagged density-dependent response was detected by AIC$_c$ and C-V. The values in boldface show the model with the highest AIC$_c$ weight per taxon.

proposed well over a century ago (Chamberlin 1890). The most-widely adopted method for this multi-model inference uses information theory based on the Akaike Information Criterion (AIC; Burnham and Anderson 2002), which employs Kullback-Leibler information as a fundamental, conceptual measure of the relative distance of a given model from full reality. Despite its obvious advantages for examining complex ecological processes, AIC has rarely been used in studies of density dependence in time series, except in a few individual case studies (e.g., Morris and Doak 2002). Bayesian methods are commonly used for model averaging (Wintle et al. 2003), but are yet to be applied in this way for the detection of density dependence.

The relative importance of endogenous vs. exogenous processes on the dynamics of real populations can be most convincingly settled by empirical means rather than a priori arguments of logic (Cooper 2001). Here we build on the work of Turchin and Taylor (1992), Woiwod and Hanski (1992), Zeng et al. (1998), and others by undertaking a diverse portfolio of analyses (AIC, BIC, C-V, NPHT) to evaluate the relative strength of evidence for density-dependent and density-independent population dynamics in long-term time series abundance data from a substantial dataset of 1198 species spanning a broad range of taxa. We demonstrate that density dependence is a pervasive feature of the population dynamics of these species, but find no important differences between the taxonomic groups (e.g., invertebrates vs. vertebrates).

METHODS

We used a set of high-quality, long-term population dynamics time series data for 1198 species (one time series per species) comprising 639 invertebrate, 529 vertebrate, and 30 plant species, and covering a wide range of taxa, biomes, and life histories (see the Appendix for the filtering methods and the Supplement for the species list and data sources). The minimum

length of these time series was eight year-to-year transitions (q) with a mean duration of 22 transitions.

There are many potential mathematical simplifications of complex population dynamics. For simplicity and generality, we used an a priori model-building strategy to arrive at a set of five population dynamics models commonly used to describe phenomenological time series data (Turchin 2003) for the MMI and model-selection methods (AIC, BIC, and C-V). The set included two density-independent models (random walk and exponential growth) and three density-dependent models (Ricker-, Gompertz-, and θ-logistic population growth). Further details can be found in the Appendix or by consulting Dennis and Taper (1994) and Sæther et al. (2002). All models were fitted using maximum-likelihood estimation assuming process error (hence, initial population size was not estimated as a separate parameter). We also separately considered a model set that included delayed (lagged) density-dependent models (Turchin 1990).

Our method of multi-model inference used Kullback-Leibler information to assign relative strengths of evidence (AIC$_c$ weights) to each model in the set (Burnham and Anderson 2002). To compare a more complex model a to a simpler model b, we employed the information-theoretic evidence ratio (ER = AIC$_c$ weight of model a ÷ AIC$_c$ weight of model b) to quantify the relative support of a vs. b, and used the least-squares R^2 value to determine structural goodness of fit of model a (test for model adequacy). For model selection (i.e., choosing a single best model) we used both BIC (Zeng et al. 1998) and C-V (Turchin 2003). For NPHT, we chose three classic tests: R (Bulmer 1974), randomization (Ran; Pollard's et al. 1987), and parametric bootstrap likelihood-ratio (PBLR; Dennis and Taper 1994).

We examined a number of potential biases regarding the detection of density dependence (see the Appendix for full details). We regressed the strength of evidence for density dependence (complementary log–log trans-

TABLE 1. Extended.

	DD detected?						Lag?	
AIC_c	BIC	C-V	Bul	Ran	PBLR		AIC_c	C-V
N	N	Y	N	N	N		N	Y
N	N	Y	N	N	N		N	Y
N	N	N	N	N	N		N	N
Y	Y	Y	Y	Y	Y		Y	Y
Y	Y	Y	Y	Y	N		Y	N
Y	N	Y	Y	Y	N		Y	N
Y	Y	Y	N	N	N		N	Y

formed AIC_c weight) against (1) log of time series length to determine whether the support for density dependence was related to length of monitoring, and (2) variance in population growth rate to test if high variability overwhelms the density-dependent signal. We also regressed realized r per generation (r_G) against log of time series length (in generations to reduce cross-species variability due to life history effects) to determine how long a population must be monitored before stabilization due to intrinsic or extrinsic regulatory processes is observed. (3) Single density-independent vs. density-dependent pairwise model comparisons were used to evaluate whether our chosen a priori model set produced a bias towards density dependence. (4) Sampling error may spuriously inflate the evidence for density dependence. Of our 1198 total species, 83 (all vertebrates) represented relatively high-precision direct-count data (e.g., mark–recapture estimates of abundance, entire colony counts) as opposed to indirect estimates of population abundance for the remaining 446 vertebrates (e.g., catch per unit effort, harvest indices). We compared the strength of evidence for density dependence between these two groups. (5) Trending time series might mask endogenous processes and provide little information about equilibrium conditions. We tested this idea by evaluating which models were best supported by IUCN-listed (predicted a priori to be declining deterministically or recovering from small numbers; almost all vertebrates in our database) vs. non-listed vertebrate species.

RESULTS

The relative support for density dependence varied widely among species (for selected examples, see Table 1). Overall, the multi-model inference (MMI) approach using five a priori population dynamics models indicated a relative support of 74.7% for density dependence over all 1198 species (Table 2). There was higher overall support for density dependence in the invertebrates (78.0%) than the vertebrates (68.9%), with insects showing the most support (79.5%) and fish the least (60.1%; Table 2). This trend was reflected in the weight of evidence for density dependence among major taxa (Fig. 1), and in the other statistical tests of density dependence (Table 2). Taxa with a large number of

representative species (i.e., birds, fish, insects, and mammals) had consistently higher support for density dependence (Fig. 1).

The number of years monitored had a strong positive influence on the evidence for density dependence (evidence ratio [ER] = 1.35×10^{32}, R^2 = 11.7%; Fig. 2A). A similar relationship was evident in some of the NPHT approaches (e.g., R^2 = 15.2% for Pollard's randomization), but not for others (e.g., R^2 = 1.1% for Bulmer's R). Species with >50% MMI support for density dependence had a mean time series length of 23.1 years (95% bootstrapped confidence interval based on 10,000 randomizations = 22.0–24.2, n = 856), whereas for those with <50% support, it was 18.0 years (95% CI = 16.9–19.2, n = 342). The estimate of the rate of population change per generation (r_G), irrespective of density, tended towards zero as the number of generations monitored increased (with no evidence for a trend in r_G: ER = 1.01, R^2 = 0.1%; Fig. 2B). Without exception, estimated r_G was near zero after monitoring for approximately $e^{4.5}$ = 90 generations (Fig. 2B).

The detection rate for density dependence was similar across the NPHTs, and substantially lower than that provided by MMI or cross-validation (Table 2). The BIC model-selection approach detected density dependence more frequently than NPHTs and less often than the AIC_c-based MMI or cross-validation. A direct comparison of AIC_c-based MMI and cross-validation requires the removal of the random walk model from the MMI model set. This produced nearly identical inferences from MMI and cross-validation (Table 2), confirming the assertion that the latter is a numerically intensive equivalent to the asymptotic approximation
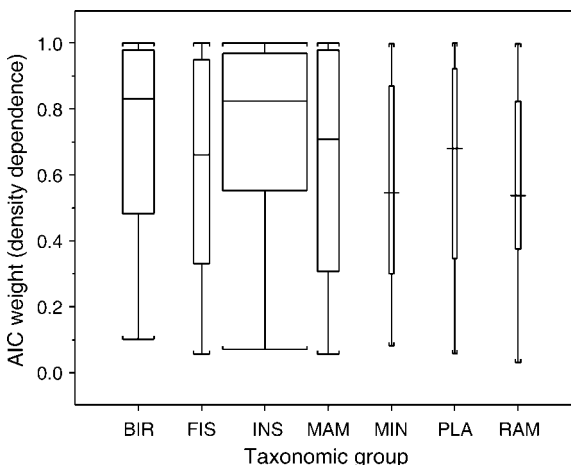

FIG. 1. Distribution of proportional support assigned to density dependence (based on Akaike's Information Criterion (AIC_c) weights for the three density-dependent models) for birds (BIR), fish (FIS), insects (INS), mammals (MAM), marine invertebrates (MIN), plants (PLA), and reptiles and amphibians (RAM). Bars represent the 50% probability density of the distribution with the width proportional to the number of species in the taxonomic group, black lines indicate the median value, and whiskers show 1.5 times the inter-quartile range.

TABLE 2. Support for density dependence in population abundance time series of 1198 species.

Taxon	n	q	AIC$_c$ model weight					ΣDD wt		DD (%)	
			RW	EX	RL	GL	TL	AIC$_c$	AIC$_{c-RW}$	C-V	BIC
All species	1198	22	0.190	0.063	0.244	0.428	0.074	0.747	0.922	93.9	66.2
Invertebrates	639	19	0.170	0.050	0.267	0.438	0.075	0.780	0.940	96.7	71.0
Vertebrates	529	26	0.223	0.088	0.217	0.401	0.071	0.689	0.918	90.5	64.1
Insects	604	16	0.158	0.047	0.276	0.443	0.076	0.795	0.944	97.2	72.2
Birds	224	20	0.149	0.054	0.253	0.455	0.089	0.797	0.937	91.6	61.2
Mammals	152	22	0.241	0.115	0.190	0.375	0.079	0.644	0.849	88.8	59.9
Fish	115	15	0.285	0.114	0.193	0.351	0.057	0.601	0.840	90.4	54.8

Notes: Shown are the number of species in each group (n), median number of yearly transitions (q), and relative strengths of evidence for five a priori population dynamics models (median AIC$_c$ weight across all species rescaled to sum to 1) encapsulating density-independent (random walk [RW], exponential [EX]) and density-dependent (Ricker-logistic [RL], Gompertz-logistic [GL], and θ-logistic [TL]) growth. The sum of AIC$_c$ weights for the density-dependent models represents the combined proportional weight for density dependence (ΣDD wt). For comparison to cross-validation (C-V; Turchin 2003), the AIC$_c$ weights without the RW model are also given (AIC$_{c-RW}$). Also shown are the percentage of species in which density dependence was "selected" using C-V, Bayesian Information Criterion (BIC), and the three null-hypothesis tests (NHT): R (Bul; Bulmer 1974), randomization (Ran; Pollard et al. 1987), and parametric bootstrap likelihood ratio test (PBLR; Dennis and Taper 1994). The final columns indicate the percentage of all species in which lagged or lagged + direct density dependence (lagged DD) was preferred over direct density dependence using AIC$_c$ and C-V.

given by AIC (Stone 1977). Between 25.5% (cross-validation) and 12.4% (AIC$_c$) of species had greater support for lagged density dependence than either direct density dependence or density independence (Table 2).

Using the full model set did not introduce a bias toward a particular conclusion because two pairwise comparisons indicated similar proportional support for density dependence: random walk (29.2%) vs. Gompertz-logistic (70.8%) and exponential (22.4%) vs. Ricker-logistic (77.6%). More variable time series showed greater support for density dependence (ER = 1.71×10^6), but explained little of the underlying variation ($R^2 = 2.5\%$). Sampling error did not spuriously inflate the evidence for density dependence: Direct-count time series had a median MMI support for density dependence of 87.0% (95% CI = 76.2–93.1%), but only 71.2% (64.9–78.2%) for the less precise indirect counts. Pollard's randomization gave a similar result (direct-count, 57.9–74.7%; indirect-count, 42.4–50.0%), but PBLR showed no difference (direct-count, 21.7–38.6%; indirect-count, 26.1–33.0%). Finally, IUCN-listed species had higher support for the exponential model relative to unlisted species as predicted (IUCN-listed median AIC$_c$ weight = 14.6%, 95% CI = 12.1–17.2%; unlisted = 8.6%, 7.6–9.6%).

DISCUSSION

We have used multi-model inference (MMI), model selection and classic Neyman-Pearson hypothesis tests (NPHT) to provide convincing evidence for pervasive density dependence in the time series data of 1198 species, yet we found little discernable difference across major taxonomic groups. These results agree with earlier work: Woiwod and Hanski (1992) used NPHT to detect density dependence in 79% of moth and aphid species where time series exceeded 20 years; Zeng et al. (1998) employed BIC to show that a density-dependent model was preferenced in 23 of 31 species examined; and Turchin and Taylor

(1992) used C-V to demonstrate support for direct or complex endogenous dynamics in all but one of 14 insect and 22 vertebrate populations. The uniqueness of our contribution in the context of the density dependence literature is twofold: (1) The number of species examined is almost three times that of the previous largest study (on moths and aphids only; Woiwod and Hanski 1992), and more than an order of magnitude larger than other cross-taxonomic comparisons (e.g., Turchin and Taylor 1992, Dennis and Taper 1994, Zeng et al. 1998). The recent analysis of 1780 abundance time series (not species) by Sibly et al. (2005) implicitly assumed density dependence in all populations and proceeded to examine its form using the θ-logistic model. (2) Multi-model inference employing AIC was used as a basis for determining the strength of evidence for density dependence and compared to the results of the more commonly applied best-model selection (BIC and C-V) and NPHT (three classic tests). The relative evidence for density dependence using these approaches was as expected. Indeed, AIC is anticipated to provide higher support for more-complex models, so it is the recommended approach in management issues attempting to capture the complexities of ecological reality. As such, AIC may over-parameterize because it does not attempt to identify the true model (whereas BIC may *under*-parameterize; Anderson and Burnham 1999). Our large sample of 1198 species and the consistent results using different methods suggest that any possible sensitivity to outliers does not alter our general conclusions.

Given the relative regularity with which density-dependent feedback mechanisms have been shown to affect vital rates such as survival, fecundity, and age at first breeding (Barker et al. 2002, Osenberg et al. 2002) and the claims that density dependence is a repeatable, measurable characteristic of a species (Wolda and Dennis 1993), it is important to understand why it is not always strongly supported in analyses of time series

Table 2. Extended.

NHT significant (%)			Lagged DD (%)	
Bul	Ran	PBLR	AIC$_c$	C-V
49.8	48.7	32.6	12.4	25.5
57.4	49.1	35.1	14.3	23.0
41.4	49.3	29.5	10.6	28.4
58.8	50.5	36.3	10.6	23.5
44.2	56.7	33.9	11.2	27.2
39.5	52.0	28.9	21.7	30.9
37.4	40.0	26.1	13.9	29.6

data. There are a number of likely explanations: (1) The time series is too short. There is ample support for an increasing likelihood of detecting density dependence or support for higher dimensional models (e.g., delayed responses) as the time over which a population is monitored lengthens (Woiwod and Hanski 1992, Hanski et al. 1993, Wolda and Dennis 1993, Dennis and Taper 1994). Our analysis confirmed this by demonstrating a relationship between length of monitoring and (a) increasing evidence for density dependence (Fig. 2A), and (b) a convergence toward zero net growth rate (implying equilibrium; Fig. 2B). The latter result is logical because species able to persist over the long term either eventually stabilize due to intrinsic or extrinsic regulatory processes or decline to extinction. The low support for lagged models (Table 2) may simply reflect the parsimony trade-off inherent in the statistical approaches. (2) Deterministic changes in population abundance (e.g., through habitat loss) can mask endogenous signals (Woiwod and Hanski 1992, Berryman and Turchin 2001), an idea supported by the result that trending species had a higher support for the exponential model. (3) Density dependence may operate at spatial scales much smaller or larger than the population unit being monitored (Ray and Hastings 1996).

The ability to discern density dependence is affected by the degree to which a population's abundance varies over the period of monitoring (Turchin 1999). In the classic logistic-growth model there are three fundamental phases (del Monte-Luna et al. 2004): exponential rise when growing from small numbers, a point of inflexion when the number of new individuals added to the population begins to decline, followed by fluctuation around some quasi-stable carrying capacity (K; Wolda 1989). It is plausible that in those time series where there was higher support for a density-independent model, the monitoring period in question corresponded mainly to either the exponential rise (exponential model) or the quasi-stable phase near K (random walk model), giving low support for density-dependent models describing all three phases (Dennis and Taper 1994, Zeng et al. 1998). Paradoxically then, species with low support for density dependence could in reality be strongly regulated, especially if other confounding exogenous factors not

included in our analysis (e.g., rainfall) mediate regulatory processes (Rothery et al. 1997, Dennis and Otten 2000). Moreover, the relationship between density and abundance may be difficult to measure when the expected per capita rate of change is relatively invariant over the population densities covered during the monitoring interval: Strong's (1986) concept of density "vagueness."

A persistent bugbear in the literature devoted to density dependence is the degree to which detection is confounded by sampling error. Large sampling errors
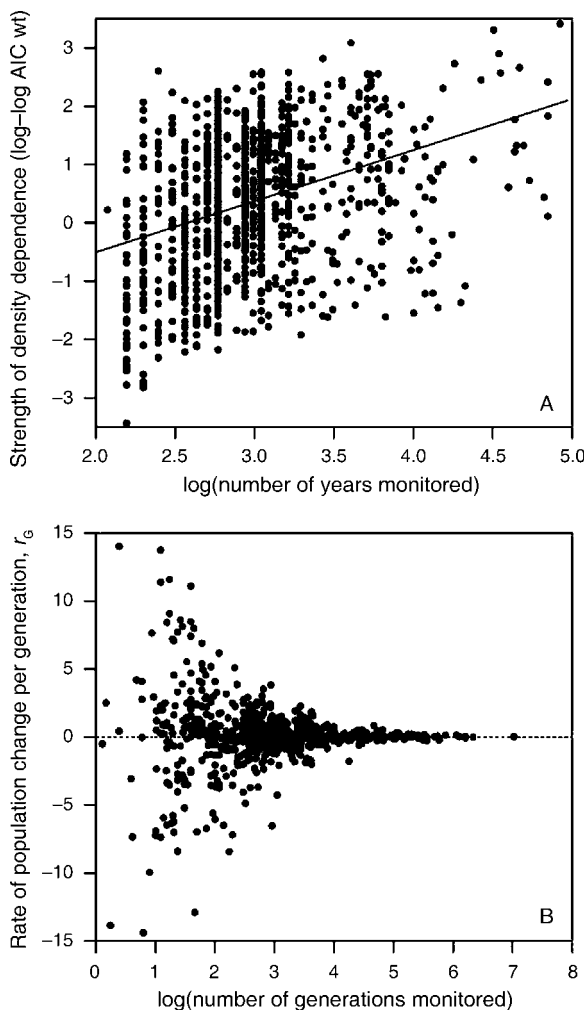

FIG. 2. Empirical relationship between density dependence and time series length for 1198 species. (A) Density regulation (complementary log–log transformation of summed Akaike's Information Criterion [AIC$_c$] weights for the three density-dependent models) plotted against the log of the number of years monitored. (B) Average rate of per-generational population change, r_G (log of the annual ratio of successive densities × generation length) plotted against the log of the number of generations monitored (number of observed annual transitions of population size ÷ generation length). The fitted line in (A) is a least-squares regression ($R^2 = 11.7\%$; AIC$_c$ evidence ratio vs. a zero slope $= 1.35 \times 10^{32}$); the dotted line in (B) represents zero net growth.

relative to actual changes in population density have been shown to inflate its spurious detection when applying various null hypothesis tests (Wolda and Dennis 1993, Shenk et al. 1998) because of first-order serial correlations in the observations (Pollard et al. 1987). Dennis and Taper (1994) found little effect of sampling error on the detection rate using the parametric bootstrap likelihood ratio test and, in fact, it appeared that sampling error increased their method's statistical power. Shenk et al. (1998) argued that a more appropriate evaluation is to assume a constant coefficient of variation rather than sampling error proportional to N. Our results comparing indirect- (i.e., presumably higher error) and direct-count data suggest that the MMI strength of evidence for density dependence is not increased erroneously by higher sampling error. The strongest MMI support was derived from the time series thought to be least affected by non-process error, and the marginal overlap in the confidence limits between the two groups suggests that sampling error reduces support for density dependence. Contrary to expectation for the NPHT, increased sampling error (1) did not spuriously inflate detection probability when using Pollard's randomization test (Pollard et al. 1987), nor (2) had any effect on the conclusions drawn from the PBLR test (Dennis and Taper 1994, Shenk et al. 1998).

Although a sustained quest of population ecology has been the search for increasingly robust tests for detecting density dependence in time series (Fox and Ridsdillsmith 1995), it is becoming more widely accepted that the reliable estimation of parameters in flexible population dynamics models, coupled with estimates of the relative importance of endogenous vs. exogenous contributions to population change, provide greater insight (Hanski et al. 1993, Turchin 1999). Berryman (1991) stressed that there is no good reason for defaulting arbitrarily to one particular outcome of the density dependence dichotomy (i.e., present or not). The evaluation of multiple models representing competing hypotheses is a philosophy better suited to an open world (Oreskes et al. 1994) that is neither entirely black (the density-independent hypothesis strictly true) or white (density independence is utterly untrue). MMI provides an analytical framework for examining the relative (not absolute) distance that any of a set of a priori hypotheses are from truth via AIC weights (Burnham and Anderson 2002). Although Zeng et al. (1998) rightly claimed that best-model selection only indicates whether data are more consistent with density dependence (or not), methods such as AIC weights or Bayesian model averaging (e.g., Wintle et al. 2003) allow inferences to be based on all models to provide a quantitative appraisal of the strength of evidence for the phenomenon (Hilborn and Mangel 1997), as demonstrated in this analysis.

CONCLUSION

The application of multi-model inference using information theory, best-model selection, and classic Neyman-Pearson hypothesis tests on an expansive empirical dataset of 1198 species abundance time series provides a convincing and broad-scale reinforcement of the theory that density dependence is a pervasive ecological process. Our findings also have important implications for models that attempt to describe the extinction probability of threatened species because density-dependent parameterization is a key modifier of extinction predictions (Ginzburg et al. 1990, Dennis and Taper 1994, Zeng et al. 1998, Drake 2005). We have made substantial progress towards achieving den Boer's (1991) "burden of proof," and as such, argue that density-dependent mechanisms should be considered valid components of hypotheses in any a priori model set that attempts to describe real-world population dynamical processes.

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REPORTS

APPENDIX

Methodological details for the data set used in this study (*Ecological Archives* E087-082-A1).

SUPPLEMENT

A data file of summary statistics of the population dynamics data set (*Ecological Archives* E087-082-S1).