

## REVISITING THE CLASSICS: CONSIDERING NONCONSUMPTIVE EFFECTS IN TEXTBOOK EXAMPLES OF PREDATOR–PREY INTERACTIONS

BARBARA L. PECKARSKY,<sup>1,12</sup> PETER A. ABRAMS,<sup>2</sup> DANIEL I. BOLNICK,<sup>3</sup> LAWRENCE M. DILL,<sup>4</sup> JONATHAN H. GRABOWSKI,<sup>5</sup>  
BARNEY LUTTBEG,<sup>6</sup> JOHN L. ORROCK,<sup>7</sup> SCOTT D. PEACOR,<sup>8</sup> EVAN L. PREISSER,<sup>9</sup> OSWALD J. SCHMITZ,<sup>10</sup>  
AND GEOFFREY C. TRUSSELL<sup>11</sup>

<sup>1</sup>*Department of Zoology, 453 Birge Hall, University of Wisconsin, Madison, Wisconsin 53706 USA*

<sup>2</sup>*Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, Ontario M5S 3G5 Canada*

<sup>3</sup>*Department of Biology, University of Texas, Austin, Texas 78705 USA*

<sup>4</sup>*Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6 Canada*

<sup>5</sup>*Gulf of Maine Research Institute, 350 Commercial Street, Portland, Maine 04101 USA*

<sup>6</sup>*Department of Environmental Science and Policy, University of California, Davis, California 95616 USA*

<sup>7</sup>*National Center for Ecological Analysis and Synthesis, 735 State Street, Santa Barbara, California 93101 and  
Department of Biology, Washington University, Saint Louis, Missouri 63130 USA*

<sup>8</sup>*Department of Fisheries and Wildlife, Michigan State University, East Lansing, Michigan 48105 USA*

<sup>9</sup>*Department of Biological Sciences, University of Rhode Island, Kingston, Rhode Island 02881 USA*

<sup>10</sup>*School of Forestry and Environmental Studies, Yale University, 370 Prospect Street, New Haven, Connecticut 06511 USA*

<sup>11</sup>*Marine Science Center, Northeastern University, 430 Nahant Road, Nahant, Massachusetts 01908 USA*

*Abstract.* Predator effects on prey dynamics are conventionally studied by measuring changes in prey abundance attributed to consumption by predators. We revisit four classic examples of predator–prey systems often cited in textbooks and incorporate subsequent studies of nonconsumptive effects of predators (NCE), defined as changes in prey traits (e.g., behavior, growth, development) measured on an ecological time scale. Our review revealed that NCE were integral to explaining lynx–hare population dynamics in boreal forests, cascading effects of top predators in Wisconsin lakes, and cascading effects of killer whales and sea otters on kelp forests in nearshore marine habitats. The relative roles of consumption and NCE of wolves on moose and consequent indirect effects on plant communities of Isle Royale depended on climate oscillations. Nonconsumptive effects have not been explicitly tested to explain the link between planktonic alewives and the size structure of the zooplankton, nor have they been invoked to attribute keystone predator status in intertidal communities or elsewhere. We argue that both consumption and intimidation contribute to the total effects of keystone predators, and that characteristics of keystone consumers may differ from those of predators having predominantly NCE. Nonconsumptive effects are often considered as an afterthought to explain observations inconsistent with consumption-based theory. Consequently, NCE with the same sign as consumptive effects may be overlooked, even though they can affect the magnitude, rate, or scale of a prey response to predation and can have important management or conservation implications. Nonconsumptive effects may underlie other classic paradigms in ecology, such as delayed density dependence and predator-mediated prey coexistence. Revisiting classic studies enriches our understanding of predator–prey dynamics and provides compelling rationale for ramping up efforts to consider how NCE affect traditional predator–prey models based on consumption, and to compare the relative magnitude of consumptive and NCE of predators.

*Key words:* behavior; consumptive effects; keystone predators; nonconsumptive effects; predator–prey cycles and interactions; trait-mediated indirect effects; trophic cascades.