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Physiological constraints on long-term population cycles: a broad-scale view

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ABSTRACT

Background: Long-term cycles in animal abundance impact the dynamics of most major ecosystems, yet the drivers of broad-scale variability in these cycles are unclear.

Aim: Examine potential relationships between the period of long-term population cycles and key life-history traits (generation time and its primary determinants – body mass and body temperature) across a broad range of primary consumer taxa (protists, zooplankton, insects, mammals, and birds).

Results: We find that long-term cycle periods vary predictably with generation time, body mass and temperature. Cycle periods decreased exponentially with increasing body temperature, and increased as a power law with increasing body mass.

Conclusions: These scaling relationships appear more consistent with predictions from models of population dynamics based on maternal effects than with those based on specialized consumer–resource interactions. More generally, the results provide a basis for understanding how changes in the size structure of populations, or the environmental temperatures populations experience, may affect their dynamics.

Keywords: macroecology, metabolic theory, population dynamics, climate change, global warming, scaling.

INTRODUCTION

Since Elton (1924) described long-term, periodic fluctuations in the abundance of animal populations nearly 100 years ago, this phenomenon has been a central focus of ecological research (Turchin, 2003; Ginzburg and Colyvan, 2004; Barraquand *et al.*, 2017; Jones, 2017). The period of these so-called 'long-term population cycles' may vary by orders of magnitude among the variety of taxa that exhibit them [e.g. protists, zooplankton, insects, mammals, and birds (Fenchel, 1982; Kendall *et al.*, 1998)], and thus have major impacts on the structure and function of ecosystems (Mattson and Addy, 1975; Holling, 1992; Ims and Fuglei, 2005; Benincà *et al.*, 2009) and their services to society [e.g. food security, sustainability (Kurz *et al.*, 2008; Murray *et al.*, 2013)]. For example, peak abundances in the 30-year cycles of *Choristoneura occidentalis* (western spruce budworm)

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may affect up to 5 million hectares of forest in a given year (Hofacker *et al.*, 1983). Thus, it is important to understand the factors that underlie heterogeneity in long-term population cycles, particularly in light of the potential for climate warming to decrease the period of cycles for groups such as insect pests (Volney and Fleming, 2000; Logan *et al.*, 2003).

Attempts to explain interspecific variation in long-term population cycle periods have generally led to two classes of explanations, both of which presume that cycles are produced by delayed negative feedback loops between population density and growth rate. The more classical ecological explanation argues that feedbacks are created by specialized consumer–resource interactions (e.g. predator–prey, host–parasite) (Lotka, 1925; Volterra, 1928; Turchin, 2003), but more recently researchers have suggested these feedbacks arise from density dependence in individual 'quality' (e.g. physiological state) that is transmitted across generations [i.e. maternal effects (Ginzburg and Taneyhill, 1994; Ginzburg and Colyvan, 2004)]. Importantly, both explanations predict that cycle periods depend in part on the life histories of species – albeit in somewhat different ways. Thus, broadly examining relationships between key life-history variables and long-term population cycle periods may help to distinguish between these hypotheses and, more generally, to link the biology of individual species to their long-term population dynamics.

Previous research in birds and mammals has suggested that long-term cycle periods depend strongly on species' biological time clocks such that smaller, short-lived animals cycle faster than larger, long-lived ones. This research was largely based on the observation that the cycle periods of species in these groups scale predictably with body mass as a power law, in a manner similar to other biological times [e.g. generation time (Calder, 1983; Peterson *et al.*, 1984; Krukonis and Schaffer, 1991; see also McNab, 1980)]. However, among invertebrates such as forest insects, body mass appears to explain little, if any, variation in long-term cycle periods (Hendriks and Mulder, 2012). Furthermore, cycle periods do not appear to scale with body mass across insects and endothermic vertebrates. For example, despite their relatively small body sizes, forest insects may cycle over decades – a period longer than many birds and mammals (Berryman, 1995; Högstedt *et al.*, 2005). This has led some to reject the generality of Calder's (1983) proposed link between cycle period and biological time clocks across taxa (Berryman, 1995; Högstedt *et al.*, 2005) in favour of other explanations, such as the lifespan of food resources (Högstedt *et al.*, 2005).

Here we perform a broad-scale analysis of the potential impacts of individual-level drivers of long-term population cycles across nearly the full range of primary consumer species known to exhibit cyclicity (protists, zooplankton, insects, mammals, and birds; 105 species). The dataset thus includes species from all major types of ecosystems (e.g. marine, freshwater, terrestrial), which span approximately 15 orders of magnitude in body mass and 40°C in body temperature. We focus on the potential effects of generation time and the primary determinants of generation time at broad scales: body mass and temperature. Biological rates and times, including generation time and intrinsic population growth rate, typically vary exponentially with temperature and as a power law with body mass as might be expected given their relationship to mass-specific metabolic rate (Gillooly *et al.*, 2001, 2002; Savage *et al.*, 2004; McCoy and Gillooly, 2008). We will specifically examine whether cycle periods (ρ; days) of diverse primary consumers vary in proportion to generation time (τ; days) and thus with body mass (M; grams) and temperature (T; degrees K) as:

$$\rho \propto \tau \propto M^{1/4} e^{0.65\left(\frac{1}{k}\left[\frac{1}{T}-\frac{1}{T_{20^\circ C}}\right]\right)} \quad (1)$$

where k is Boltzmann's constant ($8.62 * 10^{-5}$ eV/K) and 0.65 is the apparent average activation energy of metabolism (Gillooly *et al.*, 2001). For long-term population cycle periods, equation (1) describes a linear relationship with generation time, an exponential relationship with temperature, and a power law relationship with body mass. While we recognize that the proposed mass and temperature dependence shown in equation (1) remains a topic of debate, it is useful as a point of departure for explaining macroecological patterns related to individual-level physiology (see Dillon *et al.*, 2010 and references therein).

We have three primary objectives in performing this study. First, we wish to empirically evaluate any relationship between generation time and long-term population cycle periods. Generation time is often assumed to be related to cycle periods (e.g. Benincà *et al.*, 2011), but a relationship between these two variables has not been shown at this scale. Second, we wish to examine if long-term population cycles show the exponential temperature dependence described by equation (1). This would imply that a 10°C increase in temperature would lead to a roughly 250% decrease in cycle period (i.e. $Q_{10} \approx 2.5$). Previous work on *Daphnia* populations has shown relationships qualitatively consistent with this expectation (McCauley and Murdoch, 1987), but no broad-scale interspecific relationship has previously been described. We suspect that this proposed temperature dependence may explain why long-term cycle periods appear to scale with body mass within endothermic vertebrates, but not within invertebrate groups in some cases. Finally, we hope that our analyses will contribute to a better understanding of the ecological and evolutionary processes underlying variation in long-term cycle periods (e.g. maternal effects or specialized consumer–resource interactions).

METHODS

Data collection

We compiled data on long-term population cycles for field and laboratory populations of diverse species (insects, $n = 44$; protists, $n = 4$; zooplankton, $n = 7$; mammals, $n = 38$; birds, $n = 12$) that span a broad range of body temperatures (~0 to ~40°C) and body masses (~10^{-10} to ~10^{5} g). We obtained cycle period data from classical comparative studies (i.e. Calder, 1983; Peterson *et al.*, 1984; McCauley and Murdoch, 1987; Hanski *et al.*, 1991; Krukonis and Schaffer, 1991; Murdoch *et al.*, 2002; Högstedt *et al.*, 2005), and more recent studies of individual species. Studies used a variety of methods to distinguish periodic fluctuations in time series (e.g. spectral analysis, visual estimates, autocorrelation analysis). Since there is some debate as to the appropriate methodology (see, for example, Krukonis and Schaffer, 1991; Louca and Doebeli, 2015), we did not exclude any cycles because of methodology. Instead, we compiled data on statistical methodology and statistical support for periodicity to evaluate whether these variables affected the results. We restricted our analyses to cycles with periods greater than 4 generations, since this is the empirical threshold that is thought to separate short- and long-term cycles (Murdoch *et al.*, 2002; Turchin, 2003).

We limited long-term population cycles of zooplankton and protists to those observed in the laboratory because there is generally greater confidence in body temperatures and greater resolution of time series in laboratory studies of these organisms (McCauley and Murdoch, 1987). These laboratory studies used temperatures close to the species' preferred temperatures and allowed resource availability (e.g. algae for zooplankton) to fluctuate to mimic field conditions. While there are obviously still differences between the environmental conditions

experienced by these field and lab populations of zooplankton (e.g. temperature variability, photoperiod), previous studies using similar laboratory methods found the dynamics of lab populations to be comparable to those of field populations (McCauley and Murdoch, 1987; McCauley *et al.*, 1999).

For each species' cycle period, we collected data on adult body mass, body temperature, and generation time. Where direct estimates for body mass were not available, we estimated body mass using published length–weight regression equations [insects (Rogers *et al.*, 1976; Honěk, 1993); zooplankton (Peters and Downing, 1984)], or based on body volume measures assuming a density of water. Data for zooplankton and protists were from laboratory populations held at constant temperatures. Data for insects were primarily field measures from sites spanning a range of latitudes (65°N to −2°S). For these insects, we assume that body temperatures track environmental temperatures since their small body sizes generally preclude heat storage due to high convective heat loss (Stevenson, 1985). As it was not clear whether average annual environmental temperature or average growing season temperature (April–October in northern hemisphere; October–March in southern hemisphere) was the most appropriate environmental temperature to estimate insect body temperature, we performed analyses using both measures. In the main text we show results using average annual temperature, but we provide results using average growing season temperature in the Appendix (evolutionary-ecology.com/data/3111Appendix.pdf). We collected these temperature data from Worldclim (Hijmans *et al.*, 2005), which was averaged over a spatial area of ~10^6 hectares (e.g. Swetnam and Lynch, 1993; Candau *et al.*, 1998). For insects, we also included data for latitude. Latitude was important to consider in insects, since it is correlated both with environmental temperature and other factors that may influence cycle periods such as primary productivity or photoperiod. For mammals and birds, we used species-specific estimates of body temperature when available or, if not, the average body temperature of each class [mammals 36.4°C; birds 41.5°C (Clarke and Rothery, 2008)]. Finally, we collected species-specific data for generation time, defined here as the age at first reproduction of females, from a variety of sources that includes recent compilations for birds and mammals (Myhrvold *et al.*, 2015). All data and sources are given in the Appendix.

Statistical analyses

We evaluated model predictions (eqn. 1) regarding the relationship of long-term cycle periods to generation time, and to body mass and body temperature. We did so by fitting statistical models to natural log-transformed data using both ordinary least squares (OLS) and phylogenetic generalized least squares (PGLS) regression. To assess the relationship between cycle period (ρ, in days) and generation time (τ, in days), we used the following model (hereafter 'Model 1'):

$$\ln(\rho) = \ln(I) + \theta \ln(\tau),$$

where $\ln(I)$ is the intercept and θ is a parameter describing the generation time dependence of cycle period. We used 'Model 2' to assess the body mass (M, in grams) and temperature (T, in degrees K) dependence of cycle period (ρ, in days):

$$\ln(\rho) = \ln(I_o) + b\ln(M) + E\left(\frac{1}{k}\left[\frac{1}{T} - \frac{1}{T_{20^\circ C}}\right]\right).$$

where k is Boltzmann's constant, $\ln(I_o)$ is the intercept, and b and E are parameters describing the body mass and temperature dependence of cycle period, respectively. Equation (1) predicts that $\theta = 1$, $b = 0.25$, and $E = 0.65$. To plot the independent effect of temperature on cycle period, we 'body mass-corrected' cycle period as:

$$\ln(\rho/M^b) = \ln(I_o) + E\left(\frac{1}{k}\left[\frac{1}{T} - \frac{1}{T_{20^\circ C}}\right]\right),$$

where the slope E corresponds to the apparent activation energy in equation (1). Similarly, we 'temperature-corrected' cycle period to plot the independent effect of body mass on cycle period:

$$\ln\left(\rho/e^{E\left(\frac{1}{k}\left[\left(\frac{1}{T} - \frac{1}{T_{20^\circ C}}\right)\right]\right)}\right) = \ln(I_o) + b\ln(M).$$

These methods for body mass- and temperature-correcting cycle period follow from Brown *et al.* (2004).

We assessed the effects of generation time, body mass, and temperature on cycle periods within and across taxonomic groups. For analyses within groups, we considered three groups: (1) insects, (2) mammals and birds, and (3) zooplankton and protists. We chose to group mammals and birds together in our analyses to provide a sufficient range of body masses, and to remain consistent with previous studies of endotherms (Peterson *et al.*, 1984; Krukonis and Schaffer, 1991). Similarly, we chose to group zooplankton and protists together in part to provide a wider range of body masses and temperatures. More importantly, we grouped zooplankton and protists together because these populations were observed in the laboratory at constant temperatures, unlike all other populations. Thus, we avoid comparing the effects of variable temperature regimes in the field populations of insects to those of constant temperatures in the laboratory. Instead, we compare the relationships observed in each group to model predictions. Note that while growth under variable temperature regimes may affect features such as generation time in insects, any such effects do not vary predictably in either the magnitude or the direction of the effect (Colinet *et al.*, 2015).

We performed five analyses to evaluate the robustness of parameter estimates. First, we accounted for possible non-independence of data due to shared evolutionary history by performing PGLS regression analyses on data for median cycle period per species using the package 'nlme' in R (Pinheiro *et al.*, 2012). To do so, we built a phylogeny from the Open Tree of Life (Hinchliff *et al.*, 2015) using the R package 'rotl' (Michonneau *et al.*, 2016). This phylogeny included all species except *Lagopus lagopus*. We assumed Brownian trait evolution [implemented in PGLS using the R package 'ape' (Paradis *et al.*, 2004)] and equal branch lengths since divergence times of eukaryote taxa are uncertain (dos Reis *et al.*, 2015). Second, we accounted for potential pseudoreplication in data by using the R package 'boot' to perform an ordinary non-parametric bootstrapping procedure for both statistical models (Davison and Hinkley, 1997; Canty and Ripley, 2017) (see Appendix). Third, we performed analysis of covariance (ANCOVA) to evaluate possible effects of the following three categorical covariates on OLS parameter estimates (Krukonis and Schaffer, 1991): (1) the statistical methodology used to measure periodicity in time series [spectral or global wavelet analysis, average time between peaks or troughs in abundance (i.e. subjective), autocorrelation analysis, or other methods]; (2) the statistical

significance attributed to a cycle ($P < 0.05$, $P > 0.05$, and statistical significance not assessed); and (3) the number of cycles observed in the time series [< 3 or > 3 cycles observed (Kendall *et al.*, 1998; Murdoch *et al.*, 2002)] (see Appendix). Fourth, we examined potential effects of latitude on insect cycle period by performing multiple linear regression analyses to assess the combined effect of latitude, mass, and temperature on cycle period. Finally, we assessed the effect of our estimate for insect body temperature (i.e. average annual temperature vs. average growing season temperature) on the body mass and temperature dependence of cycle period within insects and across groups by performing analyses using both estimates for insect body temperature (see Appendix).

RESULTS

Long-term population cycle periods generally showed the functional relationships with generation time, and body mass and temperature, described by equation (1). Across all species, generation time explained 87% of the variation in cycle periods (OLS) and 75% of the variation in median cycle periods (PGLS; Fig. 1, Table 1). Yet, both OLS and PGLS analyses yielded slopes of ln(cycle period) vs. ln(generation time) that were significantly less than 1 (OLS: $n = 322$, $\theta = 0.87$, 95% CI = 0.83 to 0.91; PGLS: $n = 104$, $\theta = 0.73$, 95% CI = 0.59 to 0.89). Results of the bootstrapping procedure showed little bias in regression parameters for Model 1 within and across groups [the greatest bias in θ (i.e. generation time parameter) was observed within insects: $\sim 10^{-2}$; see Appendix]. Furthermore, ANCOVA analyses showed only minor deviations in OLS parameter estimates for Model 1 related to methodological covariates (see Appendix). Long-term cycle periods also showed strong relationships with body mass and temperature across all taxa, as described by equation (1) (Table 1, Fig. 2). Together, these two variables explained 89% of the variation in cycle periods, as shown by OLS regression, and 69% of the variation in median cycle period (PGLS; Table 1). For body mass, after accounting for effects of temperature, the observed slope did not differ significantly from the predicted value of $b = 0.25$ using PGLS analysis ($n = 104$, $b = 0.24$, 95% CI = 0.18 to 0.30; Table 1) and showed only a slightly steeper slope using OLS analysis ($n = 322$, $b = 0.31$, 95% CI = 0.30 to 0.32; Fig. 2a, Table 1). With respect to temperature, we observed a linear relationship between ln(body mass-corrected cycle period) and inverse temperature, with a slope that did not differ significantly from the predicted value of 0.65 in the case of OLS (OLS: $n = 322$, $E = 0.65$, 95% CI = 0.61 to 0.69; PGLS: $n = 104$, $E = 0.43$, 95% CI = 0.25 to 0.61; Fig. 2b, Table 1).

However, ANCOVA analyses revealed significant but minor effects of statistical methodology on OLS estimates for the temperature dependence of cycle period across taxa (see Appendix). Specifically, the subset of data that determined period length by spectral analysis showed a slope of $E = 0.57$ ($n = 173$; 95% CI = 0.5 to 0.64), whereas the subset of periods estimated simply as the average time between peaks or troughs showed a slope of $E = 0.72$ ($n = 117$, 95% CI = 0.66 to 0.78). In addition, OLS estimates of E were significantly affected by covariate 2, the statistical significance attributed to a cycle, with E varying from 0.56 in statistically significant cycles ($n = 103$, 95% CI = 0.47 to 0.65) to 0.70 in cycles that did not have an assessment of statistical support ($n = 162$, 95% CI = 0.65 to 0.75) to 0.31 in cycles that were not deemed statistically significant ($n = 57$, 95% CI = 0.16 to 0.45; see Appendix). The bootstrapping procedure found little bias in the OLS parameter estimates for these relationships (the estimated biases for b and E were $\sim 10^{-4}$; see Appendix).

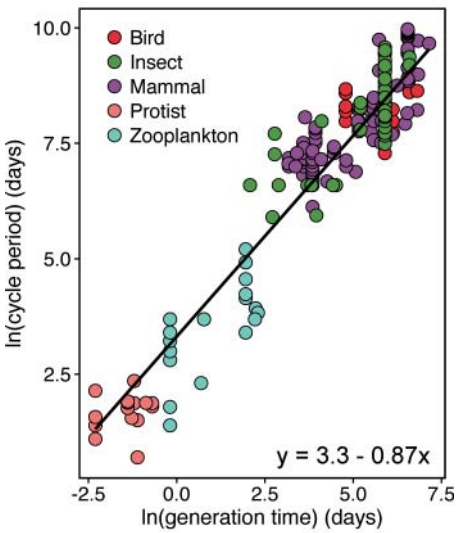

Fig. 1. Effect of the natural logarithm of generation time on the natural logarithm of long-term population cycle periods.

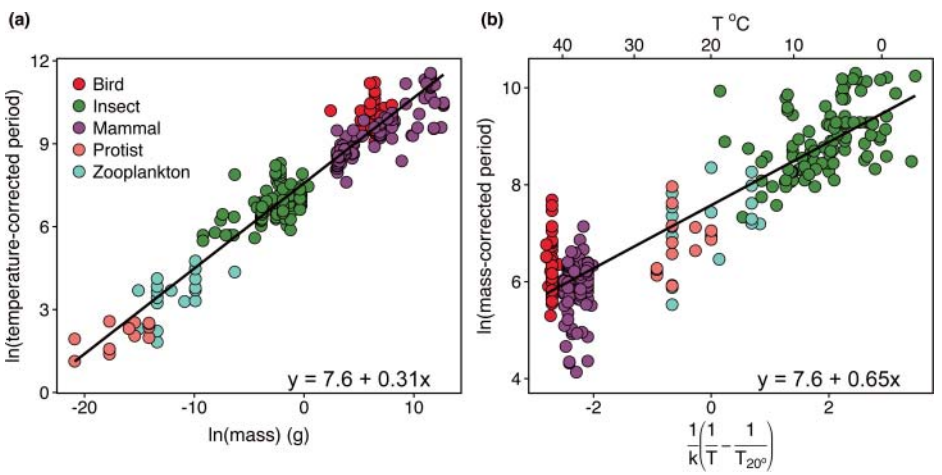

Fig. 2. The effect of body mass and body temperature on cycle periods across all taxa. (a) The natural logarithm of body mass vs. the natural logarithm of body temperature-corrected cycle period $\left(\text{days}/e^{\frac{0.65}{k}\left[\frac{1}{T}-\frac{1}{T_{20°C}}\right]}\right)$; (b) the inverse of absolute temperature vs. the natural logarithm of body mass-corrected cycle period ($\text{days}/g^{0.31}$).

Table 1. Summary of OLS and PGLS regression analyses for Model 1 and Model 2 within and across groups (i.e. insects, zooplankton, protists, mammals, and birds)

			Model 1: $\ln(\rho) = \ln(I) + \theta \ln(\tau)$				
	n	df	$\ln(I)$	P	θ	P	R^2
All groups							
PGLS	104	102	3.5 (2.4, 4.6)	**	0.73 (0.59, 0.89)	**	0.75
OLS	322	320	3.3 (3.1, 3.5)	**	0.87 (0.83, 0.91)	**	0.87
Insects							
PGLS	44	42	4.2 (2.6, 5.7)	**	0.74 (0.48, 1.00)	**	0.66
OLS	119	117	4.9 (4.2, 5.6)	**	0.56 (0.43, 0.70)	**	0.39
Zooplankton/protists							
PGLS	11	9	2.6 (1.7, 3.5)	**	0.55 (0.26, 0.85)	0.01	0.77
OLS	36	34	2.7 (2.5, 2.9)	**	0.68 (0.53, 0.83)	**	0.72
Mammals/birds							
PGLS	49	47	4.9 (3.3, 6.7)	**	0.57 (0.33, 0.81)	**	0.58
OLS	167	165	5.0 (4.6, 5.4)	**	0.58 (0.51, 0.66)	**	0.61

			Model 2: $\ln(\rho) = \ln(I_o) + b\ln(M) + E\left(\frac{1}{k}\left[\frac{1}{T} - \frac{1}{T_{20^\circ C}}\right]\right)$							
	n	df	$\ln(I_o)$	P	b	P	E	P	R^2
All groups									
PGLS	104	101	7.1 (5.9, 8.2)	**	0.24 (0.18, 0.30)	**	0.43 (0.25, 0.61)	**	0.69
OLS	322	319	7.6 (7.5, 7.6)	**	0.31 (0.30, 0.32)	**	0.65 (0.61, 0.69)	**	0.89
Insects									
PGLS	44	41	8.2 (6.8, 9.5)	**	0.23 (0.08, 0.37)	**	0.41 (0.20, 0.61)	**	0.65
OLS	119	116	7.6 (7.3, 8.0)	**	0.17 (0.12, 0.21)	**	0.48 (0.34, 0.62)	**	0.48
Zooplankton/protists									
PGLS	11	8	5.9 (3.9, 7.8)	**	0.21 (0.08, 0.33)	0.01	0.69 (0.16, 1.2)	0.03	0.81
OLS	36	33	5.9 (4.9, 6.9)	**	0.21 (0.14, 0.28)	**	0.89 (0.47, 1.3)	**	0.74
Mammals/birds									
PGLS	49	47	7.1 (5.7, 8.5)	**	0.16 (0.04, 0.28)	0.01	N/A[#]		0.34
OLS	167	165	6.5 (6.3, 6.7)	**	0.24 (0.21, 0.26)	**	N/A[#]		0.65

Note: Lower and upper bounds of the 95% confidence interval for each parameter estimate are noted within parentheses. Values of $P < 0.01$ are noted with asterisks.

[#] We did not assess the body temperature dependence of cycle period in mammals and birds because species in these groups do not span a sufficient range of temperatures.

Within groups, the body mass and temperature dependencies of cycle period were similar to those observed across all taxa. For body mass, our results corroborate the previously observed quarter-power body mass scaling of cycle period in mammals and birds [OLS: $n = 167$, $b = 0.24$, 95% CI = 0.21 to 0.26; PGLS: $n = 49$, $b = 0.16$, 95% CI = 0.04 to 0.28 (Calder, 1983; Peterson *et al.*, 1984; Krukonis and Schaffer, 1991)]. Within the insect and zooplankton/protist groups, cycle period scaled similarly to body mass (Table 1). In both groups, the

slopes were close to the predicted value of $b = 0.25$, or were not significantly different from this value, depending on whether OLS or PGLS was used (Fig. 3a,c, Table 1).

The relationship of cycle period to temperature in insects (Fig. 3b) and zooplankton and protists (Fig. 3d) was also consistent with the overall relationship across taxa shown in Fig. 2b and described by equation (1). While the estimated slope describing this relationship in insects was slightly shallower than the predicted $E = 0.65$ (OLS: $n = 119$, $E = 0.48$, 95% CI = 0.34 to 0.62; PGLS: $n = 44$, $E = 0.41$, 95% CI = 0.20 to 0.61), the slope for zooplankton and protists was indistinguishable from the predicted apparent activation energy, $E = 0.65$ (OLS: $n = 36$, $E = 0.89$, 95% CI = 0.47 to 1.3; PGLS: $n = 11$, $E = 0.69$, 95% CI = 0.16 to 1.2).

In considering the results shown in Table 1 and Figs. 1–3, and given the macro-scale

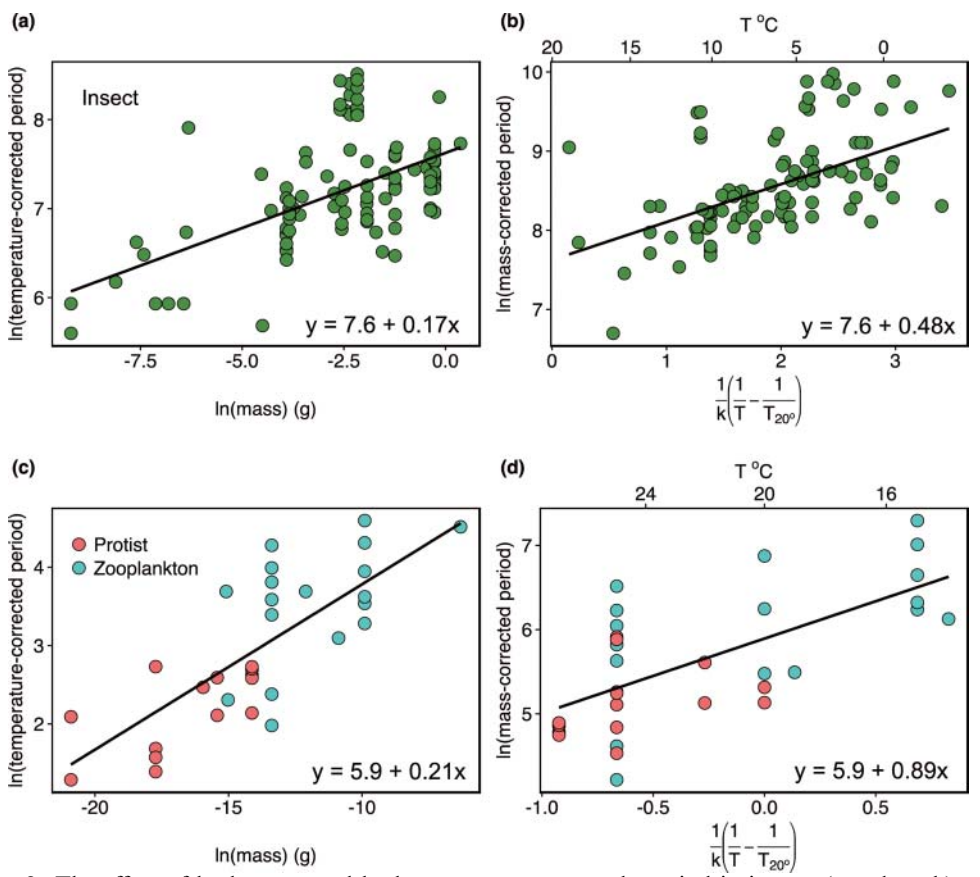

Fig. 3. The effect of body mass and body temperature on cycle period in insects (panels a, b) and in protists and zooplankton (panels c, d). Panels (a, c) show the effect of the natural logarithm of body mass on the natural logarithm of body temperature-corrected cycle period $\left(\text{days}/e^{\frac{E}{k}\left[\frac{1}{T}-\frac{1}{T_{20^\circ C}}\right]}\right)$ in insects and in protists/zooplankton, respectively. Panels (b, d) show the effect of inverse absolute temperature on the natural logarithm of body mass-corrected cycle period (days/g^b) for insects and for protists/zooplankton, respectively. Cycle periods were corrected for body mass and temperature using the values of E and b estimated for the respective group (Table 1).

nature of the study, it is important to consider at least three additional factors given their potential to affect the results. First, with respect to our estimates of body temperature in insects, we found that the observed temperature dependence described above using average annual temperature was quantitatively similar to that using average growing season temperature both for insects alone (OLS: $n = 119$, $E = 0.59$, 95% CI = 0.39 to 0.79; see Appendix, Fig. S1) and across all taxa (OLS: $n = 326$, $E = 0.84$, 95% CI = 0.78 to 0.90; see Appendix, Fig. S2). Second, within insects we found no significant effect of latitude after accounting for the effects of body mass and temperature (see Appendix, Table S1). Third and finally, our results within taxa appear to be quite robust to any effects of methodological covariates, potential biases related to pseudoreplication in data, and grouping of species for comparisons (e.g. considering zooplankton and protists together or separately; see Appendix, Table S10).

DISCUSSION

Our results show that variation in long-term population cycle periods among diverse primary consumers correlates very well with generation time and its determinants – body mass and body temperature – as described by equation (1). Thus, these cycle periods are approximately inversely proportional to species' mass-specific metabolic rates and the population-level processes controlled by metabolic rate, including generation time (Gillooly *et al.*, 2002), intrinsic population growth rate (Savage *et al.*, 2004), and natural mortality rate (McCoy and Gillooly, 2008).

However, we do not mean to imply that generation time, or body mass and temperature alone, are solely responsible for variation in cycle periods. These factors appear to be of primary importance at broad scales (e.g. from protists to mammals; Figs. 1–3), whereas other factors may explain variation in cycle periods at smaller scales. For example, small differences in the period of lemming or vole abundance cycles across northern Europe (e.g. 1–2 years) may reflect interactions with marine ecosystems (Oksanen *et al.*, 2013), geographic variation in the abundance of generalist predators (Hanski *et al.*, 1991), and/or seasonal forcing (Taylor *et al.*, 2013). Syntheses of research on long-term population cycles suggest that a broad suite of endogenous (i.e. density-dependent) and exogenous (i.e. density-independent) factors interact in complex ways to ultimately determine period length (Kendall *et al.*, 1999; Barraquand *et al.*, 2017). Perhaps these complexities explain why cycle period was found to be sublinearly related to generation time (i.e. scaling exponent < 1), contrary to predictions. Moreover, one must keep in mind that our analyses and conclusions pertain to the drivers of heterogeneity in primary consumer cycle periods – the processes that initially cause a population to cycle in abundance over long time scales is a separate question (Calder, 1983).

Still, our results show cycle periods do increase systematically with species' generation time across vertebrate and invertebrate ectotherms and endotherms (Fig. 1), as generally expected from models of population dynamics (see, for example, Turchin, 2003; Ginzburg and Colyvan, 2004). The observed body mass dependence of cycle periods provides further support for equation (1). Previous research has linked long-term population cycle periods to body mass within taxonomic groups, primarily mammals and birds (Calder, 1983; Peterson *et al.*, 1984; Krukonis and Schaffer, 1991), and to a lesser extent within insects, zooplankton, and protists (Hendriks and Mulder, 2012). We show that the body mass dependence of cycle period largely applies within and across all primary consumer groups exhibiting cyclicity, but only after accounting for the effects of temperature.

Temperature has largely been overlooked as a factor that contributes to interspecific differences in long-term population cycle periods, but the effect can be substantial. Our results show that periods decline by a factor of ~2.5 with a 10°C increase in temperature. We therefore speculate that these temperature effects may have special relevance in considering the effects of climate warming on communities and ecosystems. Note that they are qualitatively consistent with recent predictions that climate warming will increase the frequency of outbreaks for insect pests (Volney and Fleming, 2000; Logan *et al.*, 2003). For example, our results point to the potential for differences in response to warming between endothermic and ectothermic animals, since only ectothermic animals would be expected to show exponential decreases in cycle period due to increases in environmental temperature given the relatively constant body temperatures of endotherms. And importantly, the magnitude of the response to rising temperatures in ectotherms will depend on their operative body temperature (Dillon *et al.*, 2010). For example, given the exponential temperature dependence, a 5°C increase in average annual temperature for an insect species at ~25°C may lead to a decline in cycle period of ~34%, whereas the same increase in temperature for a species at ~5°C may yield a decline in cycle period of ~38% based on predictions from equation (1). Note, too, that rising temperature may indirectly affect cycle periods through effects on body size, albeit in less predictable and likely less substantial ways, in both ectotherms (Forster *et al.*, 2012; Horne *et al.*, 2015) and endotherms (Gardner *et al.*, 2011; Buckley *et al.*, 2012). In the case of ectotherms, however, effects on body size would likely be minor relative to the direct, kinetic effects of temperature. For example, a species would have to increase in mass by upwards of 40% for each °C to compensate for the exponential effects of temperature – a temperature–size relationship much greater than typically observed (Horne *et al.*, 2015).

The relationships between these individual-level traits and long-term population cycle periods shown here (Figs. 1–3, Table 1) may also help to understand the processes driving heterogeneity in long-term population cycle periods. Specifically, our results may inform recent debates regarding whether long-term cycles tend to be driven by density feedbacks related to consumer–resource interactions or maternal effects (Turchin, 2003; Ginzburg and Colyvan, 2004). To begin, our results do not appear consistent with an explanation based on interactions between primary consumers and food plant quality, since this explanation does not predict the strong body mass or temperature dependence across insects, mammals, and birds observed here (Högstedt *et al.*, 2005). Furthermore, our results appear inconsistent with predictions of consumer–resource models, specifically Lotka-Volterra (LV) and Rosenzweig-MacArthur (RM) models. Populations engaged in sustained oscillations following LV and RM dynamics cycle with a period approximately proportional to $1/\sqrt{rm}$, where r is the intrinsic population growth rate of the resource and m is the natural mortality rate of consumers (Lotka, 1925; Volterra, 1928; Yodzis and Innes, 1992; see also Schaffer *et al.*, 2001; Weitz and Levin, 2006; Hendriks and Mulder, 2012). Given that both r and m scale as

$$M^{-0.25}\, e^{\frac{-0.65}{k}\left[\frac{1}{T}-\frac{1}{T_{20^\circ C}}\right]}$$

(Savage *et al.*, 2004; McCoy and Gillooly, 2008), LV or RM models would generally predict a scaling of approximately

$$M^{0.125}\, e^{\frac{0.325}{k}\left[\frac{1}{T}-\frac{1}{T_{20^\circ C}}\right]}$$

for cycle periods of primary consumer species regardless of whether these species play the role of consumer or resource (Yodzis and Innes, 1992; but see Schaffer *et al.*, 2001). This predicted scaling is somewhat shallower than we observed here for primary consumers (Figs. 2, 3). The relationships shown in Figs. 1–3 appear more consistent with maternal effects models, which predict a one-to-one relationship between cycle period and generation time [assuming maximum per-capita offspring production per generation varies little across taxa (Ginzburg and Taneyhill, 1995; Ginzburg and Colyvan, 2004)].

However, it may also be informative to set aside the question of whether one process largely governs variability in long-term cycle periods, and consider how this variability may reflect interactions between multiple processes. Recent perspectives suggest that the diversity of long-term cycles reflects interactions among processes such as density-dependent evolution in life-history traits, pairwise consumer–resource interactions, and environmental stochasticity (Barraquand *et al.*, 2017). The expected relationships between individual-level life history and long-term cycle periods, however, are less clear under this more complicated view. The general scaling relationships described here may be useful as a point of departure for understanding how complex ecological and evolutionary processes combine to determine heterogeneity in periodic population fluctuations across diverse ecosystems.

DATA ACCESSIBILITY

All data for this study are publically available at: evolutionary-ecology.com/data/3111Appendix.pdf.

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REFERENCES

Barraquand, F., Louca, S., Abbott, K.C., Cobbold, C.A., Cordoleani, F., DeAngelis, D.L. *et al.* 2017. Moving forward in circles: challenges and opportunities in modelling population cycles. *Ecol. Lett.*, **20**: 1074–1092.

Benincà, E., Dakos, V., Van Nes, E.H., Huisman, J. and Scheffer, M. 2011. Resonance of plankton communities with temperature fluctuations. *Am. Nat.*, **178**: E85–E95.

Benincà, E., Jöhnk, K.D., Heerkloss, R. and Huisman, J. 2009. Coupled predator–prey oscillations in a chaotic food web. *Ecol. Lett.*, **12**: 1367–1378.

Berryman, A.A. 1995. Population cycles: a critique of the maternal and allometric hypotheses. *J. Anim. Ecol.*, **64**: 290–293.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. and West, G.B. 2004. Toward a metabolic theory of ecology. *Ecology*, **85**: 1771–1789.

Buckley, L.B., Hurlbert, A.H. and Jetz, W. 2012. Broad-scale ecological implications of ectothermy and endothermy in changing environments. *Global Ecol. Biogeogr.*, **21**: 873–885.

Calder, W.A. 1983. An allometric approach to population cycles of mammals. *J. Theor. Biol.*, **100**: 275–282.

Candau, J.-N., Fleming, R.A. and Hopkin, A. 1998. Spatiotemporal patterns of large-scale defoliation caused by the spruce budworm in Ontario since 1941. *Can. J. Forest Res.*, **28**: 1733–1741.

Canty, A. and Ripley, B. 2017. boot: Bootstrap R (S-Plus) Functions. R package v.1.3-12 [https://cran.r-project.org/web/packages/boot/].

Clarke, A. and Rothery, P. 2008. Scaling of body temperature in mammals and birds. *Funct. Ecol.*, **22**: 58–67.

Colinet, H., Sinclair, B.J., Vernon, P. and Renault, D. 2015. Insects in fluctuating thermal environments. *Ann. Rev. Entomol.*, **60**: 123–140.

Davison, A.C. and Hinkley, D.V. 1997. *Bootstrap Methods and Their Application*. Cambridge: Cambridge University Press.

Dillon, M.E., Wang, G. and Huey, R.B. 2010. Global metabolic impacts of recent climate warming. *Nature*, **467**: 704–706.

dos Reis, M., Thawornwattana, Y., Angelis, K., Telford, M.J., Donoghue, P.C. and Yang, Z. 2015. Uncertainty in the timing of origin of animals and the limits of precision in molecular timescales. *Curr. Biol.*, **25**: 2939–2950.

Elton, C.S. 1924. Periodic fluctuations in the numbers of animals: their causes and effects. *J. Exp. Biol.*, **2**: 119–163.

Fenchel, T. 1982. Ecology of heterotrophic microflagellates. IV. Quantitative occurrence and importance as bacterial consumers. *Mar. Ecol. Progr. Ser.*, **9**: 35–42.

Forster, J., Hirst, A.G. and Atkinson, D. 2012. Warming-induced reductions in body size are greater in aquatic than terrestrial species. *Proc. Natl. Acad. Sci. USA*, **109**: 19310–19314.

Gardner, J.L., Peters, A., Kearney, M.R., Joseph, L. and Heinsohn, R. 2011. Declining body size: a third universal response to warming? *Trends Ecol. Evol.*, **26**: 285–291.

Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M. and Charnov, E.L. 2001. Effects of size and temperature on metabolic rate. *Science*, **293**: 2248–2251.

Gillooly, J.F., Charnov, E.L., West, G.B., Savage, V.M. and Brown, J.H. 2002. Effects of size and temperature on developmental time. *Nature*, **417**: 70–73.

Ginzburg, L. and Colyvan, M. 2004. *Ecological Orbits: How Planets Move and Populations Grow*. New York: Oxford University Press.

Ginzburg, L.R. and Taneyhill, D.E. 1994. Population cycles of forest Lepidoptera: a maternal effect hypothesis. *J. Anim. Ecol.*, **63**: 79–92.

Ginzburg, L.R. and Taneyhill, D.E. 1995. Higher growth rate implies shorter cycle, whatever the cause: a reply to Berryman. *J. Anim. Ecol.*, **64**: 294–295.

Hanski, I., Hansson, L. and Henttonen, H. 1991. Specialist predators, generalist predators, and the microtine rodent cycle. *J. Anim. Ecol.*, **60**: 353–367.

Hendriks, A.J. and Mulder, C. 2012. Delayed logistic and Rosenzweig–MacArthur models with allometric parameter setting estimate population cycles at lower trophic levels well. *Ecol. Complex.*, **9**: 43–54.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. and Jarvis, A. 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.*, **25**: 1965–1978.

Hinchliff, C.E., Smith, S.A., Allman, J.F., Burleigh, J.G., Chaudhary, R., Coghill, L.M. *et al.* 2015. Synthesis of phylogeny and taxonomy into a comprehensive tree of life. *Proc. Natl. Acad. Sci. USA*, **112**: 12764–12769.

Hofacker, T.H., Loomis, R.C. and Tucker, S. 1983. *Forest Insect and Disease Conditions in the United States, 1982*. US Forest Service, Forest Pest Management.

Högstedt, G., Seldal, T. and Breistøl, A. 2005. Period length in cyclic animal populations. *Ecology*, **86**: 373–378.

Holling, C.S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecol. Monogr.*, **62**: 447–502.

Honěk, A. 1993. Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos*, **66**: 483–492.

Horne, C.R., Hirst, A. and Atkinson, D. 2015. Temperature-size responses match latitudinal-size clines in arthropods, revealing critical differences between aquatic and terrestrial species. *Ecol. Lett.*, **18**: 327–335.

Ims, R.A. and Fuglei, E. 2005. Trophic interaction cycles in tundra ecosystems and the impact of climate change. *Bioscience*, **55**: 311–322.

Jones, S.D. 2017. Population cycles, disease, and networks of ecological knowledge. *J. Hist. Biol.*, **50**: 357–391.

Kendall, B.E., Prendergast, J. and Bjørnstad, O.N. 1998. The macroecology of population dynamics: taxonomic and biogeographic patterns of population cycles. *Ecol. Lett.*, **1**: 160–164.

Kendall, B.E., Briggs, C.J., Murdoch, W.W., Turchin, P., Ellner, S.P., McCauley, E. *et al.* 1999. Why do populations cycle? A synthesis of statistical and mechanistic modeling approaches. *Ecology*, **80**: 1789–1805.

Krukonis, G. and Schaffer, W. 1991. Population cycles in mammals and birds: does periodicity scale with body size? *J. Theor. Biol.*, **148**: 469–493.

Kurz, W.A., Stinson, G., Rampley, G.J., Dymond, C.C. and Neilson, E.T. 2008. Risk of natural disturbances makes future contribution of Canada's forests to the global carbon cycle highly uncertain. *Proc. Natl. Acad. Sci. USA*, **105**: 1551–1555.

Logan, J.A., Régnière, J. and Powell, J.A. 2003. Assessing the impacts of global warming on forest pest dynamics. *Front. Ecol. Environ.*, **1**: 130–137.

Lotka, A.J. 1925. *Elements of Physical Biology*. Baltimore, MD: Williams & Wilkins.

Louca, S. and Doebeli, M. 2015. Detecting cyclicity in ecological time series. *Ecology*, **96**: 1724–1732.

Mattson, W.J. and Addy, N.D. 1975. Phytophagous insects as regulators of forest primary production. *Science*, **190**: 515–522.

McCauley, E. and Murdoch, W.W. 1987. Cyclic and stable populations: plankton as paradigm. *Am. Nat.*, **129**: 97–121.

McCauley, E., Nisbet, R.M., Murdoch, W.W., de Roos, A.M. and Gurney, W.S. 1999. Large-amplitude cycles of *Daphnia* and its algal prey in enriched environments. *Nature*, **402**: 653–656.

McCoy, M.W. and Gillooly, J.F. 2008. Predicting natural mortality rates of plants and animals. *Ecol. Lett.*, **11**: 710–716.

McNab, B.K. 1980. Food habits, energetics, and the population biology of mammals. *Am. Nat.*, **116**: 106–124.

Michonneau, F., Brown, J.W. and Winter, D.J. 2016. rotl: an R package to interact with the Open Tree of Life data. *Meth. Ecol. Evol.*, **7**: 1476–1481.

Murdoch, W., Kendall, B., Nisbet, R., Briggs, C., McCauley, E. and Bolser, R. 2002. Single-species models for many-species food webs. *Nature*, **417**: 541–543.

Murray, D.A., Clarke, M.B. and Ronning, D.A. 2013. Estimating invertebrate pest losses in six major Australian grain crops. *Austral Entomol.*, **52**: 227–241.

Myhrvold, N.P., Baldridge, E., Chan, B., Sivam, D., Freeman, D.L. and Ernest, S. 2015. An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology*, **96**: 3109.

Oksanen, T., Oksanen, L., Söderbacka, G., Hoset, K.S., Ruffino, L. and Tuomi, M. 2013. Impact of marine-subsidized predators on lemming–plant oscillations. *Evol. Ecol. Res.*, **15**: 1–24.

Paradis, E., Claude, J. and Strimmer, K. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, **20**: 289–290.

Peters, R.H. and Downing, J.A. 1984. Empirical analysis of zooplankton filtering and feeding rates. *Limnol. Oceanogr.*, **29**: 763–784.

Peterson, R., Page, R. and Dodge, K. 1984. Wolves, moose, and the allometry of population cycles. *Science*, **224**: 1350–1353.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. and Team, R.C. 2012. nlme: Linear and Nonlinear Mixed Effects Models. R package v.31–120.

Rogers, L.E., Hinds, W. and Buschbom, R.L. 1976. A general weight vs. length relationship for insects. *Ann. Entomol. Soc. Am.*, **69**: 387–389.

Savage, V.M., Gillooly, J.F., Brown, J.H., West, G.B. and Charnov, E.L. 2004. Effects of body size and temperature on population growth. *Am. Nat.*, **163**: 429–441.

Schaffer, W., Pederson, B., Moore, B., Skarpaas, O., King, A. and Bronnikova, T. 2001. Sub-harmonic resonance and multi-annual oscillations in northern mammals: a non-linear dynamical systems perspective. *Chaos Solitons Fractals*, **12**: 251–264.

Stevenson, R. 1985. Body size and limits to the daily range of body temperature in terrestrial ectotherms. *Am. Nat.*, **125**: 102–117.

Swetnam, T.W. and Lynch, A.M. 1993. Multicentury, regional-scale patterns of western spruce budworm outbreaks. *Ecol. Monogr.*, **63**: 399–424.

Taylor, R.A., White, A. and Sherratt, J.A. 2013. How do variations in seasonality affect population cycles? *Proc. R. Soc. Lond. B: Biol. Sci.*, **280**: 20122714.

Turchin, P. 2003. *Complex Population Dynamics: A Theoretical/Empirical Synthesis*. Princeton, NJ: Princeton University Press.

Volney, W.J.A. and Fleming, R.A. 2000. Climate change and impacts of boreal forest insects. *Agric. Ecosyst. Environ.*, **82**: 283–294.

Volterra, V. 1928. Variations and fluctuations of the number of individuals in animal species living together. *ICES J. Mar. Sci.*, **3**: 3–51.

Weitz, J.S. and Levin, S.A. 2006. Size and scaling of predator–prey dynamics. *Ecol. Lett.*, **9**: 548–557.

Yodzis, P. and Innes, S. 1992. Body size and consumer-resource dynamics. *Am. Nat.*, **139**: 1151–1175.