23. A. Balmford *et al.*, *Science* **291**, 2616 (1991).
24. R. P. Cincotta, J. Wisnewski, R. Engelman, *Nature* **404**, 990 (2000).
25. K. J. Gaston, T. M. Blackburn, K. K. Goldewijk, *Proc. R. Soc. London B. Biol. Sci.* **270**, 1293 (2003).
26. D. Tilman *et al.*, *Science* **292**, 281 (2001).
27. A. Duff, A. Lawson, *Mammals of the World: A Checklist* (A & C Black, London, 2004).
28. G. C. Daily, G. Ceballos, J. Pacheco, G. Suzan, A. Sánchez Azofelia, *Conserv. Biol.* **17**, 1 (2003).
29. E. Wikramanayake *et al.*, *Conserv. Biol.* **18**, 839 (2004).
30. P. M. Vitousek, H. A. Mooney, J. Lubchenco, J. M. Melillo, *Science* **277**, 494 (1997).
31. P. R. Ehrlich, A. H. Ehrlich, *One with Nineveh: Politics, Consumption, and the Human Future* (Island Press, Washington, DC, 2004).
32. Environmental Systems Research Institute (ESRI), *ESRI Data and Maps 2002* (Environmental Systems Research Institute, Redlands, CA, 2002); see www.esri.com.
33. We thank G. C. Daily, R. A. Medellin, C. Sekercioglu, R. List, and K. M. A. Chan for comments on the manuscript. This study was supported by the National University of Mexico, CONABIO (Mexico), the Center for Conservation Biology–Stanford University, EcoCiencia (Mexico), and the John Simon Guggenheim Memorial Foundation.

On the Regulation of Populations of Mammals, Birds, Fish, and Insects

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A key unresolved question in population ecology concerns the relationship between a population's size and its growth rate. We estimated this relationship for 1780 time series of mammals, birds, fish, and insects. We found that rates of population growth are high at low population densities but, contrary to previous predictions, decline rapidly with increasing population size and then flatten out, for all four taxa. This produces a strongly concave relationship between a population's growth rate and its size. These findings have fundamental implications for our understanding of animals' lives, suggesting in particular that many animals in these taxa will be found living at densities above the carrying capacity of their environments.

The way a population's size changes through time—its dynamics—depends on the way it grows when small and declines when big. More specifically, the dynamics result from the precise relationship between the population's size (N) and its per capita growth rate (pgr), defined as $^1/_N \times {dN}/{dt}$, where t is time (Fig. 1). The simplest case is a straight-line relationship, such that pgr declines linearly with increasing N (Fig. 1A, left). Linearity produces the well-known logistic population growth equation $N(t) = \frac{KN_0}{(K-N_0)e^{-r_0 t} + N_0}$, where r_0 is a parameter representing pgr when $N = 0$, N_0 is the size of the population at time = 0, and K is the population's carrying capacity (*1*).

The relationship between pgr and N is generally taken to be monotonic and decreasing and can be either concave or convex (*2*). Convex relationships (Fig. 1B) imply that pgr varies little until population size is near carrying capacity, then drops rapidly. Concavity (Fig. 1C) means that pgr is initially relatively high, so small populations grow quickly, but pgr then declines rapidly as population size increases, later flattening out so that the approach to carrying capacity is relatively slow. In a variant possible in theory and occasionally reported in nature, the slope of the relationship between pgr and N becomes positive in small populations, such that pgr actually increases with N over a narrow range of population sizes, giving an Allee effect (*2–4*).

The way in which pgr declines with population size is conventionally modeled by the theta-logistic equation, given by

$$pgr = r_0[1 - (N/K)^\theta] \qquad (1)$$

where r_0 and K are as before, and θ is a parameter describing the curvature of the relationship (*2*). In practice, population density is sometimes used in place of population size, and r_0 is best replaced by r_m, representing pgr when population size N is at a defined low value, corresponding to a population of, for example, one individual (*5*) (Fig. 2). Values of θ greater or less than 1 correspond to convex and concave relationships, respectively (Figs. 1 and 2). Mechanistically, the value of θ must depend on the ways that animals interact at different densities (*6*).

There has been a persistent suggestion that the shape of the pgr-density relationship depends on a species' life history (*5, 7, 8*). The widely cited argument (*9–14*) is as follows. Large, long-lived species generally live close to the carrying capacity of their environments, being limited mainly by resources, and are only rarely subject to natural selection for increased performance at low population density. As a consequence, these species' population growth rates are relatively unaffected until populations are nearing carrying capacity, producing the convex curve of $\theta > 1$ seen in Fig. 1. By contrast, species that spend most of their time at densities much lower than carrying capacity are selected for a high maximum rate of increase. As a result, these species are affected even at relatively low densities in their abilities to acquire foods, and so the concave relationship of $\theta < 1$ between pgr and N arises. There are a number of cases of density dependence that together have suggested that pgr-density relationships are convex for large mammals and similar species but concave for species with life histories like those of insects and some fish (*5, 7, 15*).

The form of the pgr-density relationship has implications beyond population dynamics, and it is used to make predictions and to analyze management options in areas such as conservation (*16*), pest management (*17*), risk assessment (*18*), and disease epidemiology (*19*). In spite of this, there have been few attempts to establish generalities about how pgr varies with population size (*5, 15, 20*). Here we analyze an extensive compilation of time series data from 4926 different populations in the Global Population Dynamics Database (GPDD) (*21, 22*). The GPDD is a collection of time series of population counts or indices of these, together with other taxonomic details of more than 1400 species.

After exclusion of time series that were very short, did not vary, or contained zeros, the GPDD contained 3766 time series from 1084 species (table S1). We further excluded 469 series (12%) that showed a significant decline in size with time, because unknown factors may have prevented population recovery and biased the form of the estimated pgr-density relationship, and 1% that showed positive density dependence (i.e., pgr increased with density), because these show no evidence of population regulation. We examined the remaining 3269 series for evidence of Allee relationships, but these were rare if present at all: There were only 20 cases in which a quadratic regression of pgr on N fitted better ($P < 0.05$) than a linear regression, with a turning point of the required

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type and within the range of observed values of *N*, and in only 5 was the pattern clearly non-monotonic (*22*). We conclude that there is clear evidence of Allee effects in only a small minority (0.2%) of GPDD data sets. Absence of Allee effects in bird studies has been noted by Saether *et al.* (*23*).

We fitted Eq. 1 to each of the 3269 tractable time series in the GPDD using a nonlinear least-squares procedure and discarded cases yielding relatively imprecise estimates of θ (*22*). The main taxonomic groups represented were birds (150 species), mammals (79), bony fish (64), and insects (381). Figure 3 shows the frequencies of occurrence of fitted values of θ in each of the main taxonomic groups. In each taxon, there are far more instances where θ < 1 (concave) than where θ > 1 (convex). The average proportion of cases where θ < 1 is 0.78. This is higher than the proportion (0.62) found in the only comparable study (*5*), but that was based on only 13 species of birds. The proportion of cases where θ < 1 differs only a little between the major taxonomic groups, though there is a suggestion that the proportion is higher in fish than in mammals, birds, and insects (taking the average value of θ for each species and counting species, $\chi_3^2 = 6.9$, non-significant) (Fig. 3).

It is not possible to apply explicit phylogenetic methods to these data because no phylogeny exists to describe them, but we repeated analyses using genus means and then family means as a way of controlling for the lack of independence among species (counting genera, $\chi_3^2 = 8.2$, $P < 0.05$; counting families, $\chi_3^2 = 8.0$, $P < 0.05$). θ was significantly ($P < 0.05$) different from 1 in 613 of the 1780 time series analyzed, being less than 1 in 581 cases and greater than 1 in 32. The reason only 613 estimates were significantly different from 1 is that some of the estimates are imprecise. Our strategy for dealing with imprecision was to remove very imprecise estimates (*22*), but this retained quite a number that still had wide confidence intervals. Among the small proportion (0.22) of cases where θ > 1, there are no obvious taxonomic or other patterns: All major taxonomic groups are represented. Our results suggest that in mammals, birds, fish, and insects, population regulation is generally the result of a concave relationship between a population's growth rate and its size.

The histograms of θ suggest that θ is normally less than 1, but they do not directly test the hypothesis that θ would increase with a species' body size (*7*, *8*, *15*). However, there is no suggestion of such a relationship in any of the four taxonomic groups we analyzed. In mammals, the reverse is the case: The relationship is negative, not positive as predicted [regression with one point per species: $r_{36} = -0.32$, $P < 0.05$ (fig. S2); with one point per family or genus, the relationship is still negative: $r_{11} = -0.253$, nonsignificant, and
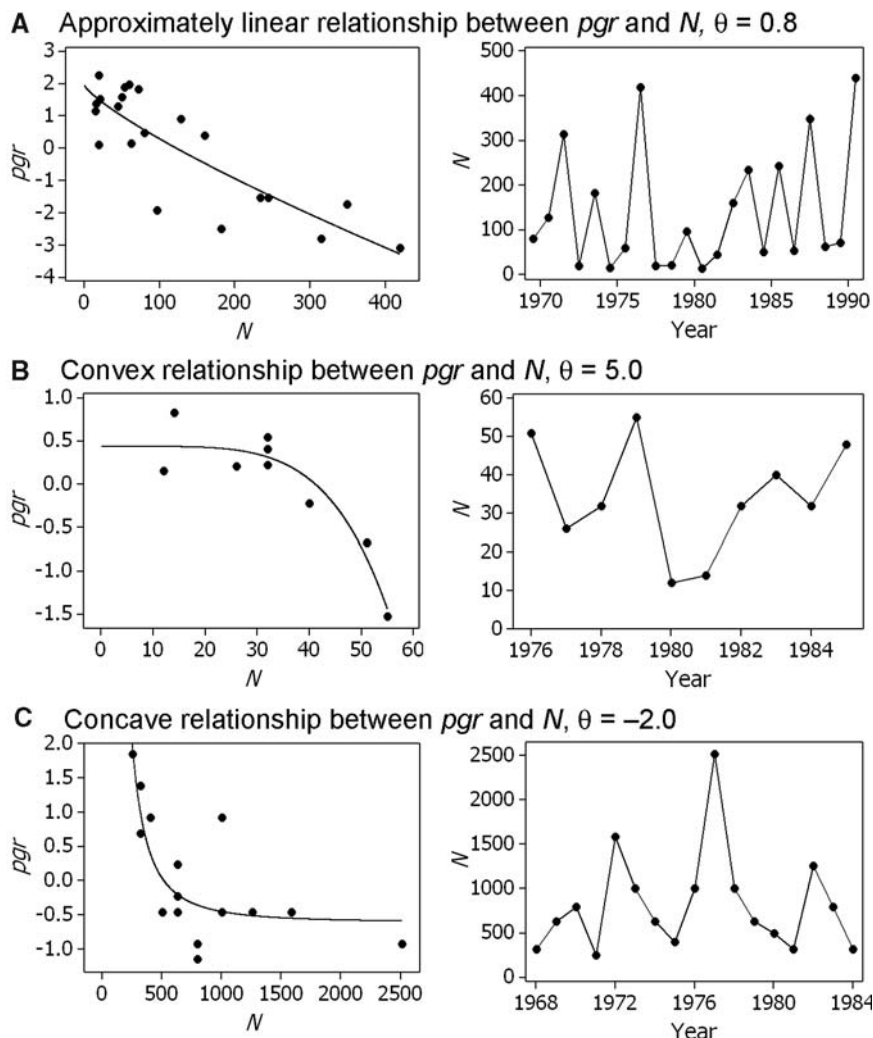

Fig. 1. (**A** to **C**) (Left) The relationships between population growth rates (*pgr*) and size (*N*) with (right) their associated population time series. The observed values on the left are calculated from the time series, and the fitted curves are of the type of Eq. 1. The data come from three insect populations in the GPDD with (A) θ ≈ 1 (*Acyrthosiphon pisum*, GPDD main ID 8383), (B) θ > 1 (*Inachis io*, ID 3276), (C) θ < 0 (*Xylena vetusta*, ID 6321). The form of *pgr-N* relationships are specific to the time and place in which the data were collected (*32*).

Fig. 2. Illustration of the curves generated by the theta-logistic equation (Eq. 1) for different values of θ. *N* represents population size or density. Each curve is constrained to go through (1, 0.1) and (100, 0); thus, the minimum population size is 1 and $r_m = 0.1$ and $K = 100$. There is no particular significance in our choice of $N = 1$ for the lower constraint; similar families of curves are obtained at other values of *N*, provided that these are nonzero and small in comparison with *K* (supporting online text).
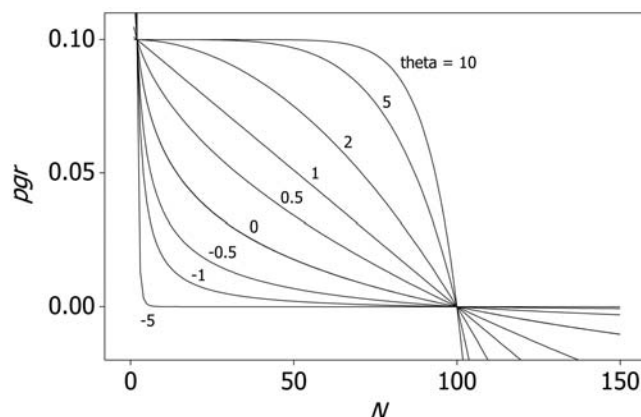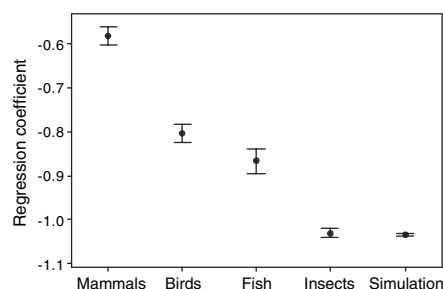
$r_{28} = -0.291$, nonsignificant, respectively]. Our results, based on a much larger data set than previous analyses, appear to rule out the possibility that the shape of the *pgr*-density relationship is strongly associated with taxonomy or body size.
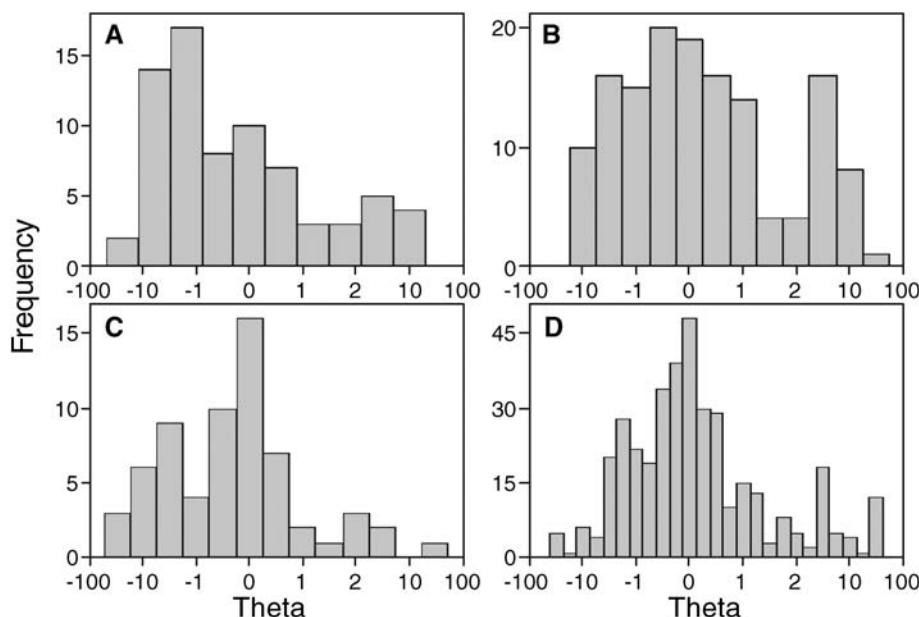
Fig. 3. Histograms of θ for the four major taxonomic groups in the GPDD database: (**A**) mammals, (**B**) birds, (**C**) fish, and (**D**) insects. A hybrid scale is used for θ, linear between −1 and 2 and $\log_{10}$ elsewhere. This scale is used to give similar weights to each of the principal regions of interest in Fig. 2. Where there existed within-species replication, we used the average value, so that each species is here represented only once.

cases analyzed here are positively skewed ($P < 0.001$, mean skewness 1.08 ± 0.024). Halley and Inchausti (*26*) obtained a similar result. Because bird and mammal populations may generally be regulated by their food supplies (*27–29*), our finding that most individuals live in environments above carrying capacity suggests they have less food than is needed for population replacement. However, other factors, such as predation and social interactions within the species, may in some circumstances override the role of food.

Factors whose effects are not felt immediately may also be important in determining population growth or decline (*30*), and we considered carefully the possibility of including time delays in our analysis. Adding two time lags would have added a minimum of two extra parameters to be estimated. Our conclusion was that the additional complexity to the model was not warranted, given the quality of data sets in our analysis. However, we believe it would be interesting to explore the possibility of including time lags in future studies.

Our conclusion that the most common *pgr*-density relationships are concave in birds, mammals, fish, and insects should have wide implications for understanding how the abundance and dynamics of populations are controlled and for our practical ability to make predictions about how such species respond to environmental change. For example, if a linear relationship is assumed and values of r_m and K are estimated from other sources—for instance, r_m is sometimes estimated from life-history data in optimal environments—then concavity means that *pgr* is overestimated when the population is below carrying capacity (Fig. 2). This would have dangerous consequences in wildlife and fisheries management, because populations would recover from disturbances more slowly than predicted. Pest control, by contrast, would be more successful than expected. Knowledge of the shapes of the *pgr*-density relationship is required in all areas of population ecology to make projections as to future abundance and population dynamics (*18, 28, 29, 31*).

Fig. 4. Slopes of regressions of *pgr* versus $\log_e$ density, showing that the observed relationships are not simply a result of measurement error. Measurement error alone predicts a slope of −1 in regressions of *pgr* against $\log_e$ density, in marked contrast to fitted slopes, except in the case of the insects. For comparison, we also show the effects of measurement error simulated with 3920 time series of length 30 and processed as for the GPDD data sets. Bars show one standard error of the mean. Frequency distributions of these regression coefficients are shown in fig. S3.

Values of θ around zero can arise from measurement error (*24*), and so it is important to exclude that possibility here (*25*). If all variation in population size arises from random measurement error, it is straightforward to derive the predicted relationship between *pgr* and the logarithm of population density. The relationship is linear with slope −1.0. We analysed the slope of the relationship between *pgr* and the logarithm of population density within each of our four taxonomic groups and for simulated data in which all variation in density was random (Fig. 4). In three of our four groups, the slopes differed markedly from −1.0 (*t* tests,

$P \ll 0.001$), suggesting that measurement error does not have a dominant role in these groups. The simulated data have, as expected, a mean very close to −1.0, and our insect populations also fall close to −1.0, possibly suggesting that measurement error has affected the estimates of θ in these populations. As a further check, we used the GPDD grading of time series to indicate perceived quality, which may in some cases be affected by measurement error (*21*). Restricting our analysis to the top two grades out of five did not affect our conclusions.

An important implication of our finding, that the relationship between *pgr* and density is generally concave, is that many animals may spend most of their time at or above carrying capacity. To see this, consider the effects of variations in population size induced by density-independent environmental factors. Assume that increases and decreases occur with similar magnitudes and frequencies and that θ < 1. For θ < 1, returns to carrying capacity are faster if the population is below than if it is above carrying capacity. The rate of return is given by the absolute value of *pgr*, and the rate of return is faster from a point below carrying capacity than from a point an equivalent distance above carrying capacity. This is seen in the dynamics of the population of *Xylena vetusta* (Fig. 1C) for which the estimated carrying capacity (where *pgr* = 0) is 512. Note that upward steps are generally larger than downward. The result is that populations spend more time above than below carrying capacity. This process will produce a tail extending to the right in the frequency distribution of population size. In line with this prediction, 88% of the 1849 GPDD

References and Notes
1. A. Tsoularis, J. Wallace, *Math. Biosci.* **179**, 21 (2002).
2. P. Turchin, *Complex Population Dynamics* (Princeton Univ. Press, Princeton, NJ, 2003).
3. P. A. Stephens, W. J. Sutherland, *Trends Ecol. Evol.* **14**, 401 (1999).
4. F. Courchamp, T. Clutton-Brock, B. Grenfell, *Trends Ecol. Evol.* **14**, 405 (1999).
5. B.-E. Saether, S. Engen, E. Matthysen, *Science* **295**, 2070 (2002).
6. T. Royama, *Analytical Population Dynamics* (Chapman & Hall, London, 1992).
7. C. W. Fowler, *Ecology* **62**, 602 (1981).
8. M. E. Gilpin, F. J. Ayala, *Proc. Natl. Acad. Sci. U.S.A.* **70**, 3590 (1973).
9. A. R. E. Sinclair, *Philos. Trans. R. Soc. London Ser. B* **358**, 1729 (2003).
10. P. Bayliss, D. Choquenot, *Philos. Trans. R. Soc. London Ser. B* **357**, 1233 (2002).
11. J. Lindstrom, H. Kokko, *Ecol. Lett.* **5**, 338 (2002).
12. R. Lande, B.-E. Saether, S. Engen, *Ecology* **78**, 1341 (1997).

13. B.-E. Saether, *Trends Ecol. Evol.* **12**, 143 (1997).
14. T. H. Clutton-Brock et al., *Am. Nat.* **149**, 195 (1997).
15. R. M. Sibly, J. Hone, *Philos. Trans. R. Soc. London Ser. B* **357**, 1153 (2002).
16. S. R. Beissinger, D. R. McCullough, Eds., *Population Viability Analysis* (Univ. of Chicago Press, Chicago, 2002).
17. G. Caughley, A. R. E. Sinclair, *Wildlife Ecology and Management* (Blackwell Science, Cambridge, MA, 1994).
18. R. A. Pastorok, S. M. Bartell, S. Ferson, L. R. Ginzburg, Eds., *Ecological Modeling in Risk Assessment* (CRC/Lewis, London, 2002).
19. R. M. Anderson, R. M. May, *Infectious Diseases of Humans: Dynamics and Control* (Oxford Univ. Press, Oxford, 1991).
20. P. Turchin, *Oikos* **84**, 153 (1999).
21. National Environment Research Council (NERC) Centre for Population Biology, Imperial College (1999), Global Population Dynamics Database, available at www.sw.ic.ac.uk/cpb/cpb/gpdd.html
22. Materials and methods are available as supporting material on *Science* Online.
23. B.-E. Saether, T. H. Ringsby, E. Roskaft, *Oikos* **77**, 217 (1996).
24. T. M. Shenk, G. C. White, K. P. Burnham, *Ecol. Monogr.* **68**, 445 (1998).
25. To identify the effects of measurement error on θ estimation, we carried out computer simulations of time series governed by Eq. 1 but subject to log-normal environmental perturbations and with measurement errors also being log-normally distributed. Preliminary results suggested that over the range of parameters of interest, θ can be recovered without appreciable bias, provided that measurement error is less than half of environmental variation, and that useful information is still obtainable when measurement error and environmental variation are equal.
26. J. Halley, P. Inchausti, *Oikos* **99**, 518 (2002).
27. A. R. E. Sinclair, in *Ecological Concepts*, J. M. Cherrett, Ed. (Blackwell Scientific, Oxford, 1989), pp. 197–241.
28. A. R. E. Sinclair, in *Frontiers of Population Ecology*, R. B. Floyd, A. W. Sheppard, P. J. De Barro, Eds. (CSIRO, Melbourne, 1996), pp. 127–154.
29. A. R. E. Sinclair, C. J. Krebs, *Philos. Trans. R. Soc. London Ser. B* **357**, 1221 (2002).
30. R. Lande, S. Engen, B.-E. Saether, *Stochastic Population Dynamics in Ecology and Conservation* (Oxford Univ. Press, Oxford, 2003).
31. S. Jennings, M. J. Kaiser, J. D. Reynolds, *Marine Fisheries Ecology* (Blackwell Science, Oxford, 2001).
32. C. J. Krebs, *Philos. Trans. R. Soc. London Ser. B* **357**, 1211 (2002).
33. We are grateful to E. Bazely-White and the NERC Centre for Population Biology at Silwood Park for generous and efficient help in supplying the data and to B.-E. Saether and A. Berryman for extensive constructive comments on an earlier version of the manuscript. Supported by NERC grant no. NER/B/S/2001/00867 (R.M.S. and M.P.).

Host Suppression and Stability in a Parasitoid-Host System: Experimental Demonstration

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We elucidate the mechanisms causing stability and severe resource suppression in a consumer-resource system. The consumer, the parasitoid *Aphytis*, rapidly controlled an experimentally induced outbreak of the resource, California red scale, an agricultural pest, and imposed a low, stable pest equilibrium. The results are well predicted by a mechanistic, independently parameterized model. The key mechanisms are widespread in nature: an invulnerable adult stage in the resource population and rapid consumer development. Stability in this biologically nondiverse agricultural system is a property of the local interaction between these two species, not of spatial processes or of the larger ecological community.

Although some consumer-resource (e.g., predator-prey) populations famously cycle in abundance, most appear to be stable, even when the predator strongly suppresses prey abundance (*1*). Yet, any theory that includes only a few basic predator properties—time lags and limited killing capacity of individual predators—generally predicts instability, i.e., large-amplitude oscillations or even predator-driven extinction of the prey (*2*, *3*). Model stability is particularly difficult to achieve when the predator can drive the prey to densities far below the limits set by the prey's own resources [the "paradox of enrichment" (*4*)], and almost all theoretically stabilizing mechanisms achieve stability only by causing the prey density to increase close to that limit (*1*).

California red scale (*Aonidiella aurantii*), an insect pest of citrus worldwide, is controlled by the parasitoid *Aphytis melinus* (*5*). This system exemplifies in extreme the features—ecological simplicity, high productivity, and severe suppression of the pest—that should engender instability. (i) It is an almost pure specialist consumer-resource interaction. Citrus groves contain, in addition to red scale, only a few, scarce, herbivore species. Under biological control, red scale are attacked mainly by *Aphytis melinus*; one other parasitoid and one or two predator species are typically present but scarce. (ii) Citrus provides a rich resource for scale. deBach (*6*) showed that when dichloro-diphenyl-trichloroethane (DDT) was applied to citrus trees (which killed *Aphytis* but not the resistant scale), scale outbreak density reached several hundred times higher than controlled populations and was not brought back under control for more than 3 years (presumably, when *Aphytis* was able to re-invade the tree). Yet, in our study area, red scale under control have persisted for >40 years (80 scale generations) with little temporal variation, at densities <1% of the limit set by the citrus plant.

Over two decades, we and our colleagues have tested and ruled out many mechanisms by which *Aphytis* might achieve this remarkable control with stability, including parasitoid aggregation to, or independent of, local host density (*7*), as well as density-dependence in the parasitoid sex-ratio (*8*). Stability also does not depend on spatial processes, including metapopulation dynamics. Dynamics were not altered when a spatial refuge from parasitism was removed, or when populations in individual trees were isolated from the larger population in the grove (*9*): Control and stabilizing mechanisms act locally within a single tree. Feasible remaining mechanisms explored in models involve life-history details, e.g., a long adult host stage invulnerable to parasitism (*10*). In previous studies, we could not detect temporal density-dependence in parasitism, host-feeding, or predation (*11*), a difficult task within the narrow range of densities of a stable system near equilibrium (*12*). A density-perturbation experiment might uncover both density-dependence and the mechanisms causing return to equilibrium. Density manipulations at the appropriate spatial scale typically are logistically daunting, but in the *Aphytis*–red scale system, the appropriate spatial scale is the individual tree (*9*).

We created experimental red scale outbreaks (*13*). We caged individual trees and increased scale recruitment over a period somewhat longer than it takes scale to develop from birth to adult (this development period defines the time unit, *t*). We followed the dynamics of these outbreak populations, together with caged and uncaged control populations, over three to five scale development times. Three separate experiments gave the same result. We present only the third experiment, which had four outbreak trees.

Control of the outbreak and stability—return to equilibrium density—occurred rapidly (Fig. 1). Scale density began to decline even before crawler additions stopped and before one scale development period had passed, and most suppression occurred by *t* = 2; i.e., within 2 months after we added scale. By

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