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ECOLOGY

Costs and benefits of living with predators

Integrating ecology and economics reveals a net monetary benefit from sea otters

By **James A. Estes**[1] and **Lilian P. Carswell**[1,2]

Although money isn't everything, today's world operates by means of capitalism. This fundamental truth has led to an intersection between economics and ecology wherein natural resources and ecological processes are often valued in monetary terms. A central challenge to the intersection of ecology and natural resource management is thus twofold—understanding ecological processes and valuing the outcomes. Nowhere has this challenge caused more confusion and debate than in the arena of decision-making about how to conserve and manage large predators. On page 1243 of this issue, Gregr *et al.* (*1*) evaluate the recovery of an apex predator—sea otters in the Canadian Pacific coast—and report that certain economies have been either negatively or positively affected by sea otter restoration, but the overall economic outcomes are positive.

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Mother and pup sea otters, *Enhydra lutris*, rest on a bed of kelp onshore in Kachemak Bay, Alaska.

Large apex predators occur in virtually all ecosystems, or once did. They were disproportionately lost or depleted during the age of exploration, discovery, and industrialization. While they are continuing to decline in some cases, they are recovering in many parts of the world following protection and purposeful repatriation. These predators commonly initiate a diverse array of effects on other species and ecological processes (*2*).

Although ecology still has much to learn about the myriad influences of apex predators, most occur through the depletion and fear-induced behavior of their prey. The most well-known ecological pathway from predator through ecosystems is the so-called "trophic cascade," wherein a predator limits the abundance and distribution of its herbivore prey, in turn enhancing the abundance and distribution of plants (*3*). Inasmuch as plants are the foundation for nearly all life on Earth, this link from predator to herbivore to plant extends broadly through nature. Many of the details are reasonably well known for various predators and ecosystems (*4*). Rarely, however, have these processes been rigorously valued on the basis of a common currency. The resulting "apples and oranges" have made it impossible to assess the net costs and benefits of predators to human societies, thereby resulting in irresolvable scientific arguments, irreconcilable management conflicts, and an inability of the responsible management agencies to establish defensible policies. The study of Gregr *et al.* is transformational because it provides a way through this conundrum. The authors conduct a cost-benefit analysis for the extensively studied and well-known case of sea otters and kelp forest ecosystems that accounts not only for shellfish depredation but also for a suite of knock-on effects of this interaction.

Sea otters prey on, and thus limit the size and abundance of, various shellfish, thereby imposing a substantial cost on shellfisheries. However, sea otters also create economic benefits by way of wildlife viewing opportunities and tourism, and through the enhancement of kelp forests that results from a reduction in the number of herbivorous sea urchins. Kelp increases coastal production and provides habitat for other species, thereby enhancing coastal fin fisheries. Kelp also sequesters carbon, thus reducing atmospheric carbon dioxide (CO_2) and ocean acidification. There are numerous other ecological influences of sea otters, although Gregr *et al.* focus on just these, from which they find that the monetary benefits of sea otters outweighed the costs sevenfold. The responsible management agencies in southeast Alaska and British Columbia heretofore have been unable to resolve the severe local conflicts that are developing because of sea otter recovery. Gregr *et al.* do not offer a solution, although they do provide the template for a more holistic and objective means of policy development.

The importance of the analysis of Gregr *et al.* is not so much in the exact findings but as a method for looking beyond depredation in assessing the costs and benefits of living with predators. In the case of sea otters and kelp forests, the web of interactions that emanate from otter predation on shellfish and the otter-urchin-kelp trophic cascade might be expanded to include other interactions that bear on human financial welfare. For example, Pacific herring spawn on kelp, are targeted by fisheries, and provide the nutritional base for other iconic and valued species, such as salmon and whales. The ecological data are not yet sufficient to assess the magnitudes of potential influence by sea otters on these and other species and ecological processes, but in the future they may be. Moreover, the details of Gregr *et al.*'s analysis are specific to the west coast of Vancouver Island, and

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these will surely vary in different places and at different times, perhaps substantially. For example, although tourism is important to many coastal economies along the west coast of Canada and the United States, this isn't so everywhere, nor is it likely that all local communities wish it to be. The ledger of net monetary benefit from sea otters would not switch to a net cost with the removal of tourism, but it would be greatly reduced, given the factors that Gregr *et al.* considered. The important point is that quantifying indirect effects broadens the base of stakeholders in natural resource management by identifying interests that could otherwise be overlooked or dismissed as trivial. Such an expanded perspective alerts the public that they may indeed have a stake in decisions made by natural resource agencies, and it directs policy-makers and managers to constituencies they may not have previously consulted.

There is also the larger question of how the monetary costs and benefits of predators affect other ecosystems. This is an important future arena for science and policy. One such scenario involves the gray wolf, which has been the focus of similar controversy and societal discord. The ecological influences of wolves in North American boreal forests are broadly similar to those of sea otters and kelp forests (*5*). One especially topical segment of the web of interactions that emerges from wolves as predators is that of disease. The removal of wolves from the midwestern and eastern United States was likely instrumental in the spread of coyotes into these regions, which in turn depleted fox populations. This led to an increase in small-mammal populations, an associated increase in tick abundance, and the rise of Lyme disease risk (*6*). Such a possibility creates an entirely new dimension to the costs and benefits of living with wolves. The analysis by Gregr *et al.* should spark a new era of ecological-economic research that can be used by natural resource policy-makers and managers to make and defend more rational, equitable, and far-sighted decisions affecting predators. ■

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MOLECULAR BIOLOGY

CRISPR at lightning speeds

Breaking the genome with the flick of a (light) switch

By **Darpan Medhi** *and* **Maria Jasin**

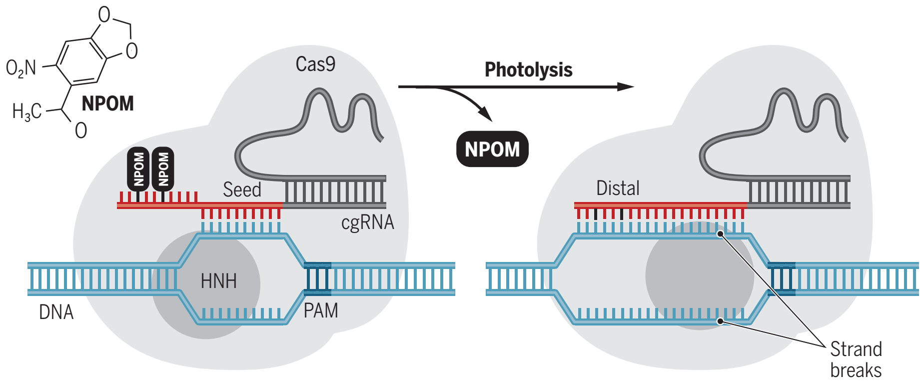
Fundamental studies since the mid-1990s demonstrated the power of targeting DNA double-strand breaks (DSBs). This work uncovered a plethora of DNA repair pathways and formed the basis for the revolution in genome modification (*1*). That revolution in its most powerful manifestation came about with the discovery of RNA-directed DNA-cleaving enzymes in CRISPR systems, allowing the simple rules of base-pairing to guide targeted DNA breakage. Yet the CRISPR-associated 9 (Cas9) endonuclease that induces a DSB at target sites (determined by guide RNAs) in gene editing has been delivered as a relatively blunt instrument, with little control over its activity. On page 1265 of this issue, Liu *et al.* (*2*) developed Cas9 into a precision instrument that is both temporally and spatially controlled. It should now be possible to interrogate the cellular response to DSBs in real time, which will allow greater understanding of how cells maintain genome integrity when faced with these potentially catastrophic lesions.

Gene-editing nucleases have historically been expressed in cells from plasmid vectors that rely on several steps (cellular uptake, transcription, and translation) before cleavage can occur. Once expressed, the nucleases may be present for days, or even permanently, if viral transduction is used. With the advent of CRISPR, direct delivery of active but relatively short-lived nucleases, in the form of Cas9–guide RNA ribonucleoproteins (RNPs) (*3*), has been feasible. However, even with RNP delivery, cleavage of genomic sites is not immediate and may not be synchronous (*3*), hampering the study of DNA breakage and repair in real time.

To overcome these limitations, Liu *et al.* developed very fast CRISPR (vfCRISPR) to enable precise control of Cas9 activity using light. Prebound to its target in genomic DNA through a modified guide RNA, Cas9 is activated to cleave DNA nearly instantaneously by shining light at wavelengths that are not phototoxic to cells (365 or 405 nm). The system uses standard CRISPR features, including protospacer adjacent motif (PAM) recognition by Cas9 and guide RNA binding close to the PAM (see the figure). However, distal guide RNA binding is blocked as a result of steric hindrance by modified deoxyribonucleotides (*4*) incorporated into the guide RNA. This "caged" guide RNA (cgRNA) effectively prevents complete R-loop (DNA-RNA hybrid) formation of the cgRNA with the target DNA (*2*), which is necessary to activate

Photoactivation of CRISPR

After protospacer adjacent motif (PAM) recognition by CRISPR-associated 9 (Cas9), the caged guide RNA (cgRNA) forms base pairs with the target DNA at the PAM-proximal "seed" sequences. However, distal cgRNA sequences are prevented from binding by steric hindrance from 6-nitropiperonyloxymethyl (NPOM) thymidine. Photolysis of NPOM (365 or 405 nm) allows distal base pairing, provoking a conformational change of the Cas9 HNH endonuclease domain. This activates DNA cleavage by both nuclease domains.



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