ESSAY

SCIENCE & SCILIFELAB PRIZE

The mechanistic pathways of trophic interactions in human-occupied landscapes

Field studies reveal more complicated relationships between African wild dogs, their prey, and the plants eaten by the prey than predicted by theory

By **Adam T. Ford***

From children's stories to the logos of professional sports teams, images on commercial products, and the icons of conservation, few organisms capture our imagination like large carnivores. From a scientific perspective, understanding the context in which predators shape ecosystem processes is one of the most pressing endeavors in modern ecology (*1*). In central Kenya, large carnivores—such as leopards and globally endangered African wild dogs—prey upon antelope, which themselves limit the abundance of plants. These wildlife species vie with commercial ranchers, as well as traditional pastoralists and their livestock for limited resources (*2*). Together, these actors interact against a backdrop of pronounced environmental variation and the unique patchwork of trees on grassland that characterizes tropical savannas. Through my dissertation research, I combined long-term monitoring of wildlife populations, high-resolution satellite imagery, fine-scale tracking of animal movements, and a series of field experiments to quantify these interactions and their consequences for ecosystem structure.

Specifically, I discovered that impala—an abundant, deer-sized antelope—are caught between "the devil and the deep blue sea": they must avoid the claws and teeth of their predators and the thorny and chemical defenses of their food (*3*, *4*). Global Positioning System (GPS) tracking reveals that impala avoid areas characterized by dense tree cover (see the figure). In such areas, leopards and wild dogs more effectively attack and kill their prey, which makes tree cover "risky" when viewed through the eyes of an impala (*3*). However, trees are also an important food source for impala, and feeding trials showed that impala prefer trees with fewer thorns, even if these less-thorny trees are better defended with noxious chemicals (*3*). This combination of habitat and food preferences means that impala deplete the abundance of their preferred (and less thorny) forage in safe habitats, yet forgo access to this preferred forage in risky habitats. Consequently, an impala's fear of being eaten increases the prevalence of thorny trees in safe areas, and safeguards less-thorny trees in risky areas.

There are three critical implications of this study (3). First, and from the perspective of a plant, there are two pathways to success—either defend yourself from herbivores by growing large thorns or thrive in areas that are risky to your enemies. Second, fear of predation and diet preference interact to shape the spatial patterning of tree species across entire landscapes (about 200 km^2). Third, because the open areas in which impala aggregate for safety arise from old (>10-year) cattle corrals, traditional pastoralism plays a key role in shaping the interactions among carnivores, their prey, and plants. The implications of this last point are profound, because it demonstrates that people are inextricably embedded within this food web. Indeed, the preferred plants that impala relinquish in risky areas could be used for livestock forage, a critical ecosystem service that may help mitigate the impact of episodic droughts that plague East Africa.

Whereas fear of predation can powerfully shape ecosystems and animal behavior (*3*, *5*), so too can the direct consumption of prey. After a 20-year absence, African wild dogs naturally recolonized areas of central Kenya and now prey upon the region's most abundant antelope, the dik-dik. Theory predicts that this strong, top-down pressure in the food chain should trigger a trophic cascade; in other words, after wild dog recovery, herbivory by dik-dik will relent and plant abundance will increase. To test this prediction, I linked the movement and diet composition of wild dog packs with changes in the size of the dik-dik population over a 14-year period. I then identified which plants are vulnerable to browsing by dik-dik. Finally, I quantified herbivory by means of a series of replicated and controlled dik-dik exclosures, separately established before and after wild dog recovery.

There were strong, top-down effects in this food chain, but no evidence that wild dog recovery caused a trophic cascade. The population of dik-dik declined by 33% because of predation by wild dogs, and dik-dik reduced the abundance of some tree species by up to 84% (*6*). However, the effect of herbivory did not diminish in the presence of wild dogs (*6*). This finding was surprising because overall plant growth (both inside and outside dik-dik exclosures) was greater following wild dog recovery. Had experiments not been used, as often is

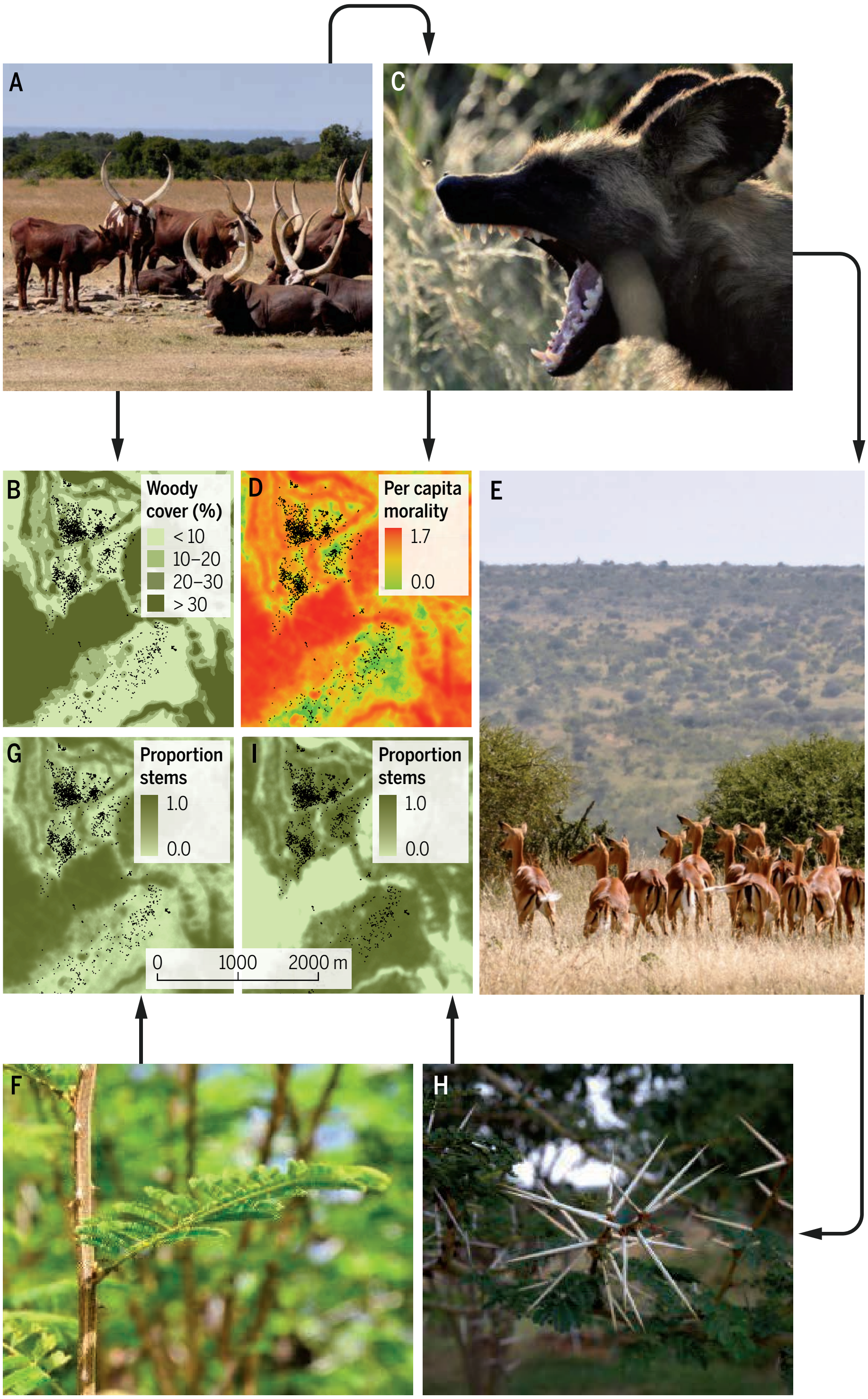
*Department of Integrative Biology at the University of Guelph, Guelph, Ontario, Canada. *E-mail: adamford@uoguelph.ca*

CATEGORY WINNER: ECOLOGY AND ENVIRONMENT

Adam T. Ford

Adam T. Ford is a wildlife ecologist interested in how predator-prey interactions are shaped by human-modified landscapes. He received a B.Sc. from the University of Victoria (British Columbia), a M.Sc. from Carleton University (Ontario), and his Ph.D. from the University of British Columbia with Assistant Professor Jacob Goheen. Ford is currently a Liber Ero Postdoctoral Fellow in Conservation Science, based at the Department of Integrative Biology at the University of Guelph (Ontario). The research described in his essay sheds new light on the relationships of people, large carnivores, their herbivore prey, and plants in an East African savanna.

PHOTO: LIBER ERO FELLOWSHIP PROGRAM



How trophic cascades emerge. Some key interactions between people, large carnivores, antelope, and plants in a savanna landscape. The creation and abandonment of (**A**) cattle corrals creates openings in (**B**) woody cover. Areas of high woody cover are used by predators, like (**C**) African wild dogs, for hunting, which coincides with (**D**) the distribution of predation risk [shown here as the per-capita risk of mortality] across the landscape. As a result, prey, like (**E**) the impala, avoid areas of high woody cover and find safety in the open areas created by abandoned cattle corrals. The GPS-recorded movements of (E) an adult female impala, are shown by the black dots in panels (B) and (D). This animal was tracked every 20 min over the course of a year. Impala prefer and suppress the abundance of less-thorny acacia plants, like (**F**) *Acacia brevispica*, compared with thorny species like (**H**) *Acacia etbaica*. As result of impala's risk-avoidance behavior and diet preference, (**G**) the proportion of stems in the tree community containing the less-thorny species is highest in the risky areas that impala avoid (see black dots tracking impala movement); whereas (**I**) thorny plants are more abundant in the open areas where impala aggregate (as shown by the black dots in GPS). Details of this study are described in (*3*).

GRAPHIC: LIBER ERO FELLOWSHIP PROGRAM

the case in large-carnivore studies, I would have incorrectly concluded the existence of a trophic cascade. My results highlight the very important finding that a positive correlation between plant and large carnivore biomass is insufficient evidence to validate a trophic cascade.

The potential for large carnivores to trigger trophic cascades has been used to justify the conservation of these iconic species and to restore landscapes (*1*, *7*). Until now, there have been significant gaps in the empirical support for this interaction, particularly when applied to savannas (*8*). Specifically, widespread reliance on correlative methods has made it challenging to attribute changes in plant and herbivore biomass to trophic cascades (*8*). These natural experiments often lack control and replication and, therefore, suffer from confounding variation (*8*). Moreover, previous work in this field has been conducted primarily in the temperate biomes of Europe and North America. In the absence of a more rigorous assessment of the trophic cascade hypothesis, and one that involves a greater diversity of species and biomes, there is a void in our knowledge of how some of the world's most recognizable and charismatic carnivores interact with their environment. Given the loss of large carnivores from many parts of the world (*1*, *7*, *9*), their recovery in other areas (*6*, *10*), and efforts being made to conserve these species in human-occupied landscapes (*11*–*13*), it is critical that we develop a clearer understanding of when and where trophic cascades will emerge. Through the pairing of experiments with landscape-level analyses, my research has unraveled the ecological contexts that determine when large carnivores generate trophic cascades in an African savanna.

REFERENCES AND NOTES

1. J. A. Estes *et al.*, *Science* **333**, 301 (2011).
2. A. T. Ford, J. M. Fryxell, A. R. Sinclair, in *Antelope Conservation in the 21st Century: From Diagnosis to Action*, J. Bro-Jorgensen, Ed., from a symposium of the same name, London, 17 and 18 November 2011 (Wiley-Blackwell, Hoboken, NJ, in press), chap. 2.
3. A. T. Ford *et al.*, *Science* **346**, 346 (2014).
4. R. M. Pringle *et al.*, *Proc. R. Soc. London Ser. B* **281**, 20140390 (2014).
5. A. T. Ford, J. R. Goheen, *J. Mammal.* **96**, 918 (2015).
6. A. T. Ford *et al.*, *Ecology* **96**, 2705 (2015).
7. W. J. Ripple *et al.*, *Science* **343**, 1241484 (2014).
8. A. T. Ford, J. R. Goheen, *Trends Ecol. Evol.* 10.1016/j.tree.2015.09.012 (2015).
9. R. Dirzo *et al.*, *Science* **345**, 401 (2014).
10. G. Chapron *et al.*, *Science* **346**, 1517 (2014).
11. A. T. Ford, A. P. Clevenger, *Conserv. Biol.* **24**, 1679 (2010).
12. A. T. Ford, A. P. Clevenger, M. P. Huijser, A. Dibb, *Wildl. Biol.* **17**, 253 (2011).
13. M. Barrueto, A. T. Ford, A. P. Clevenger, *Ecosphere* **5**, art27 (2014).

ACKNOWLEDGMENTS

I extend my heartfelt gratitude to Jacob Goheen—my Ph.D. adviser—who provided creativity, humor, guidance, and unwavering support to help me achieve my dreams.

10.1126/science.aad7134

The mechanistic pathways of trophic interactions in human-occupied landscapes

Adam T. Ford

Science **350** (6265), 1175-1176.
DOI: 10.1126/science.aad7134

Science (print ISSN 0036-8075; online ISSN 1095-9203) is published by the American Association for the Advancement of Science, 1200 New York Avenue NW, Washington, DC 20005. The title *Science* is a registered trademark of AAAS.