TROPHIC CASCADES

Cascading impacts of large-carnivore extirpation in an African ecosystem

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Populations of the world's largest carnivores are declining and now occupy mere fractions of their historical ranges. Theory predicts that when apex predators disappear, large herbivores become less fearful, occupy new habitats, and modify those habitats by eating new food plants. Yet experimental support for this prediction has been difficult to obtain in large-mammal systems. After the extirpation of leopards and African wild dogs from Mozambique's Gorongosa National Park, forest-dwelling antelopes [bushbuck (*Tragelaphus sylvaticus*)] expanded into treeless floodplains, where they consumed novel diets and suppressed a common food plant [waterwort (*Bergia mossambicensis*)]. By experimentally simulating predation risk, we demonstrate that this behavior was reversible. Thus, whereas anthropogenic predator extinction disrupted a trophic cascade by enabling rapid differentiation of prey behavior, carnivore restoration may just as rapidly reestablish that cascade.

The worldwide decline in populations of large mammalian carnivores is a major environmental concern (*1, 2*), in part because apex predators can exert a defining influence on ecosystems via trophic cascades (*3*). A trophic cascade occurs when predators indirectly affect plants through either of two mechanisms: by consumptively reducing prey abundance (*4*) or by imposing "landscapes of fear" in which prey modify their behavior to reduce predation risk. In landscapes of fear, prey are expected to forego foraging opportunities in resource-rich habitats that are risky, thereby creating spaces where palatable food plants can thrive (*5, 6*). Accordingly, the extirpation of top carnivores should create "landscapes of fearlessness" where large herbivores seek out the nutritional benefits of previously risky habitats, suppressing food-plant abundance in the process (*5*); conversely, the reestablishment of real or perceived predation risk should reverse this behavior (*7*). Although behaviorally mediated trophic cascades have been documented frequently for relatively small consumer species (*8–10*), there are few unequivocal examples involving large mammalian carnivores and herbivores (*11–13*). This gap reflects the difficulty of experimentally manipulating predation risk and quantifying its downstream effects at scales relevant to large mammals. Correlative and comparative analyses generally cannot rule out potentially confounding factors, which has fueled debates (*14–18*) and prompted calls for stronger mechanistic inference in the study of megafaunal trophic cascades (*19*).

Ecosystems in which top predators have been extirpated present valuable opportunities to test predictions of trophic-cascade theory (*4, 14, 20*). In Mozambique's Gorongosa National Park, large-mammal populations were severely reduced during the Mozambican Civil War (1977 to 1992), with >90% declines across all monitored species (*21–23*). Large-herbivore populations have subsequently increased, but leopards (*Panthera pardus*), wild dogs (*Lycaon pictus*), and hyenas (*Crocuta crocuta*) were extirpated, while lions (*P. leo*) persisted at low abundance (*23, 24*) (table S1). In this carnivore-depleted system, we evaluated evidence for a behaviorally mediated trophic cascade by using field manipulations of predator cues and herbivory, GPS telemetry of herbivore movements, spatially explicit wildlife-count data, DNA-based diet analysis, and body-condition measurements.

Gorongosa's central valley (Fig. 1, A and B) encompasses the ~750-km^2 Lake Urema floodplain and surrounding savanna woodlands (*25*). During the dry season (May to November), the floodplain is a flat, largely treeless landscape, dominated by grasses and forbs and dotted with leguminous subshrubs. Such open habitat is typically avoided by herbivores that rely on crypsis, tree cover, and known escape trails to avoid detection and capture by predators. One such herbivore species is bushbuck (*Tragelaphus sylvaticus*). This midsized antelope is a closed-habitat specialist that is "dependent on thick cover" (*26*) and "concealment to avoid predators" (*27*) and "is not found on open plains or anywhere without sufficient cover to conceal it" (*28*)

from key predators such as leopards and wild dogs (*29*). Previous studies of African ungulates have emphasized the comparative safety of open areas with high visibility (*11, 13*). For secretive forest browsers such as bushbuck, however, treeless areas should be riskier, and relaxation of predation pressure might embolden individuals to exploit what would otherwise be prohibitively dangerous open habitat. Bushbuck in Gorongosa were historically confined to woodland and thicket habitat (*30*), but in the largely predator-free contemporary environment, we have observed them venturing into the open Urema floodplain.

We quantified these initial observations by fitting GPS collars to 11 bushbuck in 2015 and collecting hourly locations for up to 8 months. The data revealed two broad patterns in habitat use. One subset of individuals was largely confined to densely wooded home ranges; another occupied the sparsely wooded floodplain margin and routinely forayed into treeless floodplain habitat, both at night and throughout the day (Fig. 1, C to E)—behavior never documented prior to predator extirpation (*30*). All available evidence indicates that this habitat shift cannot be explained by competitive interactions. In principle, carnivore extirpation might have increased woodland bushbuck densities, prompting individuals to move into the floodplain to mitigate intraspecific competition, as predicted by ideal free distribution theory (*31*). We explored this possibility by using data from six helicopter counts conducted between 2002 and 2016, when all ungulate populations were recovering from similarly severe war-induced declines (*21–23, 30*). If competition caused the habitat shift, then we would expect floodplain bushbuck densities to be negligible during the earliest counts, to increase only after woodland densities reached some threshold, and to remain lower than woodland densities throughout. To the contrary, floodplain bushbuck density was already ~50% of woodland bushbuck density in 2002, and by 2016, density was ~15% higher in the floodplain (Fig. 1F). Moreover, densities of other ungulates were also highest in the floodplain (*21*). Thus, the observed habitat shift cannot obviously be explained by either intra- or interspecific competition.

To directly test the hypothesis that predator extirpation has promoted the use of open habitat by bushbuck, we experimentally assessed the responses of GPS-collared floodplain (*n* = 7) and woodland (*n* = 5) bushbuck to simulated predator presence in August and September 2016. Habitat affiliations were determined on the basis of capture location and were subsequently verified with reference to GPS-collar locations and diet composition data (figs. S1 and S2). We exposed each individual to both predator and procedural-control cues in separate trials (in randomized order), with collars recording locations every 15 min (*32*). Treatments comprised both auditory and scent cues within the home range of each collared individual (fig. S3). Because both felids and canids prey on bushbuck, we aimed to create generalized hot spots of perceived predation risk by deploying several cues that collectively simulated multiple

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predator species. Playbacks of leopard vocalizations, artificial lion scat, and generic carnivore urine (*32*) were used to mimic predator presence; white noise, locally collected herbivore dung, and saline solution were used as sham cues in procedural-control trials (*12, 33*). We restricted our analyses to data collected between 17:00 and 06:00, the period encompassing peak bushbuck activity (*32*). For each individual, we quantified two response variables in the 48 hours immediately before and after cue deployment. First, we measured the avoidance of predator and control cues by calculating the distance between each bushbuck GPS point and the sound-cue location. Second, we measured whether

simulated risk caused floodplain individuals to increase their use of tree cover (i.e., shift back toward a more "typical" bushbuck habitat).

Bushbuck strongly avoided predator cues in both habitats but did not avoid sham cues in either habitat (Fig. 2A and table S2). Moreover, predator cues caused a significant increase in the use of tree cover by floodplain but not woodland bushbuck, whereas sham cues did not significantly alter tree-cover use in either habitat (Fig. 2B and table S2). We evaluated the statistical significance of these responses by using mixed-effects models with random intercepts for individuals (table S2). These results were robust to both GPS and habitat classification error (*32*)

(figs. S4 and S5 and table S3). That floodplain bushbuck exhibited more cautious behavior in response to even a brief exposure to simulated risk suggests that some fear of predators has been retained and is primed in more risky open habitats (*7, 12*). Our design does not enable us to distinguish the roles of specific predator cues in generating these responses, but future studies could test sound and scent cues separately.

Theory often assumes a nutritional opportunity cost of risk avoidance (*5*). We therefore hypothesized that floodplain bushbuck would consume higher-quality diets and exhibit greater size and body condition. We analyzed bushbuck diet composition by using DNA metabarcoding of
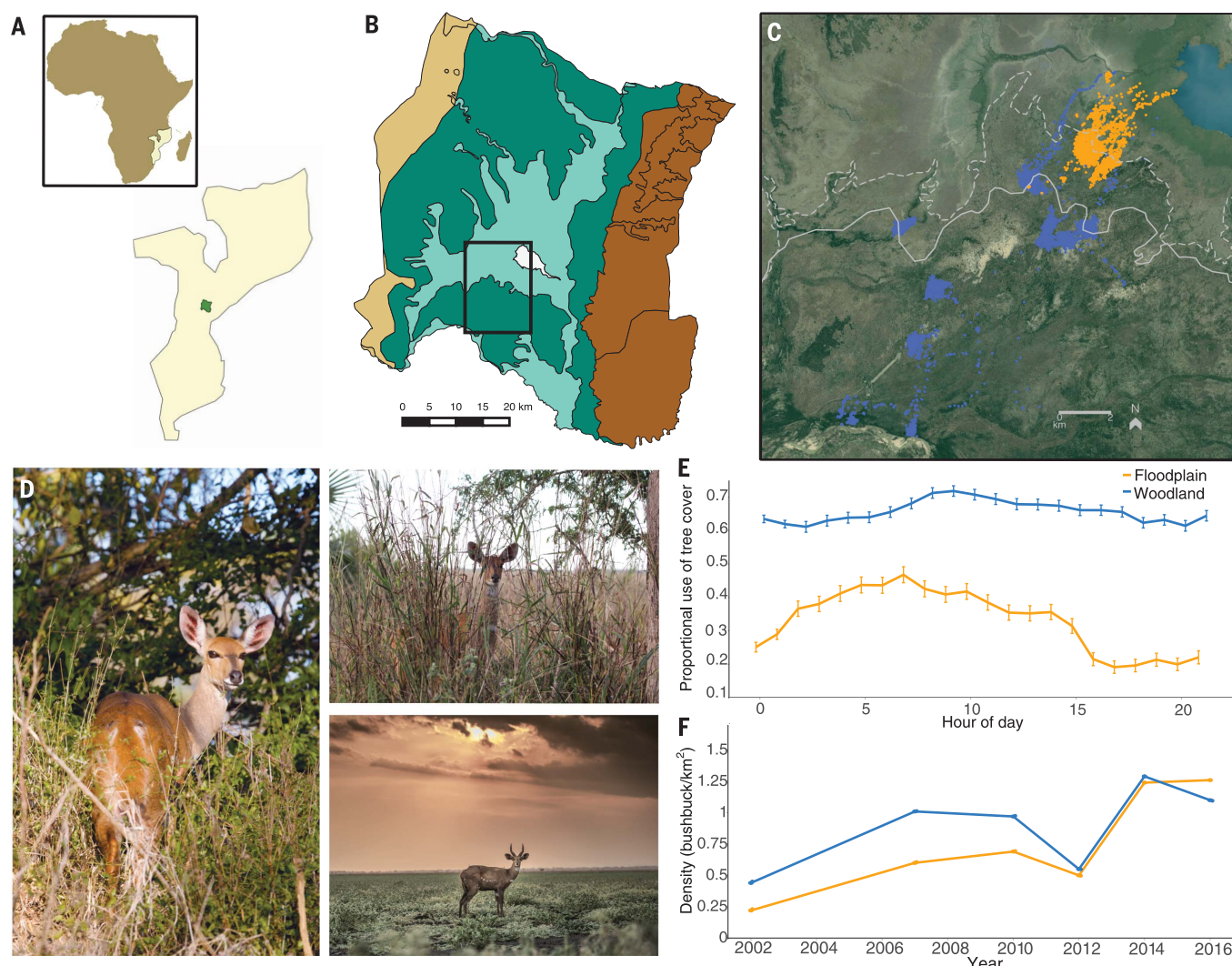

Fig. 1. Differential habitat use by bushbuck. (**A**) Map of Africa and Mozambique, showing the location of Gorongosa National Park (**B**) with its major habitat zones (*25*), from left: the western escarpment, savanna woodland (dark green), floodplain (light green), Lake Urema (white), and eastern escarpment. The boxed area indicates the region shown in the satellite image in (C). (**C**) GPS-collar locations from 11 individuals, three in the floodplain (orange) and eight in the adjoining woodland (blue), from June 2015 to March 2016. The solid line distinguishes the boundary between the floodplain and dense woodland; the dashed line distinguishes the boundary between the sparsely wooded floodplain margin and the treeless floodplain (*25*). (**D**) Bushbuck in woodland (left), the floodplain margin (top right), and the open floodplain (bottom right). (**E**) Use of woody cover by the bushbuck in (C), measured as the proportion of locations falling within a pixel classified as containing tree cover (*32*); error bars show ±1 SE. (**F**) Bushbuck densities in the floodplain and woodland, 2002 to 2016, determined via six aerial helicopter counts (*32*); here, "floodplain" refers conservatively to the treeless area surrounding Lake Urema [dashed line in (C)].

Fig. 2. Responses of floodplain and woodland bushbuck to simulated-predator and procedural-control cues. Average changes in (**A**) the distance from cues (avoidance) and (**B**) the proportional use of tree cover for bushbuck in woodland (*n* = 5) and floodplain (*n* = 7) habitats at night. Each bar (colored by habitat affiliation) represents the average difference between the 48-hour pre-cue period and the 48-hour post-cue period across all collared individuals in each category; error bars show ±1 SE. Shading indicates experimental treatment, with darker bars for the predator cues and lighter bars for the sham cues (see *x*-axis labels). *P* values from generalized linear mixed models are shown above each bar, indicating whether each response differed significantly from zero (see full model results in table S2).
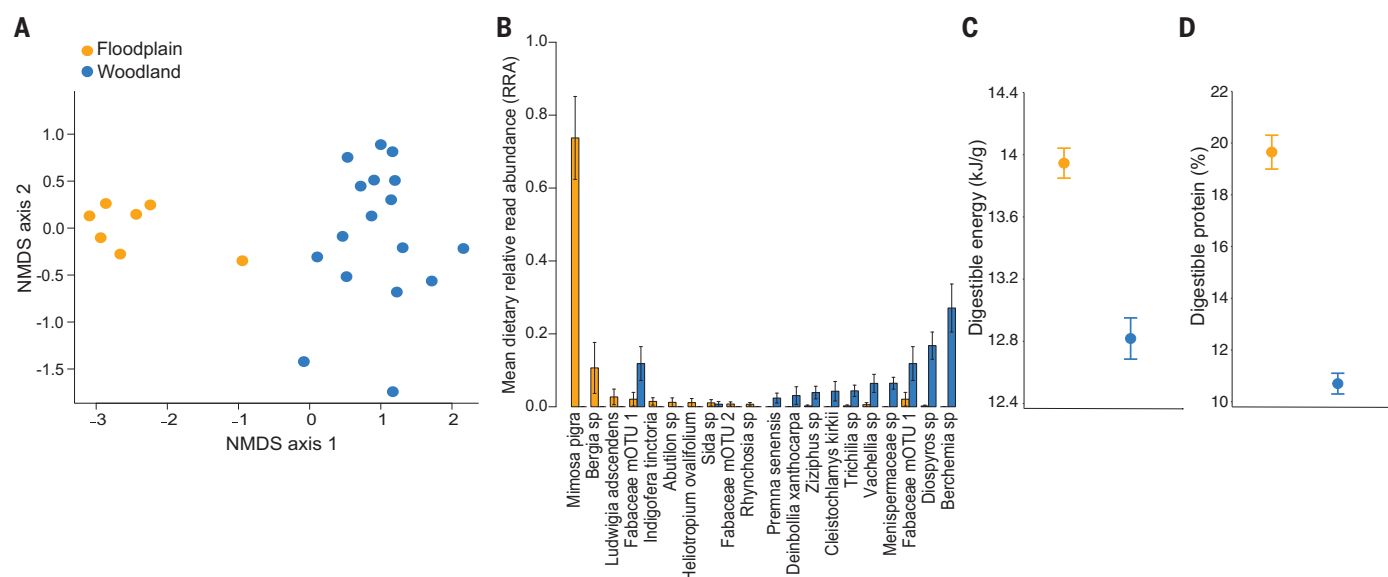

Fig. 3. Differences in composition and nutritional quality of bushbuck diets across habitats. (**A**) Nonmetric multidimensional scaling (NMDS) ordination, based on Bray-Curtis dissimilarities from DNA-metabarcoding data, showing that bushbuck diets clustered within each habitat and diverged between them. The distance between points (*n* = 7 floodplain fecal samples; *n* = 17 woodland fecal samples) reflects compositional dissimilarity. (**B**) The 10 most abundant food-plant taxa for bushbuck in the floodplain (orange bars) and woodland (blue bars). (**C**) Mean digestible energy and (**D**) protein contents of bushbuck diets, revealing higher diet quality in floodplain individuals (Wilcoxon rank sum tests; energy, *W* = 76, *n* = 18 individuals, *P* = 0.0001; protein, *W* = 77, *n* = 18 individuals, *P* < 0.0001). Error bars show ±1 SE.

fecal samples (*32, 34*). We also quantified the digestible-energy and digestible-protein contents of foliage from Gorongosa's most common browse plants. Of the 51 molecular operational taxonomic units (mOTUs) identified in bushbuck diets, 22 matched plant species for which we had nutritional-quality data, and those 22 species accounted for >83% of total diet [measured as the relative read abundance (RRA) of those mOTUs across all samples (*32*)]. We calculated weighted averages of digestible energy and protein in the diet of each sampled bushbuck, using the RRA of each plant species as the weighting factor. We

quantified the body condition of captured individuals by using principal components analysis to reduce multiple measurements of bushbuck morphology (e.g., body mass, body length, fat and muscle thickness, and standardized palpation scores) to two indices of condition: body size and body fat (*32*) (fig. S6 and tables S4 and S5).

We found pronounced differences in diet composition between floodplain and woodland bushbuck (Fig. 3A and fig. S2). The diets of floodplain bushbuck (21 mOTUs) were dominated by the leguminous shrub *Mimosa pigra* (mean RRA = 74% ± 11%) (Fig. 3B and fig. S2), with the forbs

Bergia mossambicensis (Elatinaceae; syn. *B. salaria*) and *Ludwigia adscendens* (Onagraceae; syn. *L. stolonifera*) accounting for an additional 11 and 3% of RRA, respectively. These plants had relatively high crude-protein and digestible-energy contents (fig. S2, C and D). The diets of woodland bushbuck (36 mOTUs) had greater evenness: Two tree species, *Berchemia discolor* and *Diospyros* sp., together accounted for 44% of RRA (Fig. 3B), and both species had lower crude protein and digestible energy than *M. pigra* and most other floodplain food plants (fig. S2, C and D). Overall, floodplain bushbuck diets were 8.8 and 83.6%

Fig. 4. Large herbivores suppress _Bergia mossambicensis_, a common floodplain plant. (**A**) Among all floodplain herbivore species in Gorongosa, only bushbuck consumed substantial quantities of _Bergia_. Shown are the mean changes in (**B**) the percentage of stems browsed and (**C**) the number of leaves per plant on caged versus uncaged _Bergia_ plants over a minimum of 16 days (maximum of 18 days). Herbivores also reduced (**D**) the mean number of flowers per plant, (**E**) mean height, and (**F**) mean canopy area at the conclusion of the experiment. For (D) to (F), there was no significant difference in the initial values between caged and uncaged treatment groups. Model results of the effects of herbivore exclusion on each response variable are presented in table S7. Error bars show ±1 SE.
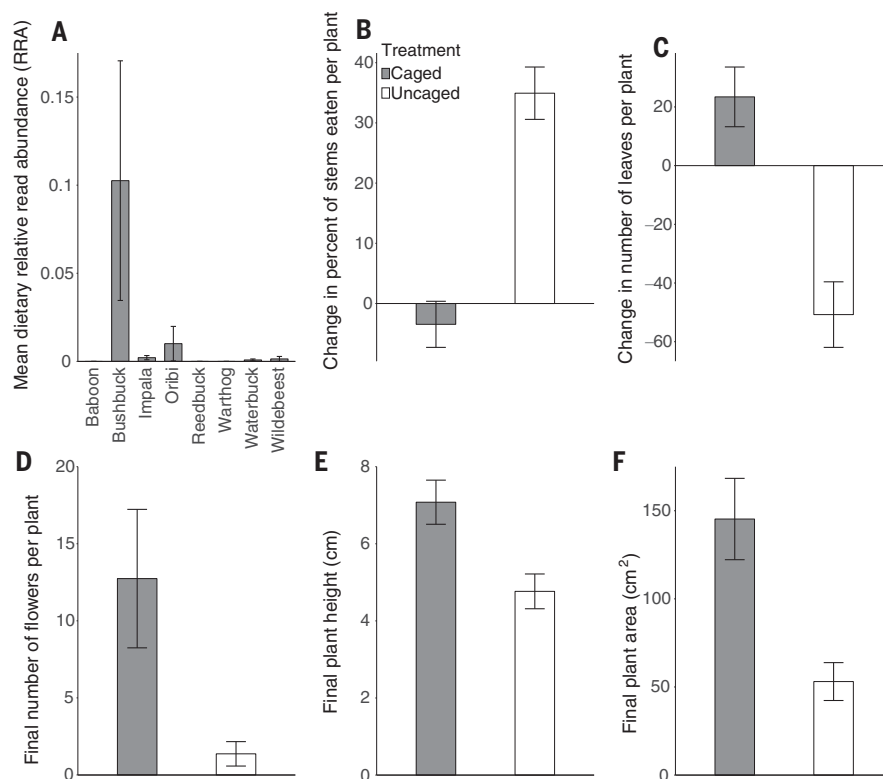
richer in digestible energy and protein, respectively, than woodland bushbuck diets (Fig. 3, C and D). Consistent with these differences in diet quality, floodplain bushbuck were in better condition than woodland bushbuck, with significantly higher scores for the body size [principal component 1 (PC1)] index (table S6). The nutritional value of the most heavily utilized plant, _M. pigra_, may help to promote floodplain use by bushbuck, but this factor alone does not provide a plausible alternative explanation for the longterm shift in habitat use. _M. pigra_ was also present on the floodplain before predator extirpation (_30_), with availability similar to that at the time of this study; if this plant drove habitat use independently of predation risk, then bushbuck should have been using the floodplain during the prewar era as well. The relative influences of risk and resource quality on bushbuck habitat use could in principle be quantified by removing _M. pigra_ at large scales; we hypothesize that this would reduce carrying capacity but not expel bushbuck from these areas.

In a final experiment, we tested whether the expansion of bushbuck into the floodplain has measurable effects on floodplain plants. Plant community responses to herbivory can be tested by using exclosures, but it would be impossible to parse the effects of bushbuck relative to those of other floodplain ungulates with overlapping diets. Thus, to isolate the effects of bushbuck, we used our diet analysis to identify an indicator plant species consumed almost exclusively by bushbuck. The waterwort _B. mossambicensis_ was the second most abundant taxon in the diets of floodplain

bushbuck but was negligible (≤1% RRA) in the diets of all other floodplain herbivores (Fig. 4A). We constructed wire-mesh exclosures around _Bergia_ plants in a randomized, paired caged-uncaged design (fig. S7) at two different floodplain sites (with 15 total pairs) (_32_). Before the experiment, and again after a minimum of 16 days, we measured the dimensions of each plant and counted all leaves, flowers, and browsed stems. The percentage of browsed stems per plant increased in uncaged plants during the experiment but did not change in caged plants (Fig. 4B and table S7). Similarly, the mean number of leaves increased in caged plants but decreased in uncaged plants (Fig. 4C). The mean number of flowers, height, and canopy area at the conclusion of the experiment were all significantly greater in caged plants (Fig. 4 and table S7). Thus, the expansion of bushbuck into open habitats was accompanied by strong suppression of growth and reproduction in _Bergia_. Although other floodplain herbivores may have contributed somewhat to this effect, only bushbuck consumed substantial quantities of _Bergia_ (Fig. 4A), suggesting that this plant would otherwise find refuge from large-mammal herbivory in the floodplain.

Altogether, our results provide evidence that the extirpation of large carnivores in the wake of the Mozambican Civil War has disrupted a behaviorally mediated trophic cascade. In the absence of apex predators such as leopards and wild dogs, a common ungulate prey species rapidly expanded into a high-risk, high-reward habitat, with concomitant shifts in diet composition and quality,

body size and condition, and the performance of a key food plant. Despite the multidecadal absence of several apex predators in Gorongosa, we found that bushbuck retained a fear of these carnivores (_7, 12_): Experimental imposition of risk cues over just 48 hours shifted habitat use toward patterns that prevailed before carnivore loss (_30_). The next phase of trophic rewilding in Gorongosa involves carnivore reintroductions (_23_), beginning in 2018 with 14 wild dogs, which should eventually enable tests of our prediction that bushbuck will vacate the floodplain. Notably, the relaxation of risk after carnivore extirpation differentially affected individual behavior within a population, leading to bimodality in habitat use and perhaps some degree of reproductive separation, which could amplify preexisting individual variation (_35_). The influence of carnivores on behavioral variation within ungulate populations, and its potential evolutionary significance, remains largely unexplored.

Our study supports the general hypothesis that the loss of top carnivores can convert landscapes of fear into landscapes of fearlessness for large mammalian herbivores, with far-reaching consequences for prey and plant populations (_6_). It further shows that the effects of fear depend on the social, foraging, and antipredator behaviors of the species involved. Whereas recent work has shown that gregarious, flight-dependent grazers and mixed feeders use open, high-visibility habitat for risk avoidance (_11, 13_), our study of a solitary, crypsis-dependent browser reveals an opposing pattern. This distinction was appreciated by early naturalists [(_36_), pp. 32–33]:

It is curious to note the different ideas of safety entertained respectively by the plain and the bush dweller. Let us say a Grant's gazelle and a bushbuck are grazing near each other on the edge of a plain when something occurs to alarm them. The bushbuck lopes quickly back into the bush, sure that in this lies his only chance of safety. The Grant's turns and gallops from the bush as if it were some deadly thing ....

Thus, although generalizations about trophic cascades involving particular species and food chains may be possible on the basis of characteristics such as herbivore size, behavior (*37, 38*), and predator hunting mode (*39*), we suggest that community-wide cascades may be dampened in diverse African large-mammal assemblages because of the orthogonal responses of different herbivore species to predation risk (*40*).

REFERENCES AND NOTES

1. J. A. Estes *et al.*, *Science* **333**, 301–306 (2011).
2. W. J. Ripple *et al.*, *Science* **343**, 1241484 (2014).
3. J. Terborgh, J. A. Estes, Eds., *Trophic Cascades: Predators, Prey and the Changing Dynamics of Nature* (Island Press, 2010).
4. J. A. Estes, J. F. Palmisano, *Science* **185**, 1058–1060 (1974).
5. J. S. Brown, J. W. Laundre, M. Gurung, *J. Mammal.* **80**, 385–399 (1999).
6. J. W. Laundré, L. Hernandez, W. J. Ripple, *Open Ecol. J.* **3**, 1–7 (2010).
7. J. Berger, J. E. Swenson, I. L. Persson, *Science* **291**, 1036–1039 (2001).
8. B. L. Peckarsky *et al.*, *Ecology* **89**, 2416–2425 (2008).
9. G. C. Trussell, P. J. Ewanchuk, C. M. Matassa, *Ecology* **87**, 2979–2984 (2006).
10. O. J. Schmitz, V. Krivan, O. Ovadia, *Ecol. Lett.* **7**, 153–163 (2004).
11. A. T. Ford *et al.*, *Science* **346**, 346–349 (2014).
12. J. P. Suraci, M. Clinchy, L. M. Dill, D. Roberts, L. Y. Zanette, *Nat. Commun.* **7**, 10698 (2016).
13. E. le Roux, G. I. H. Kerley, J. P. G. M. Cromsigt, *Curr. Biol.* **28**, 2493–2499.e3 (2018).
14. W. J. Ripple, E. J. Larsen, R. A. Renkin, D. W. Smith, *Biol. Conserv.* **102**, 227–234 (2001).
15. D. Fortin *et al.*, *Ecology* **86**, 1320–1330 (2005).
16. M. J. Kauffman, J. F. Brodie, E. S. Jules, *Ecology* **91**, 2742–2755 (2010).
17. B. L. Allen *et al.*, *Biol. Conserv.* **159**, 158–174 (2013).
18. J. Winnie Jr., S. Creel, *Food Webs* **12**, 88–94 (2017).
19. A. T. Ford, J. R. Goheen, *Trends Ecol. Evol.* **30**, 725–735 (2015).
20. J. Terborgh *et al.*, *Science* **294**, 1923–1926 (2001).
21. M. E. Stalmans, T. J. Massad, M. J. S. Peel, C. E. Tarnita, R. M. Pringle, *PLOS ONE* **14**, e0212864 (2019).
22. J. H. Daskin, M. Stalmans, R. M. Pringle, *J. Ecol.* **104**, 79–89 (2016).
23. R. M. Pringle, *Nature* **546**, 91–99 (2017).
24. P. Bouley, M. Poulos, R. Branco, N. H. Carter, *Biol. Conserv.* **227**, 233–242 (2018).
25. M. Stalmans, R. Beilfuss, "Landscapes of the Gorongosa National Park" (Gorongosa National Park, 2008).
26. J. Kingdon, *The Kingdon Field Guide to African Mammals* (Bloomsbury, ed. 2, 2015).
27. R. D. Estes, *The Safari Companion: A Guide to Watching African Mammals* (Chelsea Green, ed. 2, 1999).
28. R. D. Estes, *The Behavior Guide to African Mammals* (Univ. of California Press, 1991).
29. F. G. T. Radloff, J. T. Du Toit, *J. Anim. Ecol.* **73**, 410–423 (2004).
30. K. L. Tinley, thesis, University of Pretoria, Pretoria, South Africa (1977).
31. S. D. Fretwell, H. L. J. Lucas Jr., *Acta Biotheor.* **19**, 16–36 (1969).
32. Materials and methods are available as supplementary materials.
33. A. T. Ford, J. R. Goheen, *J. Mammal.* **96**, 918–926 (2015).
34. J. Pansu *et al.*, *J. Ecol.* 10.1111/1365-2745.13113 (2018).
35. D. I. Bolnick *et al.*, *Am. Nat.* **161**, 1–28 (2003).
36. C. H. Stigand, *The Game of British East Africa* (Horace Cox, 1909).
37. P. J. Jarman, *Behaviour* **48**, 215–267 (1974).
38. K. P. Dial, E. Greene, D. J. Irschick, *Trends Ecol. Evol.* **23**, 394–401 (2008).
39. O. J. Schmitz, *Science* **319**, 952–954 (2008).
40. N. Owen-Smith, *Oikos* **124**, 1417–1426 (2015).
41. J. L. Atkins, R. A. Long, J. Pansu, J. H. Daskin, A. B. Potter, M. E. Stalmans, C. E. Tarnita, R. M. Pringle, Data for "Cascading impacts of large-carnivore extirpation in an African ecosystem," Dryad (2019); https://doi.org/10.5061/dryad.h4r1003.

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Ecosystems feel war's effects

War ravages human lives and landscapes, but nonhuman victims are no less affected. The Mozambican Civil War resulted in the rapid decline of predators in Gorongosa National Park and led to a trophic cascade that shifted prey behaviors and plant communities. Atkins *et al.* monitored this shift and found that the absence of wild dogs and leopards resulted in a change in habitat use and plant consumption by bushbuck, which are forest-dwelling antelopes. Experiments further showed that changes in prey behavior were reversible when signs of predator activity were introduced, supporting the impact of the predator loss. These results confirm patterns seen elsewhere and go further in providing mechanistic detail about the importance of the "landscape of fear" perceived by prey animals.
Science, this issue p. 173

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