Scaling population cycles of herbivores and carnivores

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ABSTRACT
Summary: Periodicity in population dynamics is a fundamental issue. In addition to current species-specific analyses, allometry facilitates understanding of limit cycles amongst different species. So far, body-size regressions have been derived for the oscillation period of the population densities of warm-blooded species, in particular herbivores. Here, we extend the allometric analysis to other clades, allowing for a comparison between the obtained slopes and intercepts. The oscillation periods were derived from databases and original studies to cover a broad range of conditions and species. Then, values were related to specific body size by regression analysis. For different groups of herbivorous species, the oscillation period increased as a function of individual mass as a power law with exponents of 0.11–0.27. The intercepts of the resulting linear regressions indicated that cycle times for equally-sized species increased from homeotherms up to invertebrates. Overall, cycle times for predators did not scale to body size. Implications for these differences were addressed in the light of intra- and interspecific delays.

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Supplementary information: Supplementary literature is provided as appendix. Additional models are described in arXiv:0910.5057v1.

1 INTRODUCTION

Scaling already fascinated Greek philosophers like Aristotle (384–322 BC). Depending upon the assumption that mind could elucidate all the laws of the universe, in Analytica Posteriora he saw as first that knowledge generates from the discovery of causal relationships. Still, it took other two millennia before scientists became enabled by Descartes for plotting their data on Cartesian coordinates. Ecologists were fascinated by the remarkable regularity in the population oscillations observed in laboratory and field studies. Thus, the periodicity in population dynamics is still one fundamental issue in ecology. However, the relationships between oscillation period (τo) and body mass (m) have received so far surprisingly little attention. Time parameters, such as age at maturity or death, seem to scale to adult mass (e.g., Peters 1983, West et al. 1997, Gillooly et al. 2002, Brown et al. 2004, Hendriks and Mulder 2008), but allometric scaling for other groups, in particular heterotherms, invertebrates and carnivores, has to be tested. Moreover, the focus has mainly been on slopes of linear (log-log) regressions while a comparison of the differences between intercepts is equally important for understanding ongoing mechanisms. In our study, we aim to check allometric scaling of periodicity in population density for a wide range of species and trophic levels. Our null-hypothesis is that the oscillation period τo scales to body mass m with a slope of ¼, as observed for many other time variables in biology, in particular the age at maturity (tm). As an alternative, the oscillation period τo may be size-independent indicating that other factors, like environmental conditions, are more important in cycle times.

2 METHODS

The oscillation periods were collected from laboratory experiments and field surveys reported in literature (complete references provided in the Supplementary Information as appendix). All time series, including short periods, were taken into account to obtain sufficient data for regression analyses of various species groups. Adult species’ body-mass values were taken from the original studies; if adult m could not be obtained directly, it was estimated from the body size, i.e., the length, of a closely related taxon. Oscillation periods τo were usually reported as the time between two similar phases of a cycle. Together, 759 oscillation periods covering 251 species were collected; most of those values (683 cycle times) were retrieved from one data collection with standardized entries for periodic populations, the NERC – CPB ‘Global Population Dynamics Database’ available online at http://www3.imperial.ac.uk/cpb/research/patternsandprocesses/gpdd. The entire data collection was further subdivided in data sets with comparable phylogenetic and ecological characteristics. Although less comparable data were available for protists, based on a few data for very dissimilar unicellulars, those regressions were derived for completeness. Following our hypotheses, oscillation periods τo were compared to age at maturity τm.

3 RESULTS

Data on aquatic herbi-detritivores representing laboratory experiments on consumer-resource dynamics supported a close correlation between cycle times and body mass. Overall, within the common weight interval of 10⁻² – 10⁻⁷ kg, cycle times of invertebrate herbivores increased in the sequence of aquatic, herb-dwelling and tree-dwelling species. The intercepts of the homeothermic grazers were at the lower end of the range observed for the heterotherms, about a factor of three lower (Fig. 1).

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The following cases: aquatic herbivorous invertebrates (at maturity), for aquatic herbivores was just over 4 times that of the age (e.g., Krukonis and Schaffer 1991, Damuth 2007). The intercept 0.29 reported in previous studies on herbivorous homeotherms and carnivores (open symbols) were highly significant (sions (solid lines) obtained from metadata on herbivores (filled symbols) for cold-blooded species (upper panel) and warm-blooded species (lower panel). Linear regressions were within a factor of 1.3. Subdivision of fish data into all the data sources are available as separate references in the enhancement.

Cycle times for carnivores were size-independent and their averages were within a factor of 1.3. Subdivision of fish data into smaller taxonomic groups did not yield size scaling either, while the recorded number of invertebrate carnivores was too low to allow subcategories. The oscillation periods for seals, the largest mammalian predators included in the data set, were close to their maturity age. Due to these data, cycle time of mammalian carnivores decreased slightly with body size.

Slopes up to about ¼ were in agreement with the range of 0.26–0.29 reported in previous studies on herbivorous homeotherms (e.g., Krukonis and Schaffer 1991, Damuth 2007). The intercept for aquatic herbi-detritivores was just over 4 times that of the age at maturity, whereas the levels are more than 6 times higher for carnivorous Arthropoda. The oscillation periods for herbivores and carnivores are remarkable and, to our knowledge, novel. We show here that macroecology provides valuable additional viewpoints to the dynamic interpretation of periodic populations.

REFERENCES

Brown, J. H. et al. (2004) Toward a metabolic theory of ecology. Ecology 85, 1771–1789.

Carbone, C. et al. (1999) Energetic constraints on the diet of terrestrial carnivores. Nature 402, 286–288.

Danum, J. (2007) A macroevolutionary explanation for energy equivalence in the scaling of body size and population density. Am. Nat. 169, 621–631.

Gillooly, J. F. et al. (2002) Effects of size and temperature on developmental time. Nature 417, 70–73.

Hendriks, A. J. and Mulder, C. (2008) Scaling of offspring number and mass to plant and animal size: a meta-analysis and model. Oecologia 155, 705–716.

Hogstedt, G. et al. (2005) Period length in cyclic animal populations. Ecology 86, 373–378.

Jeschke, J. M. et al. (2004) Consumer-food systems: why type I functional responses are exclusive to filter feeders. Biol. Rev. 79, 337–349.

Kendall, B. 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. M. (1991) Population cycles in mammals and birds: does periodicity scale with body size? J. Theor. Biol. 148, 493–493.

Mulder, C. and Elser, J. J. (2009) Soil acidity, ecological stoichiometry and allometric scaling in grassland food webs. Global Change Biol. 15, 2730–2738.

Murdock, W. W. et al. (2002) Single-species models for many-species food webs. Nature 417, 541–543.

Peters, R. H. (1983) The Ecological Implications of Body Size. Cambridge University Press, Cambridge, UK.

Turchin, P. (2003) Complex Population Dynamics: A Theoretical/Empirical Synthesis. Monogr. Popul. Biol. 35, 1–456.

West, G. B. et al. (1997) A general model for the origin of allometric scaling laws in biology. Science 276, 122–126.

Yodiz, P. and Innes, S. (1992) Body size and consumer-resource dynamics. Am. Nat. 139, 1151–1175.
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arXiv – APPENDIX

Supplementary Literature

Values for some laboratory populations refer to experiments in which species were fed intermittently or continuously (Pratt 1943; Nicholson 1954; Huffaker 1958; Beddington and May 1975; Halbach 1979; Halbach et al. 1983). Other studies in which no additional food was added and consumers interacted with their resources (Tsuchiya et al. 1972; Levin et al. 1977; Veilléux 1979; Bohannan and Lenski 1997; Yoshida et al. 2003) were included as well. Data on field populations were taken from the statistical analysis of extensive time series on temperate species (Kendall et al. 1998). Additional information on invertebrate taxa not covered by the previous series was obtained from original studies (Utida 1957; Clark 1963; Baltensweiler 1971; Berryman 1995; Grover et al. 2000) and vertebrates (Newsome 1969; Southern 1970; Caughey 1976; Itô 1980; Calder 1983, 1984; Peterson et al. 1984; Ginzburg and Inchausti 1997; Scheffer et al. 1997; Turchin and Hanski 1997; Boonstra et al. 1998; Lambin et al. 2000). Together 759 oscillation periods were collected, 30 obtained in laboratory experiments and 729 derived from field surveys. Of the latter, 36 cycle times were taken from literature as originally reported and 693 values were retrieved from one current database with standardized entries for periodic populations (Kendall et al. 1998). Together our data collection represents 251 species. Data sets were then subdivided in groups with comparable phylogenetic and ecological characteristics. In addition, averages per individual group were calculated for comparison of oscillation characteristics that did not scale to body mass. Experiments in which food was added were assigned to a separate group. Although few comparable data were available for unicellulars, their regressions were derived for completeness ($R^2 = 91\%$, $P = 0.05$). Following our hypotheses, oscillation periods $\tau$ were compared to maturity ages $\tau_m$.

Baltensweiler, W. (1971) The relevance of changes in the composition of larch bud moth populations for the dynamics of its numbers. In Den Boer, P. J. and Gradwell, G. R. (eds.), Dynamics of Populations. PUDOC, Wageningen, pp. 208-219.

Beddington, J. R. and May, R. M. (1975) Time delays are not necessarily destabilizing. Math. Biosci. 27, 109-117.

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

Bohannan, B. J. M. and Lenski, R. E. (1979) Effect of resource enrichment on a chemoattractant community of bacteria and bacteriophage. Ecology 78, 2303-2315.

Boonstra, R. et al. (1998) Population cycles in small mammals: the problem of explaining the low phase. Ecology 79, 1479-1488.

Calder, W. A. (1983) An allometric approach to population cycles of mammals. J. Theor. Biol. 100, 275-282.

Calder, W. A. (1984) Size, Function and Life History. Harvard University Press, Cambridge, MA.

Caughey, G. (1976) The elephant problem: an alternative hypothesis. East Afr. Wildl. J. 14, 265-383.

Clark, L. R. (1983) The influence of predation by Syrphus spp. on the numbers of Cardiapa albitextura (Psyllidae). Austr. J. Zool. 11, 470-487.

Ginzburg, L. R. and Inchausti, P. (1997) Asymmetry of population cycles: abundance-growth representation of hidden causes of ecological dynamics. Oikos 80, 435-447.

Grover, J. P. et al. (2000) Periodic dynamics in Daphnia populations: biological interactions and external forcing. Ecology 81, 2781-2798.

Halbach, U. (1979) Introductory remarks: strategies in population research exemplified by rotifer population dynamics. Fortschr. Zool. 25, 1-27.

Halbach, U. et al. (1983) Population ecology of rotifers as a bioassay tool for ecotoxicological test in aquatic environments. Ecotox. Environ. Saf. 7, 484-513.

Huffaker, C. B. (1958) Experimental studies on predation: dispersion factors and predator-prey oscillations. Hilgardia 27, 343-383.

Itô, Y. (1980) Comparative Ecology. Cambridge University Press, Cambridge, UK.

Kendall, B. E. et al. (1998) The macroecology of population dynamics: taxonomic and biogeographic patterns in population cycles. Ecol. Lett. 1, 160-164.

Lambin, X. et al. (2000) Cyclic dynamics in field vole populations and generalist predation. J. Anim. Ecol. 69, 106-118.

Levin, B. R. et al. (1977) Resource-limited growth, competition and predation: a model and experimental studies with bacteria and bacteriophage. Am. Nat. 111, 3-24.

Newsome, A. E. (1969) A population study of house-mice temporarily inhabiting a South Australian wheatfield. J. Anim. Ecol. 38, 341-360.

Nicholson, A. J. (1954) An outline of the dynamics of animal populations. Austr. J. Zool. 2, 9-65.

Peterson, R. O. et al. (1984) Wolves, moose and the allometry of population cycles. Science 224, 1350-1352.

Pratt, D. M. (1943) Analysis of population development in Daphnia magna at different temperatures. Biol. Bull. Mar. Biol. Lab., Lancaster Press, Lancaster, UK.

Scheffer, M. et al. (1997) Seasonal dynamics of Daphnia and algae explained as a periodically forced predator-prey system. Oikos 80, 519-532.

Southern, H. N. (1970) The natural control of a population of Tawny owls (Strix aluco). J. Zool. 162, 197-285.

Tsuchiya, H. M. et al. (1972) Predator-prey interactions of Dicyostelium discoideum and Escherichia coli in continuous cultures. J. Bacteriol. 110, 1147-1153.

Turchin, P. and Hanski, I. (1997) An empirically based model for latitudinal gradient in vole population dynamics. Am. Nat. 149, 842-874.

Utida, S. (1957) Cyclic fluctuations of population density intrinsic to the host parasite system. Ecology 38, 442-449.

Veilléux, B. G. (1979) An analysis of the predatory interaction between Paramecium and Didinium. J. Anim. Ecol. 48, 787-803.

Yoshida, T. et al. (2003) Rapid evolution drives ecological dynamics in a predator-prey system. Nature 424, 303-306.