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Supporting Online Material

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Cyclic Dynamics in a Simple Vertebrate Predator-Prey Community

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The collared lemming in the high-Arctic tundra in Greenland is preyed upon by four species of predators that show marked differences in the numbers of lemmings each consumes and in the dependence of their dynamics on lemming density. A predator-prey model based on the field-estimated predator responses robustly predicts 4-year periodicity in lemming dynamics, in agreement with long-term empirical data. There is no indication in the field that food or space limits lemming population growth, nor is there need in the model to consider those factors. The cyclic dynamics are driven by a 1-year delay in the numerical response of the stoat and stabilized by strongly density-dependent predation by the arctic fox, the snowy owl, and the long-tailed skua.

The cyclic dynamics of boreal and arctic populations of small rodents is one of the most intensively studied phenomena in population ecology. Many (1–4), although not all (5, 6), researchers now agree that the most likely mechanism that maintains cyclic dynamics in boreal vole populations is predation by specialist mustelid predators. In contrast, interaction with food resources is thought to drive the dynamics of at least some lemming populations (7). Even in the case of vole dynamics, competition among prey for space or food is thought to play a key role in halting prey population growth at high density, thereby allowing the predator population to catch up with their faster-reproducing prey (1, 3, 8–10).

One of the simplest vertebrate predator-prey communities is that of lemmings and their dependent predators in the high-Arctic tundra in Greenland. It constitutes only one mammalian prey, the collared lemming (*Dicrostonyx groen-*

landicus), and four predators, the stoat (*Mustela erminea*), the arctic fox (*Alopex lagopus*), the snowy owl (*Nyctea scandiaca*), and the long-tailed skua (*Stercorarius longicaudus*) (11, 12). The open tundra landscape and the continuous daylight in summer in the high Arctic provide particularly favorable conditions for fieldwork on vertebrate predators. We studied the densities, breeding success, and diet of the four predators in a 75-km² area in the Karup Valley in northeast Greenland (72°30' N, 24°00' W), from 1988 to 2002.

Lemming densities were estimated with live trapping for 1998 to 2002 (11, 13) and with regression between live-trapping results and lemming winter nest counts (12, 14) for the other years (15). The winter nests of lemmings are made of grass within snow beds and are easily located on the ground after snowmelt. We made a complete count of the nest numbers in an area of 15 km² every spring for 1988 to 2002. Although a varying number of lemmings may use the same nest (16, 17), the winter nest count in our large study area should closely reflect the actual number of lemmings. The correlation between the spring densities, as estimated by live trapping, and the winter nest count for the years 1998 to 2002 is high ($R^2 = 0.99$, $P < 0.01$) (fig. S1).

The stoat density was estimated from the number of lemming winter nests predated and occupied by stoats in the 15-km² area (12, 13). Stoats always use lemming nests in winter, and stoat-occupied nests are easily distinguished by the abundance of lemming fur within the nest (12, 18).

Daily predation rates were plotted against the current (daily) lemming density (N) to estimate functional responses of predators. Daily predation rates were estimated from scat samples for arctic foxes ($n = 927$) and stoats ($n = 663$), from direct observations for skuas ($n = 475$ hours), and from pellet samples and direct observations for snowy owls ($n = 3419$ pellets and 245 hours of observation). In the open landscape and in the continuous daylight of summer, the behavior of individual predators can be closely monitored over areas as large as 5 km².

Predator densities were plotted against lemming density at snowmelt to estimate numerical responses. With the exception of the stoat, separate responses were estimated for adults and weaned or fledged young (15).

The daily consumption rate of the avian predators is somewhat higher than that of the mammalian predators, but the latter are more efficient at catching prey at low lemming densities (predation half-saturation constant < 0.2 lemmings/ha) than are the former (≥ 1) (Fig. 1, upper row). The numerical responses of the predators are species specific. The nomadic snowy owl only settles and breeds in areas where lemming density at snowmelt (N') exceeds a threshold of ≈ 2 lemmings/ha. The constant adult density in summer of the migratory long-tailed skua is five times as high as that of the snowy owl when the latter is present, but the skua breeds successfully only when $N' > 1$. The arctic fox shows elevated breeding success when $N' > 1$ but maintains a relatively constant adult density, except in peak lemming years ($N' \approx 10$) (Fig. 1, middle row), when fox density may increase greatly.

The stoat is the only predator that shows a delayed response to changes in prey density, with highest numbers seen the year after the lemming peak (Fig. 2, top). The results for the

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stoat in Fig. 2 are based on the counts of lemming winter nests occupied by the stoat, rather than on population size estimates, but our field observations support the assumption that the winter nest count gives a reliable picture of the long-term dynamics (15).

The results in Fig. 2 demonstrate a 4-year cycle in lemming and stoat numbers from 1988 to 1998. The years 1999 to 2002 show a somewhat deviating pattern, possibly indicating that this cycle will be 5 years long. The occurrence of 4-year population cycles in lemmings is sup-

ported by another source of information. The trapping records for the arctic fox in northeast Greenland from 1935 until 1960 showed distinct peaks in the winters of 1937–38, 1941–42, 1946–47, 1950–51, 1954–55, and 1958–59 (19), at intervals of 4, 5, 4, 4, and 4 years. These trapping records most likely reflect changes in lemming density.

What is maintaining the regular 4-year lemming cycle? We have constructed a model to elucidate the role of predation in lemming dynamics. In our predator-prey model, the functional responses of the snowy owl, the long-tailed skua, and the arctic fox are dependent on N , and their numerical responses are determined by N' . Hence, these responses are strict functions of spring and current (daily) lemming densities, and the impact of these predators on the lemming population is implemented in the model through the functions in Fig. 1 (15). The responses of these predators are effectively density-dependent constants and, once estimated from field data (table S1), were never altered in our modeling.

The dynamic part of the model involves the lemming and the stoat. Reproduction in the collared lemming is continuous, with overlapping generations and with a higher rate of reproduction in winter than in summer (11, 20–22). The maximum observed lemming densities were ~10 individuals per ha (Fig. 2, top). This density could potentially be much higher (11, 23–25). There is an excess of burrows available for lemmings in our study area, and there is no evidence that food is a limiting factor (15). Because there is no evidence for space or food limitation, lemming dynamics were modeled by continuous-time exponential growth, with different growth rates for winter (r_w) and for summer (r_s , from June 15 to September 25).

The dynamics of the stoat were modeled by assuming that all females produce one litter per year and that stoat mortality is an S-shaped function of lemming density (15).

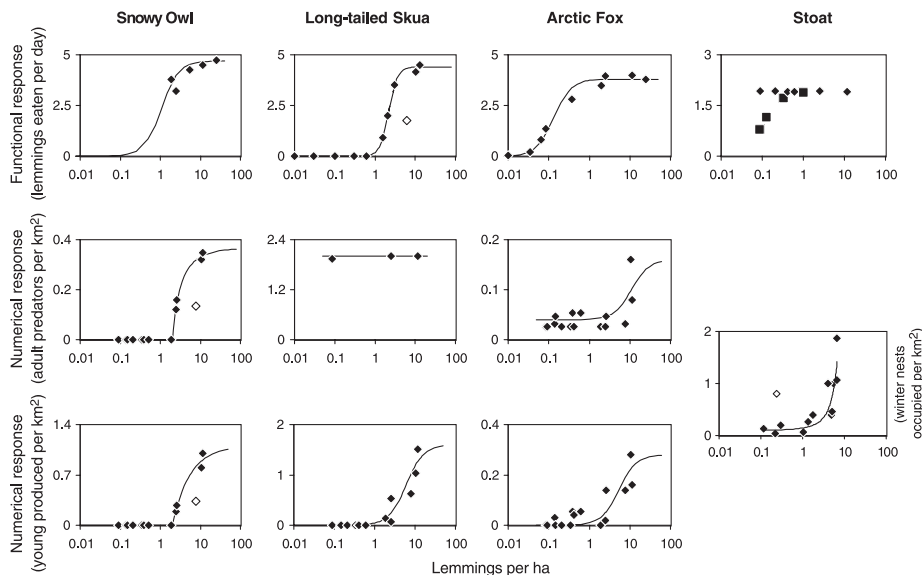


Fig. 1. Predators' responses to lemming density. Functional responses (top) are related to the current (daily) lemming density (N), whereas the numerical responses (middle and bottom) are related to the lemming density at snowmelt (N'). The numerical response of the stoat includes adults and weaned young and is delayed (x axis is the average lemming density at snowmelt for the past 2 years). The functional response of the stoat (top right) shows estimates based on winter (diamonds) and summer (square) scats. Open symbols are outliers resulting from unusual climatic or demographic situations (15). The numerical response of adult skuas could only be assessed for 1998 to 2000, when we arrived at the study area in the beginning of June and before the skuas started to flock. The species is known to have stable densities (28).

Fig. 2. Empirical (top) and model-predicted (bottom) time series for the lemming (squares) and the stoat (circles). Data points for the lemming are at snowmelt and for the stoat at midwinter. The lemming density estimate was calculated on the basis of absolute lemming winter nest counts for 1988 to 2002 and live-trapping density estimates for 1998 to 2002 (15). The gray line (bottom) shows the lemming dynamics predicted by the model; the bold black line represents the overall lemming dynamics to be compared with the empirical time series. There is a correspondence in cycle length, amplitude, and maximum lemming densities. Parameter values for the predicted series: $r_s = 0.8$, $r_w = 4$, $v = 4$, $c = 1000$, $D = 0.1$, $N_{crit} = 0.1$, $d_{low} = 0.1$, $d_{high} = 4$, and $b = 25$. v , number of weaned stoats produced per female per year; c , maximum per capita predation rate of the stoat, in lemmings per year; b , slope of the mortality function for the stoat (table S2).

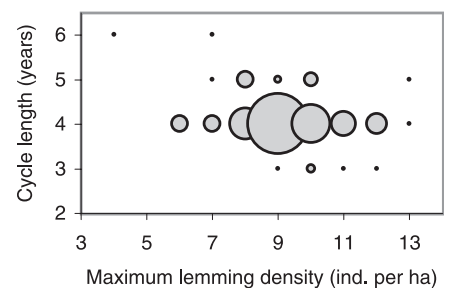
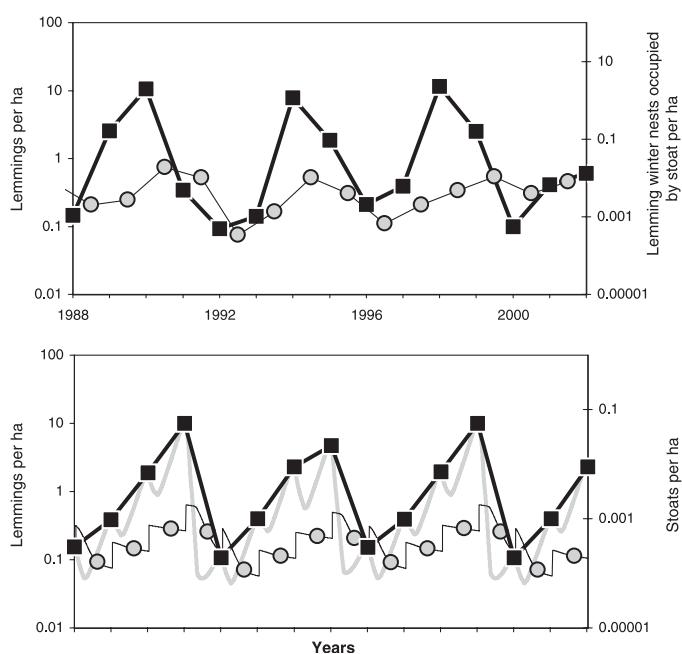


Fig. 3. Cycle lengths and maximum densities predicted by 81 parameter combinations given in table S2. Two combinations are not included that led to noncyclic dynamics or to the lemming population increasing exponentially. Circle width is proportional to the number of parameter combinations yielding the cycle length and maximum lemming density indicated in the figure (smallest circle, 1 parameter combination; largest circle, 17 combinations).

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Predation by stoat was modeled with a type III functional response (3) to incorporate the possibility of stoats finding alternative prey at lowest lemming densities, when lemmings are so dispersed (less than 10 per km²) that they must become very hard for stoats to locate (15). In this situation, with stoat density ≤ 1 per 15 km², it would be unrealistic to use a type II functional response, which assumes a steeply increasing predation rate for the lowest prey densities.

We analyzed the model numerically by keeping the parameters for the arctic fox, the snowy owl, and the long-tailed skua fixed at the values estimated in Fig. 1 and reported in table S1. Of the remaining parameters (table S2), the summer growth rate of the lemming (r_s), the predation half-saturation constant of the stoat (D), and the mortality rate parameters of the stoat (d_{low} , d_{high} , and N_{crit}) (15) have more uncertainty than the others. We ran model simulations for many combinations of these parameters (table S2). The model mostly predicts complex dynamics, but with a strong regular component, which most frequently has a period of 4 years (Figs. 2 and 3). The most notable difference between the predicted and observed dynamics is in the shape of the cycle: The increase phase of the cycle appears to be shorter in empirical results than in model predictions (Fig. 2).

Turchin *et al.* (7) have argued that Norwegian lemming oscillations, characterized by sharp and angular peaks, are driven by interactions with food plants, but our study suggests that similarly sharp peaks can also be observed for predator-regulated lemming populations.

The notable feature of the present modeling results is that there is no food or space limitation in the lemming dynamics; in other words, there is no intrinsic prey density dependence. This is supported empirically, because there is no evidence for food or space limitation in the field, or for any other mechanism, apart from predation, contributing to population regulation. The predicted dynamics are generated by a combination of destabilizing predation by the stoat and strongly stabilizing predation by the three other species of predators. This is an example of cyclic predator-prey dynamics in which the prey dynamics are entirely determined by predation.

If one of the avian predators is completely removed from the model, the dynamics change: The lemming escapes from the control of the predators. If removed, the arctic fox is less influential to lemming dynamics, which remain qualitatively unchanged, unless the summer growth rate of the lemming (r_s) is higher than 0.25 (which value is within the feasible range for r_s) (table S2). Removing the stoat, which has a much lower predation rate than the avian predators for most of the cycle (Fig. 1), does not allow the lemming to escape predator control as long as $r_s < 0.33$. However, removing the stoat

leads to noncyclic dynamics, because the delayed numerical response of the stoat is the driving force of the multiannual fluctuations. In this simple community, all the predators have distinct life histories and responses to changing prey population size, which should help them coexist on the single prey (26, 27).

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Supporting Online Material

www.sciencemag.org/cgi/content/full/302/5646/866/

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Materials and Methods

Fig. S1

Tables S1 and S2

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A Four-Base Paired Genetic Helix with Expanded Size

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We describe a new molecular class of genetic-pairing system that has a native DNA backbone but has all four base pairs replaced by new, larger pairs. The base pairs include size-expanded analogs of thymine and of adenine, both extended by the width of a benzene ring (2.4 Å). The expanded-diameter double helices are more thermodynamically stable than the Watson-Crick helix, likely because of enhanced base stacking. Structural data confirm a right-handed, double-stranded, and base-paired helical form. Because of the larger base size, all the pairs of this helical system are fluorescent, which suggests practical applications in detection of natural DNA and RNA. Our findings establish that there is no apparent structural or thermodynamic prohibition against genetic systems having sizes different from the natural one.

Previous studies aimed at making altered forms of DNA have focused mainly on changes to the phosphodiester backbone (1–5). Because the bases, rather than the backbone, encode information, it was not clear whether all of the four base pairs could be replaced and still function in specific se-

quence recognition and spontaneous self-assembly. This is particularly the case where non-Watson-Crick geometries are contemplated. Earlier studies aimed at replacing one or more of the natural base pairs (6–11) have used structures compatible with Watson-Crick purine-pyrimidine pairing.

The designs of size-expanded DNA bases are shown in Fig. 1. Each base is larger than the natural analog by 2.4 Å, the width of an inserted benzene ring, converting a bicyclic purine into a three-ring analog and a mono-

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cur on length scales far below those that are currently accessible. The most promising approach is to look not for small effects at relatively large length scales, but for large effects at the smallest possible length scales, where gravity is predicted to be strong. These probes are equally powerful for any n . For low n , they are superseded by those discussed above, but for large n , they provide the leading experimental tests.

Perhaps the most remarkable possibility for testing large n has been the realization that if gravity is strong at 10^{-19} m, tiny black holes may form in high-energy particle collisions (5–8). The formation of a black hole is expected when a large mass or, equivalently, a large energy is concentrated in a small volume (9, 10). In the conventional 3D world, gravity is so weak that the required energy density is never achieved in observable particle collisions. However, if large extra dimensions exist and gravity is intrinsically strong, very high energy particles occasionally pass close enough to each other to trigger gravitational collapse, forming microscopic black holes. Like conventional black holes, these black holes are expected to emit “Hawking radiation,” which leads to the evaporation of the black holes. In contrast to the astrophysical variety, however, they are

tiny, with diameters on the order of 10^{-19} m, and evaporate explosively after only 10^{-27} s.

Today’s particle colliders are not sufficiently energetic to produce microscopic black holes. However, ultrahigh-energy cosmic rays have been observed to collide with particles in Earth’s atmosphere with center-of-mass energies that are 100 times those available at human-made colliders. The ultrahigh-energy neutrinos that are expected to accompany these cosmic rays may create microscopic black holes. Although these black holes are extremely short-lived and hence impossible to detect directly, their explosive evaporations produce events with unusual properties (7, 8). The fact that no such events have been observed so far places strong constraints on large extra dimensions, but does not yet exclude these scenarios altogether (11).

The search for large extra dimensions will intensify. The currently operating Antarctic Muon and Neutrino Detector Array and its successor IceCube are kilometer-scale cosmic neutrino detectors buried deep in the Antarctic ice. The Auger Observatory, consisting of water Cerenkov detectors covering a 3000-km² area in the high desert of Argentina, will also begin operation in 2 to 3 years. These large projects

will provide enhanced sensitivity to the putative microscopic black holes (12, 13). The Large Hadron Collider, currently under construction in Geneva, will provide an even higher sensitivity to large extra dimensions.

If no anomalous effects are seen in these ambitious projects, the possibility of large extra dimensions will be excluded. If seen and confirmed, however, these effects will provide the first evidence for strong gravity and a radically new view of spacetime.

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ECOLOGY

Vole Stranglers and Lemming Cycles

Peter J. Hudson and Ottar N. Bjørnstad

For more than 80 years, population ecologists have been preoccupied with the rise and fall in population numbers among small mammal species, but they still cannot agree on the reasons for these cyclic variations in abundance. The controversy arises from three central questions: What are the ecological mechanisms that generate fluctuations in these cycles? Are these mechanisms common to all cyclic populations? Does understanding of these mechanisms allow us to explain why some populations are cyclic whereas others are not? The debate has been so heated among small mammal researchers that other ecologists jokingly refer to them as the “vole stranglers.” On page 866 of this issue, Gilg *et al.* (1) present their long-term field study of the cyclic dynamics of collared lemmings

(*Dicrostonyx groelandicus*) in northeastern Greenland and describe how these dynamics are affected by predators. The mathematical model that the investigators develop illustrates how the cyclic fluctuations of collared lemmings are driven by predation by the lemming specialist, the stoat, and then are molded (when lemming populations reach high densities) by three generalist predators: the arctic fox, the snowy owl, and the long-tailed skua (see the figure). The new work answers the first question and provides key insights into the third question.

The saying “Lemmings cycle—unless they don’t” (2) embodies the enigma of cyclic fluctuations in many lemming and vole populations inhabiting boreal and arctic ecosystems. The collared lemming is an excellent example: Some populations exhibit violent and periodic fluctuations in their numbers, whereas others exhibit no clear statistical pattern (3). The “vole stranglers” have come up with many hypotheses to account for this paradox. A favorite is the so-called

specialist predator hypothesis, which postulates that small mammal populations undergo periodic fluctuations in numbers in response to predation by a specialized predator (4). This hypothesis has taken center stage because the fundamental theory of predator-prey interactions—encapsulated in the worthy Lotka-Volterra model—predicts cycles in prey and predator abundance. Hence, it is natural to consider that a predator (or some other specialist consumer) is the crucial player in the cyclic dynamics of small mammal populations. At a more detailed level, theory predicts that interactions between a specialized predator and its main prey—such as the stoat’s predation of collared lemmings—should result in cycles in which the peak in predator numbers lags behind that of its prey by one-quarter of a cycle (4). This prediction is beautifully borne out by the Gilg *et al.* study (1). Indeed, this is one of those rare instances when nature appears to reflect basic theory—a textbook case.

One important feature of the specialist predator hypothesis is that a second stabilizing effect is needed at high lemming densities to slow down the growth rate of the prey and allow the specialist predator to catch up and drive prey abundance downward (5). The collared lemming is, again, a wonderful illustration. The cyclic fluctuations in lemming populations in northeastern Greenland appear to result from the tension between the

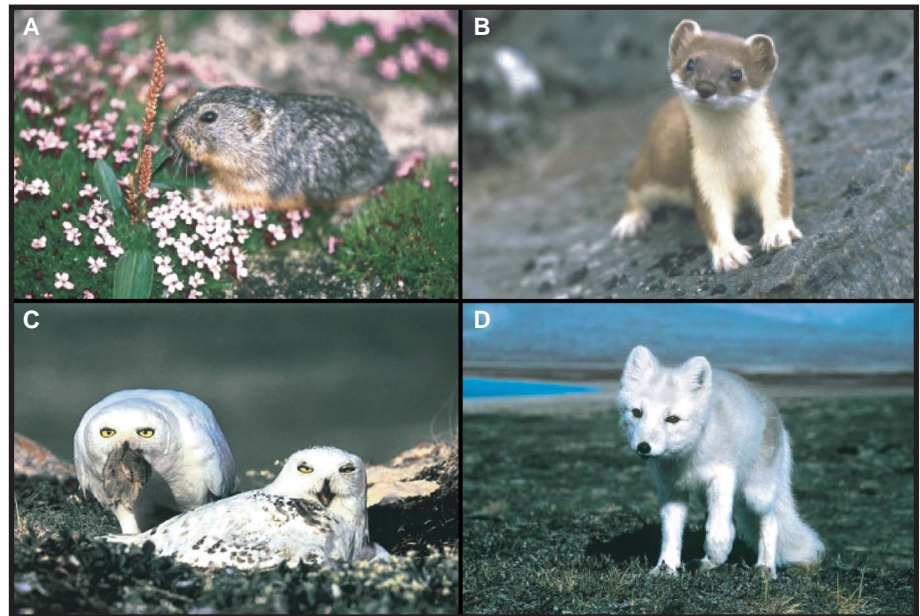
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destabilizing force of the specialist predator and the stabilizing effects of three generalist predators. The three generalist predators focus their predation on the lemmings only when populations of these rodents reach high densities. There is such a tight relationship between predator and prey that, as indeed the authors argue, these population fluctuations can be understood without having to invoke food availability, competition, or social interactions. In contrast, the noncyclic lemming populations in Arctic Canada appear to be trapped in a “generalist predator pit” where a complex guild of predators prohibits any increases in the lemming population (3). Taken together, such biogeographic comparisons provide critical insights into how the consequences of predator-prey (or, more generally, consumer-resource) interactions are affected by embedding in diverse food webs—that is, how predator-prey interactions are influenced by further consumer or competitive interactions (6, 7).

Of course, there is a difference between consistency of models and biological ground truth. The next step in the study of the collared lemmings is to use experimental manipulation of the rates of lemming predation to test the hypothesis mooted by Gilg and colleagues [e.g., (8, 9)]. Such experimental manipulations will provide a test of the theory and will reveal how to further refine the theoretical model. Sadly, ecologists rarely have the resources to “grasp the nettle” and go for such large-scale experiments. The issue for field biologists has been a tradeoff between replication of treatment and sufficient scale to ensure successful manipulation of the mechanism. Population-level experiments need to ensure that such manipulations result in effective changes in the putative ecological mechanism controlling cyclic dynamics. It could be argued that “appropriate-scaled” field experiments are logistically difficult and may have fiscal constraints that compromise the goal of effective treatment and appropriate data replication. There is some truth in this. However, even with low data replication, we can test such experiments against models and distinguish between competing hypotheses. After all, true independence of study sites is virtually impossible, as, according to the ecologist Stephen Ellner, “nature itself is just one unreplicated realization of a large stochastic process.”

Elegant manipulations of predation have been undertaken in other cyclic rodent populations but have resulted in divergent conclusions (10–12). These experiments illustrate the scientific complexities that have faced the “vole stranglers” for decades. The theories are sound and developed, the hypotheses are elegant, and the predictions are clean. At times, however, researchers have been tempt-



A choice of predator. The cyclic dynamics of collared lemming populations are determined by a range of predators. In northeastern Greenland, the collared lemming (A) undergoes cyclic fluctuations in abundance as a consequence of predation by the lemming specialist, the stoat (B). However, lemming populations could escape control by the stoat if it were not for the stabilizing predation of three generalist predators: the snowy owl (C), the arctic fox (D), and the long-tailed skua (not shown).

ed by the Popperian approach of hypothesis falsification and with one experimental falsification have “thrown a general hypothesis out with local idiosyncrasies.” A clear illustration of geographic differences regarding causes of population cycles is provided by northern European grouse. Experimental studies have identified parasites (an extreme specialist) (9, 13) and territorial behavior (14) as forces that destabilize host abundance in the British Isles. Yet there is also evidence that predation by the specialist gyrfalcon drives the cyclic fluctuations of grouse in Iceland (rock ptarmigan) (15). To understand the cycles of boreal and arctic lemmings, we sorely need more field experiments and an analysis that quantifies the changes in predator-prey interactions resulting from such field manipulations. An ultimate meta-analysis of these experiments will resolve the final question about lemming cycles: Does the same mechanism account for all cyclic lemming populations, and if not, why not?

These complexities aside, Gilg *et al.* (1) demonstrate how a simple (“few-species”) clockwork predator-prey interaction results in spectacular lemming cycles in northeastern Greenland, and how rodent dynamics are regulated in a top-down manner. Because most rodent species are found in widely divergent environments and are embedded in complex food webs involving competitors and resources, extrapolating the Gilg *et al.* findings to other cyclic rodent populations is probably unwise. However, if we turn from the apparent simplicity of high arctic ecosystems to arguably one of the most complex

predator-prey ecosystems in the world—the Serengeti plains of Tanzania in East Africa—we start to see some interesting patterns. A recent study (16) provides evidence that the abundance of small herbivores in tropical Africa is determined principally through top-down predation, whereas the larger herbivores are regulated by limited resources in a bottom-up process. We are now well on the road to explaining biogeographic variations in abundance and dynamics through species interactions and embedding in ecosystems, the sort of questions Elton was asking some 80 years ago when he first described the cyclic dynamics of small mammal populations.

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length for a fixed microwave amplitude, Chiorescu *et al.* traced out a series of damped Rabi oscillations with a decay time of about 150 ns. In two further experiments involving sequences of pulses, they obtained a decoherence time of about 20 ns and a relaxation time from the excited state of about 900 ns.

The flux qubit—the realization of Leggett's original proposal—joins the charge and phase qubits as a means of observing the coherent superposition of two quantum states in a superconducting circuit. What happens next? A major issue for all three kinds of qubits is the source of decoherence. There are many candidates, including external flux noise, Nyquist noise currents in nearby metallic objects, $1/f$ (“flicker”) noise in the critical current of Josephson junctions, spin fluctuations, the motion of charge in traps, and noise in the

measurement scheme. However, even with the available decoherence times, one could attempt to “entangle” two qubits. As a step in this direction, Pashkin *et al.* (10) have recently reported coherent mixing of quantum states by capacitively coupling two charge qubits. A classic example of entanglement is the simultaneous emission of two photons with zero net spin that move away in opposite directions: Measurement of the spin of one photon predicts the outcome of a subsequent measurement of the other, no matter how far away. It would be fascinating to examine this action-at-a-distance—known as the Einstein-Podolsky-Rosen paradox (11)—with superconducting circuits. Tests of quantum mechanics versus macroscopic realism may be within reach (12).

Entanglement is also necessary for quantum computation. Whether or not a large-scale quantum computer can ever be

realized—with superconducting qubits or otherwise—remains to be seen, but in the meantime, the quest for it is likely to drive many beautiful experiments.

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ANTHROPOLOGY

Overkill and Sustainable Use

Martyn Murray

For over two decades, the international conservation lobby has advocated economic development as the primary means of achieving sustainable living (1). This goal has proved elusive even when biological resources are controlled by local communities (2, 3).

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Nevertheless, many development agencies have accepted commercial incentives and regulations as the mainstay of their conservation effort (4), apparently without taking into account humankind's long history of exploiting wild living resources. Consideration of episodes of overkill and sustainable use in human history may inform the prevailing conservation paradigm.

“Overkill”—a conspicuous decline in a population of hunted animals without prospect of stabilization or recovery—is often coupled with trade in animal products and wastage of less valuable parts of the carcass. It has been cited in the late Pleistocene extinctions of large mammals in Australia, New Guinea, and the Americas (5); the extinction of large flightless birds in New Zealand in the 14th century (6); the North American fur trade in the 17th and 18th centuries (7, 8); and the current harvest of wild meat from increasingly accessible tropical forests in west and central Africa (9).

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In contrast, sustainable harvesting ensures that wildlife populations remain numerically stable. It is usually assumed implicitly that hunters could kill at a higher rate if they so chose. Sustainable harvesting has been claimed in red deer stalking in the Scottish Highlands in the 19th and 20th centuries (10); the hunting of wildlife by Bushmen in the Kalahari in the mid-20th century (11); and the hunting of game animals on private farmland in southern Africa in the late 20th century (12).

Onset of Overkill

Four triggers are commonly associated with unsustainable hunting: occurrence of naïve prey, vulnerable animals, new technology, and trade.

Naïve prey is believed to have played a key role when paleolithic hunters crossed the Bering land bridge in about 12,000 B.C. and spread across North and South America, all the while hunting native large mammals so effectively as to bring about their extinction (5). The hunters invading the Americas may have been more effective than those in Africa and Asia because their prey

lacked awareness of humans as predators (13).

Top predators and highly specialized species may be vulnerable to overexploitation because they reproduce slowly. Migratory animals may be at risk because of the perception that their populations are limitless.

The northern Plains Indians believed that the bison herds disappeared each season to graze beneath the water on pastures where they bred in countless numbers (8). At the same time as the near extinction of bison, the passenger pigeon became extinct. One of John Muir's characters remarks that “they were made to be killed, and sent for us to eat as the quails were sent to

God's chosen people” (14). Prey animals are also vulnerable if another primary source of food is available to their predator, allowing the latter to persist at high density even when its prey has been reduced. Hence, Australian marsupials are vulnerable to foxes, which have rabbits as their primary prey (15).

New technology is often incriminated in wildlife overkills. The extinction of Pleistocene mammals in Africa has been linked to the development of hand axe cultures (16). Soon after Europeans arrived in the Americas, Native Americans began trading pelts for guns and steel traps that contributed to the decline in large mammals. In Africa, wire snares set in lines are one of the most effective overkill technologies. Declines in freshwater and marine



Rock painting of a Bushman hunter from the Western Cape of South Africa.

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fisheries have followed the introduction of ever more sophisticated and indiscriminating fishing craft and gear.

Efficient technology also tends to divorce hunters from their prey by reducing, or dispensing with, the respect often found in the human-wildlife relationship of indigenous peoples (17). Among modern recreational hunters, this respect is reflected in the notion of sportsmanship, which disapproves of methods that kill easily or indiscriminately.

Powerful market forces are frequently implicated in the overexploitation of animals and plants. For example, the ivory trade has long affected the fortunes of African elephants. According to Pliny (23 to 79 A.D.), demand for ivory in the Roman Empire was so great that the elephants of North Africa succumbed. From the 16th to the early 20th century, the booming African ivory trade with Europe led to a continental decline in elephants. In the latter part of the 20th century, trade in ivory with Japan and Hong Kong precipitated yet another decline.

Overkill is thus clearly not a new phenomenon. Nor, however, is it the inevitable consequence of human utilitarianism in relation to hunting. The archaeological record indicates that certain pre-agricultural societies may have lived within the regeneration capacity of wildlife populations over long periods (18). Late Stone Age hunters seem to have adapted to their impoverished faunas after they had exterminated Pleistocene vertebrates. How they did so is seldom discussed.

Sustainable Harvesting

Three factors are associated with sustainable hunting: availability of alternative sources of food, ownership of wildlife resources, and existence of cultural and spiritual beliefs.

Alternative sources of food were available to Bushmen occupying traditional territories in the central Kalahari. When game was in short supply, the Bushmen could survive on plants. But rather than using their plant-based subsistence to exterminate local prey species, they reduced their hunting and created a sustainable life-style (11). Their nomadic system of utilization is thought to have lasted for at least 2000 years, without evidence of environmental degradation or species loss. Only in recent decades have wildlife populations declined. This coincided with the Bushmen being dispossessed of their land and the right to manage their natural resources.

Control of wildlife resources has also been instrumental in creating one of the success stories in African conservation. Since a change in legislation provided commercial farmers in southern Africa with effective

ownership of wildlife on their lands (12), a lucrative wildlife industry has arisen based on trophy hunting, wildlife harvesting, and tourism. Wildlife populations have increased on many farms and ranches.

It has been suggested that a spiritual relationship with nature may preclude overexploitation (7). After the overkill episodes of the Pleistocene, Native Americans coexisted with the remaining prey species [though some late Holocene cultures depressed populations of large fishes and mammals (19)]. The environment of the precontact peoples of eastern Canada seems to have been filled with spirits that imbued animals, plants, and everyday objects with power and influence, the people apparently maintaining amicable relations with these spirits.

It has, however, been pointed out that such a close spiritual relationship with game animals, despite dictating good conduct, does not necessarily prevent overexploitation (8). Native Americans believed that by honoring a slaughtered animal in a prescribed manner they could ensure its reappearance in future hunts. In this case, should beavers disappear from a region, the intensity of trapping would not be implicated. Rather, greater care would be taken to obey the proscribed taboos. The game animals may therefore have persisted through the Holocene owing to their lack of vulnerability—just as they had survived the Pleistocene extinction.

Given our limited knowledge of the precontact relationship between Native Americans and wildlife, it is difficult to assess the relative influence of these rival expositions. But in the case of the Bushman hunter-gatherers, there is evidence of a direct association between cultural beliefs and environmental policy. Among the G/wi, it was important that respect be shown to all creatures created by N!adima (the supreme being) because each has its own place in his world, being a part of his property. Killing more than one head of game at a time would anger N!adima. Anthropologists living with isolated bands have reported that the Bushmen understood the balance between the material needs of their groups and the productivity of their semi-arid environment (11, 20).

Social Disruption

If cultural or spiritual restraints underpin sustainable living, then episodes of overkill might be expected during periods of social disruption. When infectious diseases were brought to the New World by Europeans, the Native American peoples were devastated even before most had made direct contact. It has been suggested that the ensuing epidemics undermined the shamans' ability to influence the supernatural realm and invalidated the peoples' sacred rela-

tionship with wildlife. This apostasy may explain the enthusiastic participation of Native Americans in a trade that locally exterminated many valuable species (7). Others have argued that the material value placed on European goods by Native Americans alone brought about the overkill of fur-bearing animals (21). In either case, some Native American groups have reestablished sustainable forms of hunting several centuries after the disruption initiated by European contact (7).

At first thought the notion of sustainable harvesting may appear to be a precarious and unlikely human enterprise, particularly in regions with expanding human populations. As previously stated, there is some suggestion in the archaeological and anthropological records that a few subsistence economies have been stable over long periods (18). Perhaps times of overexploitation punctuate rather than dominate human history.

It is generally agreed that a stable society with a secure sense of ownership of prey animals is crucial for a sustainable use of wildlife. Here, the term "ownership" refers to the sense of exclusive access or use that in modern society can be traced back to the Norman game laws in the 11th century (22). The term could also convey an intimate spiritual connection with animals and the environment. Ownership might furthermore be linked to an understanding of the habits and behavior of prey animals. Constantly knowing where one's prey is and what it is doing may elicit proprietary feelings, whereas if the behavior of prey animals is virtually unknown—for example, because they migrate quickly through the hunter's range—there is little incentive to care for them.

The latter type of ownership was probably absent among the bands of Paleolithic hunters moving swiftly into new hunting grounds each year, and among the Europeans of the 15th to 19th century in America, Africa, and elsewhere. All three senses of ownership would suffer in severely disrupted societies.

Conclusions

Conservationists wishing to reduce overkill are presented with two main options: make animals harder to market through restrictions in access, trade, and the use of modern technology, or provide resource users with a greater sense of ownership. The conservation community currently places much emphasis on granting exclusive rights to commercial harvesting, be it on private, state-owned, or common lands. The spiritual and knowledge-based dimensions of ownership are usually ignored. Possibly the spiritual relationship is seen as aboriginal and irrele-

vant to modern management, while the knowledge-based relationship is sidelined as academic and equally impertinent. When modern society does recognize these dimensions, it often employs them defensively: The inspiration from natural beauty is used to establish protected areas, and biological knowledge is used to set limits to the catch or bag. By contrast, the biological knowledge and spiritual understanding of the traditional hunter enhanced his sense of identity with the prey.

The role of indigenous peoples in sustaining wildlife resources is beginning to be recognized. In a few pioneering ventures, indigenous peoples have participated in the management of protected areas (23). There is room for much greater appreciation and wider incorporation of traditional beliefs, values, and knowledge in contemporary conservation and development. An ongoing exploration of these dimensions in the global context would also constructively broaden the current economic focus.

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BOTANY

Relieving DELLA Restraint

Nicholas P. Harberd

According to an old English nursery rhyme: “Oats and beans and barley grow, ..., nor you nor I nor anyone knows how oats and beans and barley grow.” On page 1896 of this issue, Sasaki *et al.* (1) bring us closer to understanding the age-old mystery of plant growth.

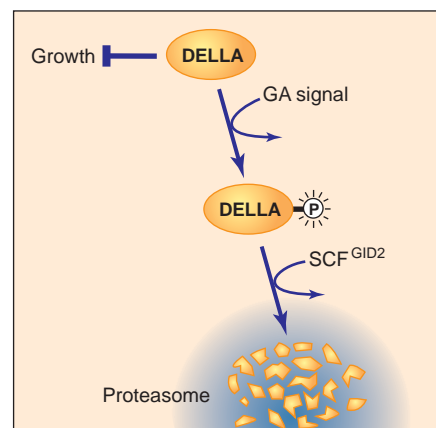
The phytohormone gibberellin (GA) controls plant growth. Mutant plants deficient in GA are dwarfed, and treating these plants with GA restores normal growth (2). It is unclear exactly how plant cells detect GA, but our understanding of downstream GA signaling events is more advanced. A family of proteins, the DELLA proteins, are key intracellular repressors of GA responses (3, 4). The “relief-of-restraint” model proposes that DELLA proteins restrain plant growth, and that growth is promoted by a GA signal that relieves plants of DELLA-mediated growth restraint (2, 3).

Recent advances have put some biochemical and cellular flesh on the bones of the restraint model. For example, DELLA proteins are known to be localized in the nucleus of plant cells but disappear rapidly in response to GA (5, 6). In addition, the disappearance of the DELLA proteins in-

duced by GA requires both protein phosphorylation and a functional 26S proteasome, the cellular organelle that degrades proteins (7).

Targeted degradation of regulatory proteins by the proteasome is an important mechanism for controlling cellular and developmental signaling in a wide variety of organisms. For example, the phytohormone auxin regulates plant development through proteasome-mediated degradation of members of the AUX/IAA family of auxin signaling proteins (8). Sasaki *et al.* (1) now rewrite the relief-of-restraint model in terms of specific GA-promoted targeting of DELLA proteins to the proteasome. First, they describe the properties of rice *gid2* mutants. These mutants exhibit a dwarf phenotype resembling that conferred by GA deficiency. However, unlike GA-deficient rice mutants, *gid2* mutants exhibit reduced GA responses and do not resume normal growth when treated with GA.

Molecular cloning revealed that the *GID2* gene encodes a protein containing an F-box domain. F-box domains are found in specific components of the multisubunit SCF E3 ubiquitin ligase complex. This enzyme complex targets proteins for destruction in the proteasome by tagging them with a chain of ubiquitin molecules. *GID2* may be part of an SCF complex and may interact with another



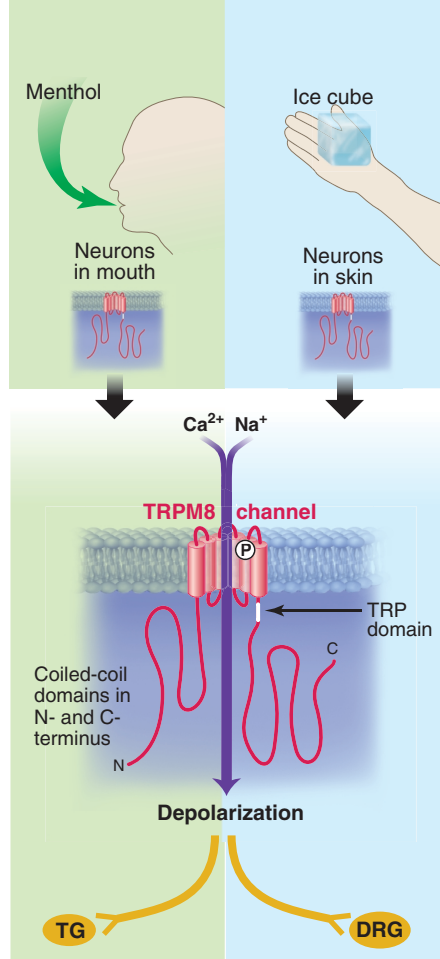
A restraining order for plants. The DELLA proteins, such as SLR1 in rice, restrain plant growth. In response to a GA signal, the DELLA proteins are first phosphorylated, then targeted for destruction in the proteasome by polyubiquitination. The addition of a polyubiquitin chain is catalyzed by the SCF^{GID2} E3 ligase. Degradation of the DELLA proteins releases the restraint on plant growth.

SCF complex component called OsSkp2. In addition, *GID2* turns out to be a rice ortholog of the *SLY1* gene of *Arabidopsis*. *SLY1* also encodes a positive regulator of GA signaling (9), which suggests that *GID2* and *SLY1* have similar functions.

Now that *GID2* is established as a likely candidate component in a GA-specific SCF E3 ligase complex, what is the substrate of this complex? Could it be the rice DELLA protein SLR1 (6)? Sasaki *et al.* (1) show that in rice *gid2-1* mutants SLR1 accumu-

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SCIENCE'S COMPASS



Cool mint. Mildly cool temperatures (25° to 15°C) and the cooling agent menthol activate the TRPM8 ion channel. This channel is expressed by sensory neurons in the mouth that project to the trigeminal ganglia (TG) in the brain, and by sensory neurons in the skin that project to the dorsal root ganglia (DRG) of the spinal cord. When activated, TRPM8 channels open, allowing Ca²⁺ and Na⁺ ions into neurons, which then become depolarized. TRPM8, like other TRPM channels, is a tetramer with each subunit containing six transmembrane domains and unusually long amino and carboxyl termini.

amino acids in length, is in the class of TRP channels that has extremely long amino and carboxyl termini rather than in the vanilloid class of temperature-sensing TRPs containing ankyrin repeat domains. This class of long or melanostatin-related TRPs was thought to be involved in cell division, although the best-characterized TRP channels are all sensory: The *Drosophila* TRP channel is involved in vision, and the vanilloid TRPs sense temperature or osmotic changes.

It is intriguing that although TRPM8 was already identified, its sensitivity to temperature and menthol remained undiscovered. First, the classification of TRPM8 in the TRPM family may have been somewhat misleading because it does not bear close homology to TRPM class members. Also, presumably due to low levels of mRNA, TRPM8 did not show up in commercially available Northern blots of nervous tissue. Finally, because most cells in patch-clamp recordings are equilibrated at ~22°C, the TRPM8 current would have been only weakly activated.

The two studies are in reasonable agreement about the threshold for activation of TRPM8 (22° to 26°C), and the ~5°C shift induced by subactivating concentrations of menthol. Also, both studies agree that the channel is expressed in small-diameter neurons, consistent with the known sensitivity to temperature of unmyelinated C and thinly myelinated A δ primary afferent sensory neurons. However, the papers do come to some different conclusions. In cultures of mouse trigeminal sensory neurons, McKemy *et al.* found that ~50% of neurons expressing TRPM8 also expressed TRPV1 (VR1). This suggests that some neurons are both heat and cold sensors, potentially explaining the confusing sensations that we humans can have with hot and cold stimuli. As McKemy *et al.*

point out, simultaneous contact with warm and cool surfaces (such as a thermal grill) evokes a sensation of burning pain. Also, mild cold can induce a feeling of burning pain after elimination of large nerve fibers by nerve block or injury. Using in situ hybridization in trigeminal ganglia from adult mice, Peier *et al.* found that TRPM8 was not expressed in TRPV1 (VR-1)-containing neurons, suggesting that there exist distinct subpopulations of neurons expressing either TRPM8 or TRPV1. Peier *et al.* also propose that the TRPM8 channel is uniquely associated with neurons that express the TrkA growth factor receptor; indeed, TRPM8 mRNA was not present in newborn mice lacking TrkA. The issue of whether heat and cold sensors are in the same neurons could be efficiently resolved in further studies of freshly isolated human and mouse nerve tissue.

Besides the complex road ahead for determining how neurons recognize and evaluate temperature, another set of interesting mysteries remains to be solved. The thermosensors TRPV1, TRPV2, and TRPM8 are expressed not only in neurons but also in nonneuronal cells. What could these receptors be doing in such tissues as the prostate? Finally, it will be intriguing to learn the native chemical messengers in neurons that open these channels.

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PERSPECTIVES: ECOLOGY

Of Predators, Prey, and Power Laws

Pablo A. Marquet

Power laws, in which one quantity can be expressed as some power of another, are ubiquitous in physical and social systems. They have been used to describe phenomena as diverse as the frequency of earthquakes of different magnitudes (the Gutenberg-Richter law), the distribution of income among individuals

(Pareto's law), and the rank-frequency distribution of city sizes, or words in natural languages (Zipf's law) (1, 2). Power laws in the form of scaling or allometric relationships are used by biologists to express how physiological, ecological, and life-history attributes relate to body size (W) raised to a power, usually a multiple of 1/4 (3). Among the vast number of biological power laws, those related to energy acquisition, transformation, and delivery are of fundamental importance, because energy sustains life. Thanks to the work of Max

Kleiber in the 1930s, we know that the amount of energy organisms need to extract from their environments to sustain themselves, metabolism (M), scales with body mass according to $M \propto W^{3/4}$ (Kleiber's law) (4). This simple power law represents a fundamental first principle whose consequences for the structure and operation of ecological systems we are just beginning to appreciate. On page 2273 of this issue, Carbone and Gittleman (5) demonstrate that the interaction between metabolic requirements and locally available energy can account for the observed power law relation between carnivore population density and body size. Their approach illustrates the importance of incorporating local ecological information if we are to understand large-scale patterns in biodiversity.

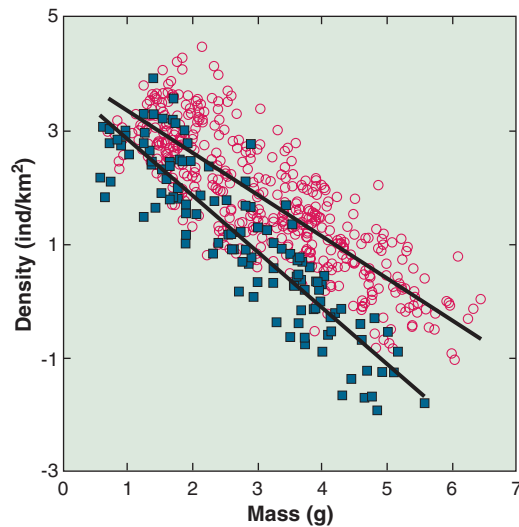
It follows from Kleiber's law that a lim-

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ited amount of available energy per unit area will sustain a larger number of individuals of a small-sized species than of a bigger species. Thus, assuming energy limitation, population densities (N) of large species are expected to be lower than those of smaller ones because of their higher total metabolic demands, and both are expected to conform to a power law of the form $N \propto W^{-3/4}$. Available estimates, based on the compilation of data from different ecosystems worldwide, show that mammalian primary consumers (herbivores) conform well with this expectation (6). Furthermore, because the energy available to secondary consumers (those feeding on other animals) is less than that available to primary consumers (7), it is expected that carnivores will reach lower population densities than similar-sized herbivores. Available data for mammalian species also support this expectation (8, 9). However, what has puzzled ecologists for a long time is that the allometric exponent of this power law is considerably smaller (that is, steeper slopes in the range -1.0 to -0.8) than $-3/4$ (see the figure). Explanations for this discrepancy have been elusive, and are usually based on presumed systematic (allometric) variations in prey biomass and productivity with predator body mass (8). However, Carbone and Gittleman present data showing that the relation between population density and size in mammalian carnivores (species of the order Carnivora) is constrained by metabolic rate and by variability in their resource base (prey species) such that the $-3/4$ power law only emerges if the local productivity of prey species, experienced by a carnivore population, is taken into account. Thus, the answer to the anomalous scaling of mammalian secondary consumers is found in local resource availability.

Carbone and Gittleman incorporate resources available to carnivore species into allometric equations by assuming that under energy limitation, the maximum density N_{\max} that a species can attain is related to the rate of resource supply per unit area (R) and to the average rate of resource use per individual (M) by $R \propto N_{\max} \times W^{3/4}$, which amounts to $N_{\max}/R \propto W^{-3/4}$ (Equation 1) (10). Most studies, however, have implicitly or explicitly assumed that the rate of resource supply in different environments is constant and bounded within similar levels, reducing the previous equation to $N_{\max} \propto W^{-3/4}$. But, as Carbone and Gittleman show, this is not a safe assumption for secondary consumers, carnivores in particular,

because there is a positive relation between available resources and carnivore population density, which (assuming energy limitation) renders misleading comparison across secondary consumer species using data from populations experiencing environments that differ in the availability of resources. These authors demonstrate that density estimates should first be made comparable by standardizing them by the amount or rate at which they become available to each population. To accomplish this, Carbone and Gittleman standardize carnivore density according to their available resources, estimated as biomass and productivity of available prey. Thus, using



Carnivores on a slippery slope. The power law in mammalian population densities. The relation between the logarithms of population density and body mass in mammalian primary (open circles) and secondary (filled squares) consumers. The relation for primary consumers (herbivores) has a slope of $-3/4$, whereas the slope for secondary consumers (such as carnivores) is much steeper. Population density and body mass data are from a worldwide compilation by Damuth (11).

Equation 1 and assuming that carnivore density does in fact scale with carnivore mass as $W^{-3/4}$, they accurately predict the allometry of carnivore numbers per 10,000 kg of prey and per unit productivity of prey, accounting for a larger proportion of the variance in carnivore population density. This result lends support to the energy limitation hypothesis and underscores the importance of prey density for the persistence of carnivore populations.

The study by Carbone and Gittleman raises several questions with important implications. In particular, why do herbivore populations show a $-3/4$ power allometric scaling without the need for standardizing by resource availability? The wide variability observed in the density of similar-sized species of herbivorous mammals suggests

that they might be affected by local resource availability, but that this variability is averaged out when considering a large number of species and populations. This would imply that small samples of herbivorous species might show steeper slopes, similar to the one observed for secondary consumers. A simple bootstrap analysis of a data set reported by Damuth (11) reveals that the slopes characterizing secondary consumers are significantly steeper ($P = 0.0005$) than expected from sampling alone (see the figure) (12), suggesting that the density-size power law for herbivores reflects the scaling of their metabolic demands (6). Considering that plant species density follows the same $-3/4$ power law (13) as do the herbivores that feed on them, a related question is why the power law in herbivore density does not map onto one with a similar allometric exponent for carnivores such that it is necessary to correct for prey abundance? The answer to this question probably lies in constraints upon the prey size spectrum available to predators of different body sizes, competition for prey species, and ecosystem productivity. A definitive answer to this and related questions, however, will benefit from detailed allometric studies of food webs within local communities.

Finally, Carbone and Gittleman illustrate that our understanding of power laws, and other macroecological patterns in ecosystems, can be enhanced by going beyond the compilation of published data devoid of local ecological context. As has been demonstrated (14), power laws are ubiquitous within local ecosystems and may hold the clue to understanding large-scale patterns in the structure and function of biodiversity.

References and Notes

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