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 These probes are equally powerful for any n. For low n, they are superseded by those discussed above, but for large n, they provide the leading experimental tests.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-km^2 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.

References

1. N. Arkani-Hamed, S. Dimopoulos, G. R. Dvali, *Phys. Lett. B* **429**, 263 (1998).
2. E. G. Adelberger *et al.*, http://arXiv.org/abs/hep-ex/0202008 (2002).
3. S. Cullen, M. Perelstein, *Phys. Rev. Lett.* **83**, 268 (1999).
4. L. J. Hall, D. R. Smith, *Phys. Rev. D* **60**, 085008 (1999).
5. S. B. Giddings, S. Thomas, *Phys. Rev. D* **65**, 056010 (2002).
6. S. Dimopoulos, G. Landsberg, *Phys. Rev. Lett.* **87**, 161602 (2001).
7. J. L. Feng, A. D. Shapere, *Phys. Rev. Lett.* **88**, 021303 (2001).
8. L. A. Anchordoqui, H. Goldberg, *Phys. Rev. D* **65**, 047502 (2002).
9. D. M. Eardley, S. B. Giddings, *Phys. Rev. D* **66**, 044011 (2002).
10. H. Yoshino, Y. Nambu, *Phys. Rev. D* **66**, 065004 (2002).
11. L. A. Anchordoqui *et al.*, http://arXiv.org/abs/hep-ph/0307228 (2003).
12. M. Kowalski, A. Ringwald, H. Tu, *Phys. Lett. B* **529**, 1 (2002).
13. J. Alvarez-Muniz *et al.*, *Phys. Rev. D* **65**, 124015 (2002).

ECOLOGY

Vole Stranglers and Lemming Cycles

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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

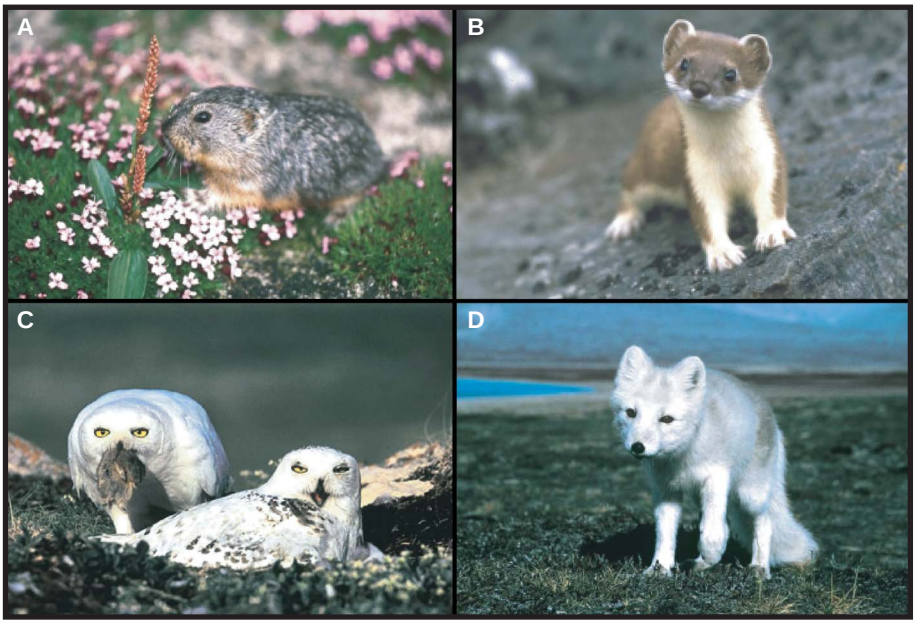
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destabilizing force of the specialist predator and the stabilizing effects of three generalist predators. The three generalist predators focus their predation on the lemmings only when populations of these rodents reach high densities. There is such 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 tempted 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 gyr falcon 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.



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).

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References

1. O. Gilg, I. Hanski, B. Sittler, *Science* **302**, 866 (2003).
2. I. Hanski, *Trends Ecol. Evol.* **2**, 55 (1987).
3. D. G. Reid, C. J. Krebs, A. Kenney, *Ecol. Monogr.* **67**, 89 (1997).
4. W. M. Murdoch, C. Briggs, R. M. Nisbet, *Consumer Resource Dynamics* (Princeton Univ. Press, Princeton, NJ, 2003).
5. I. Hanski, L. Hansson, H. Henttonen, *J. Anim. Ecol.* **60**, 353 (1991).
6. E. McCauley, R. M. Nisbet, W. W. Murdoch, A. M. De Roos, W. S. C. Gurney, *Nature* **402**, 653 (1999).
7. O. N. Bjørnstad, N. C. Stenseth, T. Saitoh, O. C. Lingjære, *Res. Popul. Ecol.* **40**, 77 (1998).
8. C. J. Krebs *et al.*, *Science* **269**, 1112 (1995).
9. P. J. Hudson, A. P. Dobson, D. Newborn, *Science* **282**, 2256 (1998).
10. E. Korpimaki, K. Norrdahl, *Ecology* **79**, 2448 (1998).
11. J. Sundell, *Oikos* **101**, 416 (2003).
12. I. M. Graham, X. Lambin, *J. Anim. Ecol.* **71**, 946 (2002).
13. P. J. Hudson *et al.*, *Philos. Trans. R. Soc. London* **357**, 1259 (2002).
14. F. Mougeot, S. M. Redpath, F. Leckie, P. J. Hudson, *Nature* **421**, 737 (2003).
15. O. Nielsen, *J. Anim. Ecol.* **68**, 1034 (1999).
16. A. R. E. Sinclair, S. Mduma, J. Brashares, *Nature* **425**, 288 (2003).