

## The macroecology of population dynamics: taxonomic and biogeographic patterns in population cycles

Bruce E. Kendall,<sup>1</sup> John Prendergast,<sup>2</sup> and Ottar N. Bjørnstad<sup>1,3</sup>

<sup>1</sup>National Center for Ecological Analysis and Synthesis, University of California, 735 State St., Suite 300, Santa Barbara, California 93101-5504, U.S.A. After 1 January 1999: Donald Bren School of Environmental Science and Management, University of California, Santa Barbara, CA 93106, U.S.A. E-mail: kendall@nceas.ucsb.edu

<sup>2</sup>Centre for Population Biology, Imperial College at Silwood Park, Ascot, Berkshire, SL5 7PY, U.K.

<sup>3</sup>Division of Zoology, Biological Institute, University of Oslo, N-0316 Oslo, Norway.

### Abstract

Regular cycles in population abundance are fascinating phenomena, but are they common in natural populations? How are they distributed among taxa? Are there differences between different regions of the world, or along latitudinal gradients? Using the new Global Population Dynamics Database we analysed nearly 700 long (25 + years) time series of animal field populations, looking for large-scale patterns in cycles. Nearly 30% of the time series were cyclic. Cycle incidence varied among taxonomic classes, being most common in mammal and fish populations, but only in fish did cycle incidence vary among orders. Cycles were equally common in European and North American populations, but were more common in Atlantic fish than Pacific fish. The incidence of cycles increased with latitude in mammals only. There was no latitudinal gradient in cycle period, but cycle amplitude declined with latitude in some groups of fish. Even after considering the biases in the data source and expected type I error, population cycles seem common enough to warrant ecological attention.

### Keywords

Complex population dynamics, latitudinal gradients, long-term population data, population cycles, time-series analysis.

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### INTRODUCTION

Cycles in abundance have long fascinated population ecologists, and have helped shape modern theories of population regulation. Despite detailed studies of some highly cyclic species, however, the taxonomic or geographical extent of such periodic fluctuations remains unknown. Hassell *et al.*'s (1976) influential analysis led to a widespread view that cycles were uncommon in nature. Recent studies (Krukonis & Schaffer 1991; Ellner & Turchin 1995) uncovered many cyclic populations, but these were biased samples (the authors actively sought populations with oscillatory dynamics). An assessment of the commonness of population cycles would be valuable, given recent interest in the evolution of complex population dynamics (Ferriere & Gatto 1993; Rand *et al.* 1994; Doebeli & Koella 1995).

Population cycles have long been thought to be more likely at high latitudes (Dymond 1947). Recent models suggest that two latitudinally varying factors can influence population cycles: the strength of seasonality (Aron & Schwartz 1984; Rinaldi *et al.* 1993) and food-web complexity (Hanski *et al.* 1991; Turchin & Hanski 1997). Within cyclic populations, period scales with body size in herbivorous

birds and mammals (Calder 1983; Peterson *et al.* 1984; Krukonis & Schaffer 1991); given Bergmann's rule (body size increases with latitude), this suggests that period should increase with latitude in many animals. However, latitudinal gradients in cyclicality, period, and amplitude have only been reported in a few mammal and bird species (Butler 1951; Adams 1959; Buehler & Keith 1982; Potts *et al.* 1984; Angelstam *et al.* 1985; Hansson & Henttonen 1985; Williams 1985; Lindén 1988; Bjørnstad *et al.* 1995; Turchin 1996).

A major impediment to testing the generality of patterns in population cycles has been the apparent dearth of long-term data. An ongoing project assembling published population time series reveals that such data are now abundant. Taking advantage of this collection, we analysed 694 animal population time series to address three questions: How common are population cycles? Does the incidence of cycles vary among taxa? Are there general biogeographic patterns of cyclicality?

### MATERIALS AND METHODS

We analysed data from the Global Population Dynamics Database (GPDD), selecting time series of annual abun-

dances that are at least 25 years long, and eliminating time series that encompass extremely large areas. Very few such time series currently in the database are from the southern hemisphere (and none are from the tropics), so we analysed only northern populations. The GPDD contains 694 time series of 220 species (all animals) that fulfil these criteria.

We detrended each time series (with a LOESS smooth, using a span of half the data) and transformed the density to stabilize the variance (choosing the Box-Cox transform of 0, 1/4, 1/2, or 1 that minimized the squared residuals from the smooth). We performed spectral analysis using the Lomb normalized periodogram, allowing us to analyse time series with missing values (Lomb 1976; Press *et al.* 1992). We estimated the statistical significance of the spectral peak by  $P = 1 - (1 - e^{-z})^n$ , where  $z$  is the height of the peak and  $n$  is the number of points in the time series (Horne & Baliunas 1986; Press *et al.* 1992). We defined all populations with  $P < 0.05$  as ‘‘cyclic’’. We called a species cyclic if at least one population was cyclic; we also used a Bonferroni correction. For cyclic populations we recorded the period and measured the amplitude as  $s = \text{SD}(\log N)$ . We tested for differences (among taxonomic groups and locations) in the incidence of cycles with the  $G$ -test.

We used logistic regression to examine latitudinal patterns in the incidence of cycles. We performed ordinary least squares regression of period and amplitude on latitude for cyclic populations. We performed these regressions on the entire dataset, and within the best-represented taxonomic groups and geographical regions.

## RESULTS

Approximately 29% of the populations (representing 26%–31% of the species) exhibited statistically significant periodicity at a nominal 5% level (Table 1). The incidence

of cycles varied among taxonomic classes ( $G = 44.54$ , d.f. = 6,  $P \ll 0.001$ ), being most common in fish and mammal populations. Fully 70% of the fish and mammal species comprised at least one cyclic population (63% and 48% with Bonferroni correction). Only fish showed differences among taxonomic orders in the incidence of cycles ( $G = 6.42$ , d.f. = 2,  $P = 0.04$ ), with Gadiformes (cod) being most cyclic.

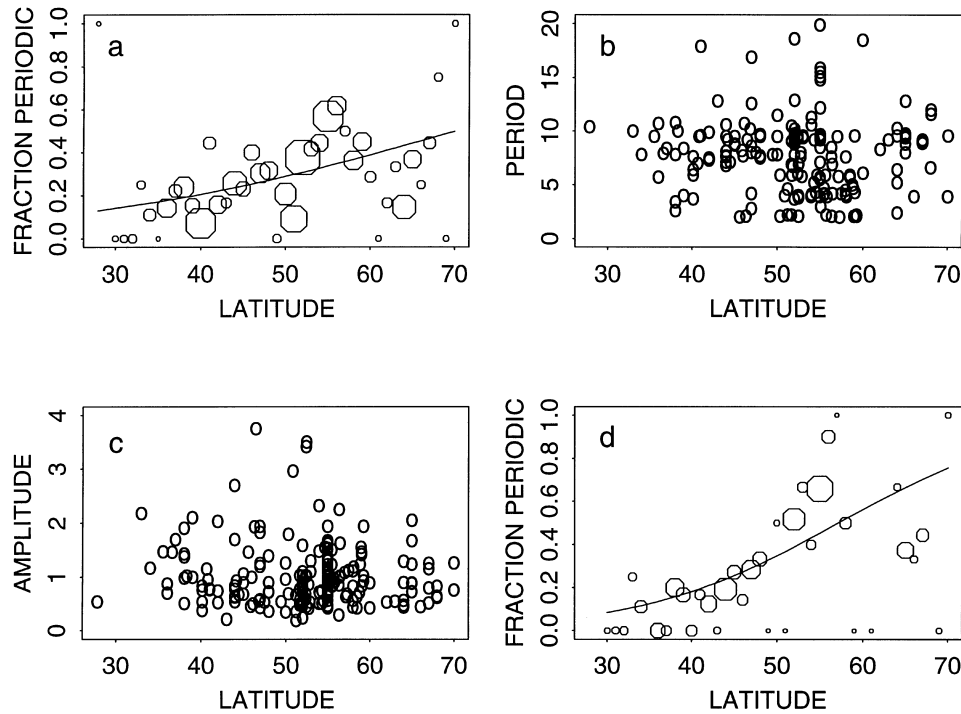
There were no detectable differences between European and North American terrestrial animals in the tendency to cycle. Among fish, Atlantic and North Sea populations were more likely to be periodic than Pacific populations ( $G = 11.05$ , d.f. = 2,  $P = 0.004$ ).

The fraction of cyclic populations increased with latitude up to about 55°N, tapering off at higher latitudes (Fig. 1). This pattern was caused entirely by the mammals, in particular by North American carnivores and British lagomorphs (Table 2). Across the whole dataset there were no latitudinal trends in cycle period or amplitude (Fig. 1), nor did period change with latitude within taxonomic classes or orders. Cycle amplitude declined with latitude in insects and in Atlantic, Pacific, and salmonid fish. A single highly variable population caused the insect pattern, but the fish patterns appeared to be genuine trends.

The mammalian latitudinal gradient in cycle incidence was confounded by the fact that time series length was also correlated with latitude (length =  $0.92 \times$  latitude,  $P \ll 0.01$ ) and cycle incidence was correlated with series length ( $\log[p/(1-p)] = -4.0 + 0.067 \times$  length,  $P \ll 0.01$ ). To control for these correlations, we repeated the analysis using just the first 30 years of each time series. The mammalian gradient in cycle incidence remained, although the slope was shallower ( $\log[p/(1-p)] = -4.5 + 0.066 \times$  latitude,  $P \ll 0.01$ ).

**Table 1** Distribution of periodic and nonperiodic populations and species among taxonomic classes of animals. Confidence intervals are based on the binomial likelihood function of the true probability given the observed incidence and sample size. Under species, the ‘‘raw’’ classification includes every species with at least one cyclic population; in the ‘‘Bonferroni’’ classification the critical significance level is divided by the number of populations in the species

Taxon	Populations			Species		
	Number	Number periodic	Fraction periodic (95% CI)	Number	Fraction periodic (95% CI)	
					Raw	Bonferroni
Birds	139	18	0.13 (0.08, 0.20)	89	0.18 (0.11, 0.27)	0.16 (0.10, 0.25)
Mammals	328	109	0.33 (0.28, 0.39)	27	0.70 (0.51, 0.84)	0.48 (0.31, 0.66)
Fish	129	56	0.43 (0.35, 0.52)	27	0.70 (0.51, 0.84)	0.63 (0.44, 0.78)
Insects	79	13	0.16 (0.10, 0.26)	68	0.17 (0.10, 0.28)	0.16 (0.09, 0.27)
Crustaceans	12	6	0.50 (0.25, 0.75)	3	0.33 (0.07, 0.81)	0.33 (0.07, 0.81)
Gastropods	3	1	0.33 (0.07, 0.81)	3	0.33 (0.07, 0.81)	0.33 (0.07, 0.81)
Bivalves	3	1	0.33 (0.07, 0.81)	3	0.33 (0.07, 0.81)	0.33 (0.07, 0.81)
All populations	694	204	0.29 (0.26, 0.33)	220	0.31 (0.26, 0.38)	0.26 (0.21, 0.33)



**Figure 1** Latitudinal patterns in population cycles. (a) The propensity to cycle. For each degree latitude, the fraction of populations that are cyclic at  $P < 0.05$  is shown; the area of the symbol is proportional to the number of populations it represents. The solid curve represents the logistic regression (Table 2). (b) The period of the cyclic populations. (c) The amplitude ( $s$ ) of the cyclic populations. (d) The latitudinal gradient in the propensity to cycle for mammals, with the logistic regression.

**Table 2** Latitudinal patterns in cycles for the taxonomic groups most abundant in the database. For each of fraction periodic and amplitude, we give the linear regression coefficient, the  $P$  value for a test of its difference from zero, and the number of populations

Taxon	Fraction periodic			Amplitude ( $s$ )		
	Slope	$P$	$n$	Slope	$P$	$n$
Birds	0.005	0.89	139	0.009	0.34	18
Galliformes	-0.020	0.84	16	0.027	0.48	5
Passeriformes	-0.044	0.51	70	-0.006	0.54	8
Mammals	0.088	<0.01	328	-0.009	0.12	109
Carnivora	0.098	<0.01	262	-0.008	0.18	96
Lagomorpha	28.849	<0.01	13	0.059	0.47	5
Rodentia	0.008	0.15	50	-0.026	0.14	10
Fish	-0.024	0.36	129	-0.011	0.39	56
Atlantic Ocean	-0.075	0.07	32	-0.014	0.05	16
North Sea	0.165	0.07	17	0.025	0.43	8
Pacific Ocean	-0.085	0.25	16	-0.054	0.03	6
Salmonidae	0.048	0.40	60	-0.090	0.03	24
Insects	-0.078	0.10	80	-0.116	0.03	13
Lepidoptera	-0.069	0.34	40	-0.243	0.03	8

**DISCUSSION**

Our analysis of 700 northern hemisphere animal population time series found that 30% of the populations were

cyclic. Cycles were most common in fish and mammals and less common in insects and birds. Cycle incidence did not differ between Europe and North America, but did differ among the oceans. Cycle incidence increased with

latitude in mammals alone. There were no latitudinal patterns in cycle period, and cycle amplitude declined with latitude in certain fish groups.

The populations studied here are certainly not a “random” sample of animal populations in general, although they were not selected for their dynamics. North American fur-bearing carnivores dominate the mammal data, and most of the fish are commercially harvested populations. Thus the higher incidence of cycles in mammals and fish might represent something special about harvested species (e.g. they tend to be high on the food chain), or even be a result of the harvesting activity. Within birds (which constitute the most representative sample) cycles seem particularly common in grouse, but are evenly distributed over taxonomic orders (Table 3). They are found in predatory, insectivorous, and granivorous species, ranging in size from the House Wren to the Whooping Crane.

We expect roughly 5% of the populations to be classified as cyclic just by chance. Cycle incidence substantially exceeds 5% in all major taxonomic groups. If we take birds as the most representative taxon, and subtract the 5% of potentially spurious results, we find cycles in 3%–15% of populations. Thus population cycles are sufficiently common to be of general ecological interest. This is in contrast to the apparent absence of delayed density dependence in a large collection of British insect populations (Woiwood & Hanski 1992); the difference may lie in the greater statistical power associated with the longer time series in this study. Using the first 24 years of each time series (the length of the longest series in Woiwood & Hanski), we detected periodicity in only 6% of the bird populations.

Our results suggest that there is no general latitudinal gradient in the incidence of population cycles. This may

reflect the absence of a universal latitudinal gradient in the relevant environmental variables. For example, ocean temperature variation declines towards the poles, and although many birds and insects can mitigate the effects of seasonality by migrating or diapausing, few of the mammals in this analysis do so. An important question for future work is whether the mammal gradient is general or restricted to North American carnivores, British lagomorphs, and Fennoscandian voles.

The absence of a latitudinal gradient in period is puzzling, given the known period–body size and body size–latitude relationships. Our taxonomic categorizations might be too crude, and careful attention to life history and ecological traits could produce different results. The latitudinal gradient in cycle amplitude is opposite to that observed in Fennoscandian voles (Hansson & Henttonen 1985; Turchin 1996).

The value of this broad-scale analysis of population time series is clear. As the GPDD continues to grow we may be able to correct the bias towards harvested populations in mammals and fish, and include tropical and southern populations. Some taxonomically and geographically extensive surveys, notably in birds and insects, will soon become long enough to be analysed in this way. Combining this sort of time-series analysis with information about the physiology, life history, and ecology of the species in question may allow us to go beyond pattern description and address generalities about the determinants of population dynamics.

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**Table 3** Distribution of periodic and nonperiodic populations and species among taxonomic orders of birds. Confidence intervals and species classifications as in Table 1

Taxon	Populations			Species		
	Number	Number periodic	Fraction periodic (95% CI)	Number	Fraction periodic (95% CI)	
					Raw	Bonferroni
Charabriiformes	5	1	0.20 (0.04, 0.64)	4	0.25 (0.05, 0.72)	0.25 (0.05, 0.72)
Ciconiiformes	1	0	0.00 (0.00, 0.84)	1	0.00 (0.00, 0.84)	0.00 (0.00, 0.84)
Columbiformes	5	0	0.00 (0.00, 0.46)	4	0.00 (0.00, 0.52)	0.00 (0.00, 0.52)
Cuculiformes	2	1	0.50 (0.09, 0.91)	2	0.50 (0.09, 0.91)	0.50 (0.09, 0.91)
Falconiformes	12	1	0.08 (0.02, 0.36)	8	0.12 (0.03, 0.48)	0.12 (0.03, 0.48)
Galliformes	16	5	0.31 (0.14, 0.56)	6	0.50 (0.18, 0.82)	0.33 (0.10, 0.71)
Gruiformes	1	1	1.00 (0.16, 1.00)	1	1.00 (0.16, 1.00)	1.00 (0.16, 1.00)
Passeriformes	70	8	0.11 (0.06, 0.21)	51	0.16 (0.08, 0.28)	0.14 (0.07, 0.26)
Pelecaniformes	12	0	0.00 (0.00, 0.25)	2	0.00 (0.00, 0.71)	0.00 (0.00, 0.71)
Piciformes	13	1	0.08 (0.02, 0.34)	8	0.12 (0.03, 0.48)	0.12 (0.03, 0.48)
Strigiformes	2	0	0.00 (0.00, 0.71)	2	0.00 (0.00, 0.71)	0.00 (0.00, 0.71)

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## BIOSKETCH

Bruce Kendall is a quantitative population ecologist working to understand the causes of population cycles, predict the fates of small populations, and explore the consequences of spatial structure for population dynamics.

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