

Single-species models for many-species food webs

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Most species live in species-rich food webs; yet, for a century, most mathematical models for population dynamics have included only one or two species^{1–3}. We ask whether such models are relevant to the real world. Two-species population models of an interacting consumer and resource collapse to one-species dynamics when recruitment to the resource population is unrelated to resource abundance, thereby weakening the coupling between consumer and resource^{4–6}. We predict that, in nature, generalist consumers that feed on many species should similarly show one-species dynamics. We test this prediction using cyclic populations, in which it is easier to infer underlying mechanisms⁷, and which are widespread in nature⁸. Here we show that one-species cycles can be distinguished from consumer–resource cycles by their periods. We then analyse a large number of time series from cyclic populations in nature and show that almost all cycling, generalist consumers examined have periods that are consistent with one-species dynamics. Thus generalist consumers indeed behave as if they were one-species populations, and a one-species model is a valid representation for generalist population dynamics in many-species food webs.

Conventional approaches to nonlinear time-series analysis focus on dynamical invariants such as the dimension of the series, which has recently been used to infer the number of strongly interacting

species in a system^{9,10}. These are powerful methods, but require time series much longer than those typically available for field populations¹⁰. In contrast, cycle period can be estimated from relatively short series and, when the organism's maturation time is used to fix the timescale, provides useful dynamical information. Theory for stage-structured populations leads us to consider three classes of cycles. Single-species populations with direct density dependence in vital rates can exhibit 'single-generation cycles' with cycle period one to two times the maturation time^{7,11,12}. Single-species populations can also exhibit 'delayed-feedback cycles' that typically have periods two to four times the maturation time^{12–14} (though longer periods may be possible in models with extremely large-amplitude cycles¹⁵). Models of a specialized consumer, tightly coupled to a resource population so that each controls the dynamics of the other, show longer-period, true 'consumer–resource cycles'. However, approximately constant resource recruitment in these consumer–resource models induces weak coupling and a collapse to single-species dynamics; direct or delayed density dependence in the consumer can then produce single-generation cycles or delayed-feedback cycles in the consumer, with the period determined by consumer development time^{4–6}.

We first establish that specialist consumer–resource cycles can be distinguished from single-species cycles by their scaled periods (cycle period divided by time to maturity). If T_C and T_R are the maturation times of the consumer and resource respectively, then cycles in single-species models have periods that seldom exceed $4T_C$, as noted, whereas consumer resource cycles have periods seldom less than $4T_C + 2T_R$ (Box 1).

Next, the collapse from consumer–resource dynamics to single-species dynamics caused by weak coupling suggests the following prediction. Generalist consumers should typically be weakly coupled to any one of their prey populations because, when feeding on many different species, they cannot be strongly coupled to any one of them. In particular, total resource recruitment rate will be largely independent of the abundance of the consumer and of any particular resource population. We therefore predict that, among cyclic species, generalists should typically show single-species cycles. Specialist species, on the other hand, should more typically show consumer–resource cycles, although strong density dependence

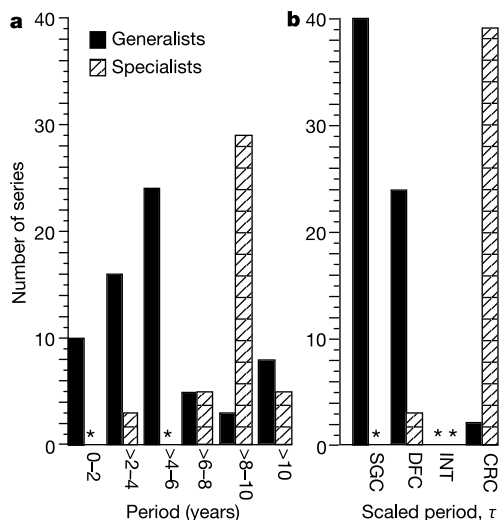


Figure 1 Cycles classified by period. Asterisk indicates zero series in the class. **a**, Number of cyclic populations with various periods, in years. **b**, Distribution of cycles among classes defined by scaled period. SGC, single-generation cycles ($\tau=1$); DFC, delayed-feedback cycles ($2 \leq \tau \leq 4$); CRC, consumer–resources cycles (period in years $\geq 4T_C + 2T_R$). No cycles fall in the intermediate class (INT) between single-species and consumer–resource cycles.

Table 1 Species analysed

Generalists	Specialists
<i>Phylloscopus trochilus</i> , willow warbler	<i>Bupalus piniarius</i> , pine looper (2)
<i>Grus americana</i> , whooping crane	<i>Hyloicus pinastri</i> , pine hawkmoth
<i>Milvus milvus</i> , red kite	<i>Lymantria dispar</i> , gypsy moth
<i>Bucephala albeola</i> , bufflehead	<i>Zeiraphera diniana</i> , larch budmoth
<i>Parus major</i> , great tit	<i>Dendrolimus pini</i> , pine-tree lappet
<i>Esox lucius</i> , pike	<i>Lymantria monacha</i> , black arches
<i>Rutilus rutilus</i> , roach (2)	<i>Epirrita autumnata</i> , autumnal moth
<i>Coregonus albula</i> , vendace	<i>Exapate duratella</i>
<i>Perca flavescens</i> , yellow perch	<i>Panolis flammea</i> , pine beauty
<i>Merlangius merlangius</i> , whiting	<i>Lepus americanus</i> , snowshoe hare
<i>Oncorhynchus gorbis</i> , pink salmon (8)	<i>Lepus europaeus</i> , brown hare
<i>Oncorhynchus nerka</i> , sockeye salmon (21)	<i>Lepus timidus</i> , mountain hare (2)
<i>Salmo salar</i> , Atlantic salmon	<i>Lynx canadensis</i> , Canadian lynx (15)
<i>Pleuronectes platessa</i> , plaice	<i>Mustela vison</i> , North American mink (10)
<i>Gadus morhua</i> , cod (3)	<i>Ondata zibethicus</i> , muskrat (3)
<i>Clupea harengus</i> , Atlantic herring	
<i>Castor canadensis</i> , beaver (4)	
<i>Taxidea taxus</i> , American badger	
<i>Ursus americanus</i> , black bear (3)	
<i>Sus scrofa</i> , wild boar (2)	
<i>Ovibus moschatus</i> , muskox (2)	
<i>Cancer magister</i> , Dungeness crab (5)	
<i>Calathus melanocephalus</i> , carabid beetle	
<i>Pterostichus versicolor</i> , carabid beetle	
<i>Vespa sp.</i> , wasp	

Except as noted, generalists had single-species cycles and specialists had consumer–resource cycles. Species were chosen based on match between life-history features and discrete-time theoretical models (Methods and Supplementary Information 3). All appropriate series for a species were analysed (Methods) and, if this exceeded 1, the number of series analysed is in parenthesis. *L. monacha* and two of the mink series showed single-species cycles. Each of the two carabid beetle species showed consumer–resource cycles.

Box 1

A lower bound for periods of consumer–resource cycles

A family of consumer–resource models has the property that periodic or quasi-periodic solutions have period greater than six¹⁶. These models assume that both the consumer and resource species reproduce only once, and have the same development time. Here we generalize the work of ref. 16 to include species with arbitrary development times and show that, with biologically reasonable parameter values, appropriately scaled periods are seldom likely to drop much below six, even when the strict mathematical conditions for that bound are relaxed.

We consider a tightly coupled consumer–resource model of the general form:

$$R_t = \lambda R_{t-1} f(R_{t-1}, C_{t-1}) + S_R R_{t-1} \quad (1)$$

$$C_t = \lambda R_{t-1} (1 - f(R_{t-1}, C_{t-1})) + S_C C_{t-1} \quad (2)$$

where R_t and C_t represent the density of adults in the resource and consumer populations in year t , λ is the geometric rate of resource increase, $f(R_t, C_t)$ is the fraction of the resource population that survives attack by the consumer, and S_R , S_C are the fractions of the resource and consumer populations surviving to the next year.

We assume that the system has only one non-trivial equilibrium state (R^* , C^*). The characteristic equation defining the conditions for local stability of the equilibrium is:

$$\mu^2 + A_1 \mu + A_2 = 0 \quad (3)$$

with $A_1 = -1 - \alpha - \beta - S_C$, $A_2 = \alpha(\lambda + S_R) + S_C(1 + \beta)$, where $\alpha = -\lambda R^* f_C(R^*, C^*)$, $\beta = \lambda R^* f_R(R^*, C^*)$, f_i implies a partial derivative with respect to i for $i = R$ or C and μ is an eigenvalue. With forms of the functional response most appropriate for specialist consumers (types 1 or 2), α and β are both non-negative.

On the local stability boundary, $A_2 = 1$, and the period of the cycles is

$$P = 2\pi / \tan^{-1} \left(\sqrt{\frac{4}{(1 + \alpha + \beta + S_C)^2} - 1} \right) \quad (4)$$

which always exceeds six. With some additional algebra, it can be shown that the cycle period approaches six for large λ only if $\beta = 0$ and $S_C = 0$. If either $\beta > 0$ (as with a type 2 functional response) or $S_C > 0$ (adult consumers may live for more than a year), the limiting period is greater than six. Cycle period increases as λ decreases from the limit to lower, and biologically realistic, values.

Resource density dependence can reduce the period, but only slightly. We analysed a variant of the above model with the standard Nicholson–Bailey assumption, $f = \exp(-\alpha C_t)$, implying $\beta = 0$, but with either Ricker or Beverton–Holt density dependence in the resource population. A period of six is no longer a lower bound, but we found that consumer–resource periods always exceeded 5.5 with $\lambda < 10$, typically the upper limit in natural populations (Supplementary Information 3). (Delayed-feedback cycles (a period of two) arise in the Ricker version with sufficiently strong resource density dependence.)

A generalization of model (1) that allows for different juvenile development times, T_R and T_C , for resource and consumer respectively, has equations:

$$R_t = \lambda R_{t-T_R} f(R_{t-T_R}, C_{t-T_R}) + S_R R_{t-1} \quad (5)$$

$$C_t = \lambda R_{t-T_C} (1 - f(R_{t-T_C}, C_{t-T_C})) + S_C C_{t-1} \quad (6)$$

With the same restrictions as before ($\beta = 0$ and $S_C = 0$), and one additional assumption ($S_R = 0$), we can prove that the cycle period approaches a limiting value of $2T_R + 4T_C$, as $\lambda \rightarrow \infty$. An outline of the proof is in Supplementary Information 1. We have not managed to prove that this limit is a lower bound as was true with a period of six, but extensive numerical studies suggest that it is.

The above analyses are strictly valid only on the stability boundary. However, such calculations are typically a good indicator of the periods of all but very large-amplitude quasi-cycles or limit cycles. With large-amplitude limit cycles, periods are typically longer than would be predicted from our analysis¹⁷, supporting our interpretation of $2T_R + 4T_C$ as a lower bound.

might sometimes reduce these to single-species cycles.

We analysed 108 time series from natural populations (comprising 40 species), each of which exhibited statistically significant cycles and met criteria ensuring a rigorous test of the predictions (Methods). We classified each species into one of two trophic roles (Methods). ‘Generalist’ consumers (for example, predatory fish) feed on many resource species over their lifetime and in turn are not preyed on by specialist consumers. ‘Specialists’ (for example, lynx) feed largely on one species, or are prey of a specialist predator (for example, snowshoe hares). We then estimated cycle periods and calculated scaled periods. Our focus was on generalists, because the specialists in the database are known, in general, to have long-period cycles. We used the distribution of specialist cycle periods as a basis for comparison and to test the Box 1 prediction that scaled long periods are not less than $4T_C + 2T_R$.

Our predictions are well supported. The generalists and specialists did not separate cleanly when we examined period measured in years (mainly because a substantial fraction of generalist periods are longer than four, or even six, years; see Fig. 1a) but they did so almost perfectly when we used the scaled period (Fig. 1b). All but two of the 66 generalist consumer series show single-species cycles, including those with periods greater than four years. There are no cycles with intermediate scaled period, that is, between $4T_C$ and $4T_C + 2T_R$, in spite of the fact that many periods lie between four and six years (Fig. 1a). As expected, the great majority of cyclic series from specialists are true consumer–resource cycles (Fig. 1a), and none of these periods is less than $4T_C + 2T_R$, as predicted by Box 1. Furthermore, as predicted by the theory discussed above, when specialists have shorter periods (only three cases), they are single-species periods rather than intermediate periods (Fig. 1b).

Single-species cycles occur in a broad taxonomic range but are especially prevalent in fish (Table 1). True consumer–resource cycles are restricted in this data set to forest Lepidoptera and mammalian carnivores and their prey, but probably occur in other taxonomic groups that were excluded because the species have multiple generations per year.

Our results suggest not only that single-species models are often appropriate for describing population dynamics of individual species in many-species food webs, but that prey species diversity, a prevalent feature of natural systems, itself facilitates such simplification. Remaining challenges include adding taxonomic variety to the database, developing appropriate theory on cycle periods for multivoltine species, and determining whether the simplification applies in non-cyclic generalist populations. □

Methods

The time series are from the Global Population Dynamics Database⁸, plus the three additional series found while searching the literature for relevant natural history information (Supplementary Information 2). Criteria for excluding time series of field populations from the analysis (see Supplementary Information 3) and the main groups excluded, are as follows:

(1) We could not determine the species’ trophic role (nine series from insects and game birds).

(2) There is strong evidence the population has no causal role in the cycle (43 series from high-latitude species, mainly foxes, entrained by the lynx–snowshoe hare cycle or, less often, by microtine (voles, lemmings, and so on) cycles; these populations track but do not cause the cycles^{19–21}). Mink and muskrat series were analysed because there is evidence that they are causally involved in a distinct cycle¹⁹, as were the mountain and brown hare series²².

(3) To conform to the discrete-time theory, series were excluded if maturation takes less than one year and breeding is more frequent than annual. Theory on cycle periods is not available for seasonally driven, properly age-structured, consumer–resource models of species with more than one generation per year. This excludes 31 series, mainly from voles.

(4) For statistical power, we focused on time series at least 25 years long, and excluded any results in which the estimated period was more than one-third of the series length. To avoid biologically meaningless results, we only analysed data with mean counts of more than 10 individuals and cycles in which the maximum population was on average at least twice the minimum.

Information from the literature on trophic role was supplemented by discussions with appropriate experts. Generalist consumers—usually top predators with broad diets—could typically be categorized easily and unambiguously. Lepidopteran forest pests were classified as specialist prey (of parasitoids)²³, although some cycles may be specialized

pest–plant cycles or even single-species dynamics with second-order delays such as maternal effects, which lead to periods of over $6T$ (ref. 24). The last would increase the prevalence of single-species dynamics.

Scaled period, τ , was calculated by dividing the period (in years) by time to maturity (in years), T_C (sources in Supplementary Information 3). For cases in which $\tau > 4$, we then asked if the cycle period in years exceeded $4T_C + 2T_R$; in series involving lynx (average maturation time = 1.5 years) this sum was eight years; in all others, where consumer and resource species develop in one year, it was six. Because maturation times and cycle periods are approximations, estimates of τ were rounded to the nearest integer. Periods with $\tau = 1$ were assigned to single-generation cycles; those with $2 \leq \tau \leq 4$ were assigned to delayed-feedback cycles.

The series were analysed ‘blind’, without knowledge of the species name or trophic role. We used multitaper spectral analysis^{25,26} using the algorithm described in ref. 27. This technique avoids the often arbitrary choice of data tapering by using a series of optimal slepian tapers. We classified a series as periodic if there was both a clear peak in the power spectrum (of either the transformed or the untransformed data) and the corresponding P -value was < 0.05 . If there were missing values, we analysed the longest continuous segment of the data. If, upon visual inspection, only part of the series appeared cyclic, we analysed that segment. We analysed the data both with and without a logarithmic transformation, and removed any linear trend in both cases. If several series were available from any given area and time period, we analysed only one series, and only the predator if predator and prey series were available.

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Precise inhibition is essential for microsecond interaural time difference coding

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Microsecond differences in the arrival time of a sound at the two ears (interaural time differences, ITDs) are the main cue for localizing low-frequency sounds in space. Traditionally, ITDs are thought to be encoded by an array of coincidence-detector neurons, receiving excitatory inputs from the two ears via axons of variable length (‘delay lines’), to create a topographic map of azimuthal auditory space^{1,2}. Compelling evidence for the existence of such a map in the mammalian ITD detector, the medial superior olive (MSO), however, is lacking. Equally puzzling is the role of a—temporally very precise³—glycine-mediated inhibitory input to MSO neurons. Using *in vivo* recordings from the MSO of the Mongolian gerbil, we found the responses of ITD-sensitive neurons to be inconsistent with the idea of a topographic map of auditory space. Moreover, local application of glycine and its antagonist strychnine by iontophoresis (through glass pipette electrodes, by means of an electric current) revealed that precisely timed glycine-controlled inhibition is a critical part of the mechanism by which the physiologically relevant range of ITDs is encoded in the MSO. A computer model, simulating the response of a coincidence-detector neuron with bilateral excitatory inputs and a temporally precise contralateral inhibitory input, supports this conclusion.

Sensitivity to ITDs, which can be in the order of only micro-seconds⁴, requires neuronal processing with a temporal acuity far beyond that normally observed in the mammalian central nervous system. Traditionally, ITD processing in mammals and birds is explained by means of an elegant model devised by Jeffress more than 50 years ago¹. The model assumes the existence of arrays of coincidence-detector neurons receiving excitatory inputs from the two ears. Neurons respond maximally when stimulus-evoked action potentials, phase-locked to the stimulus waveform, converge from each ear simultaneously. Different conduction delays from each ear, assumed to result from a system of delay lines, provide a means by which different coincidence-detector neurons encode different ITDs. A systematic arrangement of such delay lines is assumed to create a topographic representation of ITDs and, thus, a map of sound positions in the azimuthal plane.

For nucleus laminaris, the ITD-processing structure in birds, the existence of such an arrangement has been confirmed^{5,6}. However, for the mammalian equivalent, the MSO (Fig. 1a), direct confirmation of such an arrangement is lacking. Spherical bushy cells from each cochlear nucleus provide binaural excitatory input to MSO neurons^{7,8}, which *in vivo* recordings demonstrate to be sensitive to ITDs^{9,10}. However, MSO neurons also receive prominent