ECOLOGY

It's a Wonderful Gift

Rolf O. Peterson

How Species Interact
Altering the Standard View on Trophic Ecology
by Roger Arditi and Lev R. Ginzburg
Oxford University Press, Oxford, 2012. 184 pp. $59, £40. ISBN 9780199913831.

It is not often that mathematical theory is tested with a machine gun. In 1981 Dave Kelleyhouse, a wildlife biologist employed by the state of Alaska, submitted a purchase requisition for an automatic rifle to shoot wolves from aircraft in order to increase moose hunter success. If removing wolves was the management goal, it seemed to make sense to accomplish this as efficiently as possible. "Machine-gun Kelleyhouse" didn't reckon that public opinion would play a role and that, once the public weighed in, his supervisors would be displeased (*1*).

It is doubtful that elegant math was really on the wildlife biologist's mind. But 11 years later, when the "experimental results" of killing wolves entered the scientific literature, it was packaged as a field test of a theory based on very seductive mathematical equations and graphs. The idea was that, if wolves and wolf kill rates could be brought to a very low level, low-density moose populations would increase and then remain at high density even when wolves were allowed to recover (*2*). Alas, the general result of temporary, intensive killing of wolves did not result in abundant moose, much less a "Serengeti of the North" (*3*). Instead, in almost all cases, as wolves recovered, there was a proportional reduction in moose density.

Proportional change in predator and prey populations is the theme of *How Species Interact*, the slimness of which belies its actual importance. In it, theoretical ecologists Roger Arditi (AgroParisTech) and Lev Ginzburg (Stony Brook University) provide a comprehensive summary of their long journey to recast scientific understanding of predator-prey dynamics. The authors continue to nudge ecologists beyond the classical Lotka-Volterra paradigm to a more realistic view they have termed "ratio dependence." Although their argument seemingly focuses on a small, arcane arena of population biology, few areas within ecology could be more fundamental (*4*).

Over two decades ago, Arditi and Ginzburg published a provocative paper in which they argued that ecologists had been misled during the previous half-century (*5*). Notwithstanding the elegant experimental work by Gause (*6*), Holling (*7*), and others in the decades following the much-cited work of Lotka (*8*) and Volterra (*9*), Arditi and Ginzburg contend that theories of coupled predator-prey dynamics rest on an incorrect premise: that predator kill rate is a function of prey density. Their contrarian view is that predator kill rate is best understood in relation to the ratio of prey to predator. At a fundamental level, predators represent a "conversion" of biomass from their prey, so logically one would expect a proportional relationship.

It would be a vast understatement to say that prey-dependent models based on Lotka-Volterra dynamics are the entrenched, majority view, for they are the foundation of most of the scientific literature on predation over the past century. Never mind that the outcome of the basic Lotka-Volterra model is very sensitive to initial conditions; that the only model outcome, if the parameters are carefully adjusted, is an everlasting predator-prey cycle; and that no serious student of predation believes the model suitably depicts the real world. For over two decades, Arditi and Ginzburg have picked away at the reigning paradigm, all the while championing their alternative ratio-dependent model. Amassing compelling evidence from mathematics, logic, field data, and experimental studies, they have gradually gained support.

Only dedicated specialists will have closely followed the debate over ratio dependence. The present book usefully distills the theory in a grand narrative, albeit one written by the challengers to prevailing opinion. Arditi and Ginzberg have studied carefully the arguments of their critics and respond with a hypothesis based on "gradual interference" along a gradient of predator density. By this notion, predators that exist at moderate to high density interfere or indirectly compete with one another, leading to a "reduction in consumption rate due to sharing available prey with their neighbors." Perhaps satisfyingly, gradual interference accommodates both prey-dependent and ratio-dependent perspectives, each operating in pure form at the extremes of predator density.

After a career in field biology that's led to an appreciation for the inherent complexity of predator-prey dynamics, I admit to being impressed by the immediate usefulness of viewing predation through ratio-dependent glasses. Elegant mathematics that describes the essential core dynamic is a "wonderful gift" to our understanding of the natural world, which physicist Eugene Wigner said "we neither understand nor deserve" (*10*). Imagine reaching the following insights through mathematics and critical thinking: Whereas the presence or absence of predators greatly affects prey numbers, annual variation in predator density does not. Killing a wolf will not likely improve moose-, elk-, or deer-hunting success for humans. Improving habitat will increase prey numbers more successfully than will controlling predators. Biological control of insect pests can actually work, even in a (mainly) ratio-dependent world. The mutual dependency of predator and prey is fundamentally asymmetrical—prey matter to predator populations far more than vice versa.

In reviewing the progress in scientific understanding of predator-prey systems, Arditi and Ginzburg decry the gap that exists between theory and application. Microbiologists quickly confirmed and accepted the basics of consumer-resource dynamics, but many applied ecologists (e.g., in my own field of wildlife management) have an unfortunate phobia for all things mathematical. Readers

CREDIT: ROLF PETERSON/MICHIGAN TECHNOLOGICAL UNIVERSITY

The reviewer is at the School of Forest Resources and Environmental Science, Michigan Technological University, 1400 Townsend Drive, Houghton, MI 49931, USA. E-mail: ropeters@mtu.edu

Downloaded from www.sciencemag.org on January 23, 2013

who do not fully understand the equations of Arditi and Ginzburg will not appreciate all of the elegance and evidence in *How Species Interact*. Yet all ecologists will certainly gain by grasping the conclusions and philosophy found in the book.

References

1. B. Hampton, *The Great American Wolf* (Holt, New York, 1997).
2. W. C. Gasaway *et al*., *Wildl. Monogr.* **120**, 3 (1992).
3. National Research Council, *Wolves, Bears, and Their Prey in Alaska: Biological and Social Challenges in Wildlife Management* (National Academies Press, Washington, DC, 1997).
4. J. Terborgh, J. A. Estes, *Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature* (Island, Washington, DC, 2010).
5. R. Arditi, L. R. Ginzburg, *J. Theor. Biol.* **139**, 311 (1989).
6. G. F. Gause, *Science* **79**, 16 (1934).
7. C. S. Holling, *Can. Entomol.* **91**, 293 (1959).
8. A. J. Lotka, *Elements of Physical Biology* (Williams and Williams, Baltimore, MD, 1924).
9. V. Volterra, *Leçons sur la théorie mathématique de la lutte pour la vie* (Gauthier-Villars, Paris, 1931).
10. E. Wigner, *Commun. Pure Appl. Math.* **13**, 1 (1960).

10.1126/science.1232024

Downloaded from www.sciencemag.org on January 23, 2013