

INDIRECT EFFECTS OF LARGE HERBIVORES ON SNAKES IN AN AFRICAN SAVANNA

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Abstract. Many large mammal species are declining in African savannas, yet we understand relatively little about how these declines influence other species. Previous studies have shown that the removal of large herbivorous mammals from large-scale, replicated experimental plots results in a dramatic increase in the density of small mammals, an increase that has been attributed to the relaxation of competition between rodents and large herbivores for food resources. To assess whether the removal of large herbivores also influenced a predator of small mammals, we measured the abundance of the locally common olive hissing snake, *Psammophis mossambicus*, over a 19-mo period in plots with and without large herbivores. *Psammophis mossambicus* was significantly more abundant in plots where large herbivores were removed and rodent numbers were high. Based on results from raptor surveys and measurements of vegetative cover, differences in snake density do not appear to be driven by differences in rates of predation on snakes. Instead, snakes appear to be responding numerically to greater abundances of small-mammal prey in areas from which large herbivores have been excluded. This is the first empirical demonstration of the indirect effects of large herbivores on snake abundance and presents an interesting example of how the influence of dominant and keystone species can move through a food web.

Key words: Africa; indirect effects; large herbivore; *Saccostomus mearnsi*; small mammal; snake; *Psammophis mossambicus*.

INTRODUCTION

Dominant and keystone species are recognized by their profound impacts on the composition, dynamics, and functioning of ecological communities (Power et al. 1996). Direct effects of these species on their prey, predator, or competitor species are relatively apparent, but in most cases constitute only a portion of their total effect on community dynamics. Indirect effects are also essential components of food web ecology, but are often more difficult to detect. Indirect effects or interactions follow when one species produces a change in a variable associated with a second species by changing one or more other variables, at least one of which is associated with a third species (Wootton 1994, Abrams et al. 1996). The general role and importance of indirect effects in food web ecology have been extensively considered (Schoener 1993, Menge 1995, Abrams et al. 1996, Schmitz et al. 2004). Indirect effects of dominant or keystone species typically are examined in the context of trophic cascades, defined as the impact of predators on abundance or biomass of prey that penetrates at least two trophic levels below the predator (Pace et al. 1999).

Other indirect pathways for the influence of these species, for example via competition for shared resources or bottom-up penetrance through multiple trophic levels, are less often considered.

In African savannas the dominant species are often native large herbivorous mammals (hereafter “large herbivores”). Native African large herbivores are declining as a result of habitat destruction, poaching, disease, and competition with domestic stock (du Toit and Cumming 1999, Ottichilo et al. 2000, Georgiadis et al. 2003). Several indirect effects of the loss of large herbivores from African savannas have already been well-documented. For example, the removal of large herbivores has been demonstrated to cause an increase in the density of small mammals, particularly rodents, probably as a result of decreased competition for food (Keesing 1998, 2000, Caro 2001, 2002, 2003).

Janzen (1976) provided a number of prescient hypotheses concerning how large herbivores might also indirectly contribute to the depression of reptile biomass in Africa, although these hypotheses have remained untested. In this experiment, we attempted to determine if the removal of large African herbivores could indirectly affect the abundance of snakes, an important predator of small mammals in African savannas. Previous studies have indicated that the fitness of snakes might be positively correlated with prey abundance

(Ford and Seigel 1989, Bronikowski and Arnold 1999, Madsen and Shine 2000a, b). Thus, we hypothesized that if snakes were capitalizing on increased abundances of rodent prey made available following the removal of large herbivores, then we would find more snakes in experimental plots where large herbivores were absent as compared to control plots where large herbivores were present.

In addition to surveying the abundance of snakes in areas with and without large herbivores, we evaluated potential mechanisms by which snakes might be responding to the absence of large herbivores by (1) measuring small-mammal abundance by live trapping, (2) estimating the amount of vegetation cover available for snakes to use as refuge from predators, and (3) surveying densities of raptors that prey upon snakes.

METHODS

Study site

We conducted this research from April 2002 to January 2005 at the Mpala Research Centre (MRC) in the Laikipia District of Kenya (0°20' N, 36°53' E). The study site is in *Acacia drepanolobium* savanna-woodland on "black cotton" soil. Rainfall is weakly trimodal with peaks in April–May, July–August, and October–November, and a distinct dry season in January–February. There is considerable year-to-year variation in total rainfall. Total precipitation at the study site was 547 mm in 2002, 740 mm in 2003, and 826 mm in 2004 (Kenya Long-Term Exclusion Experiment project records).

Woody vegetation on the site is dominated by *A. drepanolobium*, with trees of this species accounting for >97% of the overstory vegetation (Young et al. 1998). The herbaceous understory is dominated by five grasses and, to a lesser degree, six forbs (Young et al. 1998). Ten species of large wild mammalian herbivores and domestic cattle are present at the site (Young et al. 1998, Keesing 2000). Resident snake species include the olive hissing sand snake (*Psammodon mossambicus*), puff adder (*Bitis arietans*), spitting cobra (*Naja nigricollis*), Battersby's green snake (*Philothamnus battersbyi*), and white-lipped snake (*Crotaphopeltis hotamboeia*). The small-mammal community is dominated by the northern pouched mouse (*Saccostomus mearnsi*); six other species are also present in lower numbers (Keesing 2000).

All experiments were conducted within the Kenya Long-Term Exclusion Experiment (KLEE), which was established in 1995 (Young et al. 1998). The KLEE site consists of three 400 × 600 m (24-ha) blocks. Each block in turn consists of six 200 × 200 m (4-ha) plots, each of which excludes a particular combination of large mammals. For our experiments we used only treatment plots that excluded all large herbivores >15 kg ($n = 3$) and unfenced control plots where all animals had free access ($n = 3$). See Young et al. (1998) for details of the enclosure plots and site characteristics.

Snake surveys

We used cover boards to monitor snake abundance (Fellers and Drost 1994). We placed eight 1 × 1 m plywood boards 50 m apart along the perimeter of the inner hectare of plots with and plots without large herbivores in KLEE. No two boards in different plots were closer than 140 m. Boards were placed in April 2002 and were allowed to sit undisturbed for 16 mo before we began regularly monitoring them for snakes.

Surveys of snakes were conducted July 2003–January 2005. Boards were checked approximately twice monthly, with slight variation due to impassable roads and the occasional presence of dangerous wildlife on the survey sites. We completed 23 surveys during the study. All surveys were conducted between 0600 and 0900 hours, before diurnal snakes left the boards to forage. We alternated the order in which we surveyed boards. If we were unable to complete surveys in all of the replicate blocks by 0900 hours, we suspended our work after completing paired plots and resumed the following morning. Snakes were identified to species following Spawls et al. (2002).

The most abundant snake detected in KLEE was the olive hissing snake, *Psammodon mossambicus*, a medium-sized diurnal colubrid common in many parts of East Africa and known to feed upon small mammals, lizards, snakes, amphibians, and birds (Spawls et al. 2002). We initially marked captured snakes by clipping ventral scales. In November 2003, we switched to marking snakes with PIT tags (AVID; Greeley, Colorado, USA) as this proved to be a superior means of identification. The total length of new captured snakes was measured.

We used two separate measures to compare snake abundance between enclosure and control plots: "sightings," the number of snakes (including both recaptured and untagged) observed under boards; and "individuals," the number of snakes captured under boards and PIT-tagged for the first time. This approach was necessary because snakes are too rare in KLEE to allow for estimation of densities using standard mark and recapture programs. Both of these abundance metrics are likely to be underestimates of the actual population sizes of *P. mossambicus* in study plots (with "individuals" representing the absolute minimum number of snakes in a plot). We put more emphasis on the importance of the number of sightings, because this is probably a better proxy for actual snake abundance and because this measure has been demonstrated in other snake studies to approximate closely the patterns produced by mark and recapture program estimates (Lind et al. 2005). The total numbers of sightings and individuals summed over the 23 sampling sessions were normally distributed. We used a one-way ANOVA to test for the effects of block and treatment on total snake sightings and individuals from each of the two treatments over the three replicates. In order to guard against loss of statistical precision possibly engendered by

comparing totals, we also employed a permutation test (randomly permuting observations between blocks and comparing the permutation distribution of the Euclidean length of the component-wise t statistic to the observed value [see Lehmann and Romano (2005) for details]) to test for block effect on each treatment (exclosure and control) for sightings and individuals. Because results from these permutation tests demonstrated no significant effect of block on snake abundance, we pooled data from each of the three blocks for sightings and individuals and analyzed the effect of herbivore exclusion using an unpaired two-tailed t -test. We compared the total lengths of all snakes at first capture also using an unpaired two-tailed t -test.⁷

Small-mammal sampling

Small mammal populations in KLEE have been monitored continuously since 1995 (Keesing 1998, 2000). In conjunction with this research, we trapped plots with and without large herbivores five times before the onset of snake surveys (from January 2002–June 2003) and five times during snake surveys (from September 2003–March 2005). One large folding Sherman trap was placed at each point on a permanent 10 × 10 m grid with 10-m spacing, the grid positioned in the inner hectare of each plot. Traps were baited with a mixture of oats and peanut butter. Trapping was conducted for two to three consecutive nights in each plot during each session. Captured individuals were marked with ear tags.

Abundances of all small mammals except the pouched mouse, *Saccostomus mearnsi*, were determined using direct enumeration, because abundances were generally too low for reliable mark–recapture estimates. Abundances of *S. mearnsi* were calculated with Program CAPTURE (Rexstad and Burnham 1992) using the model of homogeneity of captures. We used a factorial repeated measures ANOVA to compare abundances through time.

Vegetation cover

Understory vegetation in KLEE has been monitored continuously since 1995 (Young et al. 1998, 2005). During this study, we measured vegetative cover in plots with and without large herbivores in June 2003, February 2004, and June 2004. Understory aerial cover was determined using a 0.5 m wide pin frame with 10 pins. The pin frame was placed at every small-mammal trap station in the inner hectare, for a total of 100 placements per plot. At each placement, we recorded the number of pins contacting vegetation, and the number of pins contacting no vegetation. For exclosure and control plots from each of the three surveys, we

calculated the mean number of pins contacting vegetation and compared these using a repeated measures ANOVA.

Raptor surveys

We surveyed plots with and without large herbivores for raptors during January 2001–March 2004. Surveys were conducted once a month, except during March 2001–July 2001, when surveys were made bimonthly. No surveys were conducted during four months due to impassable roads, giving a total of 40 surveys. All surveys were carried out between the hours of 0900 and 1200 when air thermals had developed and raptors were active. During the first five monthly surveys, one observer was placed in a plot with large herbivores and one observer was placed in the corresponding plot without large herbivores, so that areas could be surveyed simultaneously. Observers walked once around the 800-m perimeter of the plots and then once along each of the two diagonals bisecting plots, taking ~30 min to cover this distance. Observers counted, identified, and made note of the activity of all birds of prey seen within the boundaries of each respective plot. Identifications were made to the species level when possible following Zimmerman et al. (1996), but owing to the difficulty of identifying raptors in flight, observations to group level were also included. From June 2001 until March 2004, both observers began surveying the same plot together to increase observer safety. Only sightings of raptors that were identified in the literature as predators of snakes, reptiles, or small vertebrates were considered for this analysis (henceforth considered “potential snake-eating raptors”). The mean number of potential snake-eating raptors recorded per observation was calculated for exclosure and control plots, and these averages were compared using an unpaired two-tailed t test.

RESULTS

Snake surveys

Two species of snakes were found under the boards during our surveys: olive hissing sand snakes (*Psammophis mossambicus*) and puff adders (*Bitis arietans*). *P. mossambicus* was by far the most common, accounting for 94% ($N = 49$) of total snake sightings under boards. There were approximately twice as many snake sightings and individuals in plots without large herbivores vs. plots with large herbivores (Fig. 1). One-way ANOVAs demonstrated that there was no effect of block on either total number of snake sightings ($F_{2,3} = 0.28$, $P = 0.77$) or total individuals ($F_{2,3} = 0.07$, $P = 0.94$), and there was a significant effect of herbivore removal on both total snake sightings ($F_{1,4} = 15.6$, $P = 0.017$) and total individuals ($F_{1,4} = 9.1$, $P = 0.039$). Permutation test results likewise demonstrated no effect of block on treatment for both sightings (no large herbivores, $P = 0.52$; large herbivores, $P = 0.49$) and individuals (no large herbivores, $P = 0.59$; large herbivores, $P = 0.67$),

⁷ All statistics were computed using R: A language and environment for statistical computing. Version 2.1.1. 2005. (R Foundation for Statistical Computing, Vienna, Austria) (<http://www.Rproject.org>)

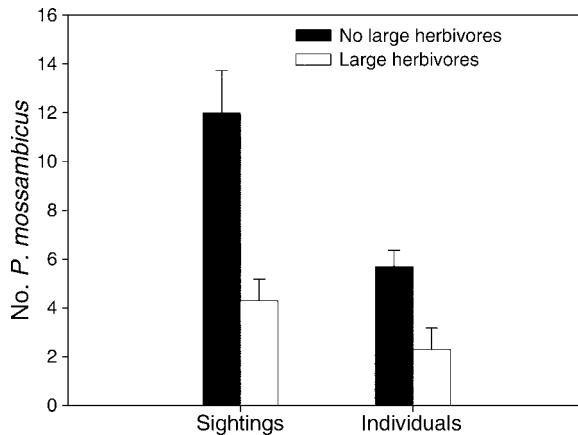


FIG. 1. Abundance of *Psammophis mossambicus* in plots with and without large herbivores (mean number per plot; with bar indicating SE). The mean number of snake sightings ($F_{1,4} = 15.6$, $P = 0.017$; $t = 2.82$, $P = 0.006$) and individual snakes ($F_{1,4} = 9.1$, $P = 0.039$; $t = 1.89$, $P = 0.062$) was higher for plots without large herbivores.

while t test results showed a significant effect of the removal of large herbivores on sightings ($t_{128} = 2.82$, $P = 0.006$) and a marginally nonsignificant effect on individuals ($t_{85} = 1.89$, $P = 0.062$). There was no significant difference between plots with and without large herbivores in the length of snakes at the time of first capture ($t_{15} = -0.4$, $P = 0.66$).

The 11 recaptured snakes were all caught on the same plots on which they were tagged. We were not able to compare movement patterns of the snakes in areas with and without large herbivores, because only one of these recaptures was made in plots with large herbivores.

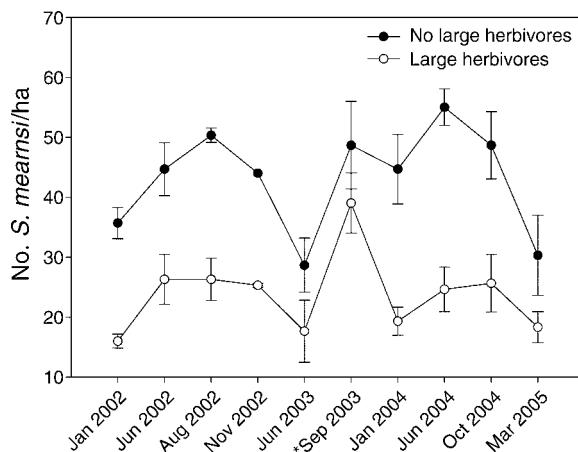


FIG. 2. Density of the most abundant small mammal *Saccostomus mearnsi* on plots with and without large herbivores (\pm SE). Surveys of snakes began in September 2003, as indicated by the asterisk. *Saccostomus mearnsi* were significantly more abundant on plots without large herbivores in the year prior to ($F_{1,4} = 76.7$, $P < 0.001$) and the year of snake surveys ($F_{1,4} = 14.6$, $P = 0.02$).

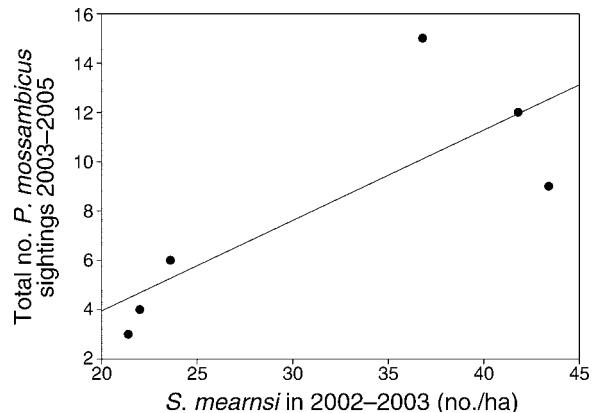


FIG. 3. Relationship between snake abundance (total number of sightings for *Psammophis mossambicus*) and density of *Saccostomus mearnsi* in year prior to snake survey ($R^2 = 0.64$, $P = 0.05$). The three points grouped at bottom left are from plots with large herbivores, and the three points grouped in the top right are from plots without large herbivores.

Small mammal sampling

Seven species of small mammals were captured during the course of this study. The abundance of all small mammals was significantly higher on plots without large herbivores in the year prior to surveying snakes ($F_{1,4} = 40.5$, $P = 0.003$) and in the year during snake surveys ($F_{1,4} = 49.1$, $P = 0.002$). The most abundant small mammal at the site during both years, representing 75% of all captures, was the northern pouched mouse, *Saccostomus mearnsi*. There were also significantly more *S. mearnsi* in the plots without large herbivores in the year prior to snake surveys ($F_{1,4} = 76.7$, $P < 0.001$) and the year of snake surveys ($F_{1,4} = 14.6$, $P = 0.02$) (Fig. 2). There was a significant positive relationship between total number of sightings of snake *P. mossambicus* and mean density of *S. mearnsi* ($R^2 = 0.64$, $P = 0.05$) (Fig. 3) and density of total small mammals ($R^2 = 0.65$, $P = 0.05$) from the year preceding snake surveys in each plot. A similar positive relationship was found between total number of snake individuals and densities of *S. mearnsi* ($R^2 = 0.53$, $P = 0.10$) and total small mammals ($R^2 = 0.48$, $P = 0.13$) from the year preceding snake surveys, although these trends were not significant.

Vegetation surveys

In general, there was high understory aerial cover on all plots. There was no significant difference in understory aerial cover in the presence (mean percentage pins contacting vegetation per framing, $93.6\% \pm 1.5\%$) vs. the absence (mean percentage pins contacting vegetation per framing, $96.4\% \pm 1.0\%$) of large herbivores over the course of the experiment ($F_{1,4} = 5.0$, $P = 0.09$). Other measures of vegetation cover based on the proportion of pins hitting each species of vegetation were also not significant ($F_{1,4} = 0.62$, $P = 0.47$).

Raptor surveys

We recorded 15 species of raptors that could potentially feed upon snakes. There was no difference in densities of potential snake-eating raptors between plots with and without large herbivores ($t_{77} = 0.198$, $P = 0.84$). One of these raptors, a snake specialist, the Black-chested Snake Eagle (*Circaetus pectoralis*), was observed five times in plots with large herbivores and five times in plots without large herbivores. Throughout the course of the observations, five raptor individuals were observed actively hunting in plots without large herbivores and four raptor individuals were observed actively hunting in plots with large herbivores.

DISCUSSION

Plots without large herbivores consistently had significantly higher abundances of *P. mossambicus* snakes (Fig. 1). How could removing large herbivores from a habitat cause an increase in snake abundance? Three possible mechanisms seem most likely: snakes could be negatively affected by trampling of large herbivores; snakes could be subject to lower predation rates in plots without large herbivores; and/or snakes could be occupying habitats without large herbivores to take advantage of higher prey densities. We evaluate the evidence for each of these possibilities.

We have no data to support or refute the possibility that large herbivores are significantly affecting snake abundances by trampling. However, *Psammophis mossambicus* is a fast-moving, visually oriented snake very capable of eluding capture and presumably equally able to avoid being trod upon. Furthermore, *P. mossambicus* and other snake species in this habitat often use refugia (termite mound holes, fallen logs, rodent holes) when at rest, and while in them are safe from large herbivores. No trampled snakes have ever been recorded in the Kenya Long-Term Exclusion Experiment (KLEE) site, despite thousands of hours of researcher presence over the past ten years.

Greater vegetative cover can provide increased protection from predators for small-bodied animals (Birney et al. 1976, Peles and Barrett 1996). The presence of large herbivores in the control plots could decrease cover via feeding and disturbance. If this decrease in cover were great enough, snakes might be more vulnerable to predation and consequently less abundant in areas with large herbivores. However, vegetative cover in enclosure and control plots during the period of the snake surveys did not differ significantly. The lack of a difference in vegetative cover might be partly explained by the high densities of herbivorous rodents in the exclusion plots, which might consume much of the surplus vegetation made available by the removal of large herbivores (Keesing 2000). However, it should be noted that in some earlier surveys, cover in plots with large herbivores did exceed cover in the exclusion plots, at least during extended dry periods (Young et al. 2005).

Our data on snake predators in KLEE allow us a means to indirectly measure whether any of these differences in cover actually translated into differences in predation pressure on snakes. Surveys of raptors demonstrated that there were many bird species present in KLEE that could potentially feed upon snakes. However, there was no difference in abundance or activity patterns of these predators between enclosure and control plots. Raptors are not the only potential snake predators in this experiment. Several species of small carnivores that eat snakes are also present in KLEE (e.g., mongooses and felids). We were not able to directly compare numbers of small carnivores between plots with and without large herbivores without disturbing ongoing experiments. However, using scat and track data, we were able to determine that they are present in both enclosure and control plots and not significantly deterred by the enclosure fencing (Keesing 1998; F. Keesing, unpublished data). Moreover, data from an experiment conducted in KLEE using plasticine snake models to measure predation rates (Madsen 1987, Webb and Whiting 2005) yielded only a single predator attack during 56 observation days, suggesting that predation pressure on snakes of any kind is generally low in KLEE and not different between plots with and without large herbivores (J. Peters and F. Keesing, unpublished data).

There were twice as many small mammals in plots without large herbivores as in plots with large herbivores (Fig. 2). Specific data on the diet of *P. mossambicus* in KLEE is lacking. However *S. mearnsi*, the most abundant small mammal in this habitat, is an important, if not the most important, prey source for *P. mossambicus* in KLEE. We identified hair samples collected from the stomach contents of two dead *P. mossambicus* recovered in KLEE as being from *S. mearnsi* (Teerink 1991, Riordan 1997) and observed *P. mossambicus* hunting *S. mearnsi* released from traps. The positive relationship between density of *S. mearnsi* in the year prior to snake surveys and snake abundances (Fig. 3) suggests that the predator *P. mossambicus* could have been responding to increases in the density of this prey species. Body size in snakes has been shown to reflect food intake (Forsman and Lindell 1991, 1996, Madsen and Shine 2000a). If snakes in the plots without large herbivores were not utilizing increased *S. mearnsi* densities, we would have expected crowding to negatively affect their length, as compared to the length of snakes in plots with large herbivores (Lindell and Forsman 1996). However, total lengths of *P. mossambicus* in plots with and without large herbivores were not significantly different. Because we did not sex or weigh captured snakes (in order to minimize handling stress and thus risk to future sampling), we are not able to report similar comparisons of snake body condition (length–mass relationship). We cannot eliminate the possibility that trampling or differences in predation pressure engendered by differences in cover or some

other unmeasured variable might be contributing to the differences in snake abundance observed between plots. Nevertheless, our data suggest that the major variable driving these changes in snake abundance was the difference in rodent density.

We are unable to say definitively whether the increases in snake density we observed represented a behavioral shift of snakes (i.e., feeding forays from outside home bases), or whether they indicate higher rates of snake reproduction or survival. However, our mark and recapture data do not support a behavioral explanation. Because all snakes were sampled early in the day before they ventured out to forage, location of capture represents where they took refuge for the night and should be indicative of their residence areas. Furthermore, marked snakes were not observed to move between plots and some snakes stayed in the plots for considerable periods of time (maximum time between capture and recapture was 251 d for an individual snake in a plot with no large herbivores). Although home range size in snakes appears to be highly variable, researchers have recorded ranges of movement and home range sizes of less than one hectare for other colubrids (Tobin et al. 1999, Rodriguez-Robles 2003). Thus, we tentatively conclude that the carrying capacity for snakes increased when large herbivores were removed.

Our enclosure fences experimentally simulate how predation by apex carnivores (humans included) can depress populations of large herbivores. In the absence of large herbivores, rodents are released from competition for a basal resource and become nearly twice as abundant. This increase seems to contribute significantly to a pronounced increase in the number of snakes. If our hypothesized mechanism is correct, then the influence of this experimental perturbation moves down from apex predators, to large herbivores, to a resource base, where it then reflects back up through the savanna food web to small herbivores and their predators. There are few examples in the literature where trophic cascades are "reflected" in this manner (Thompson et al. 1991, Berger et al. 2001, Reisewitz et al. 2005; R. M. Pringle, unpublished data). We suspect that the rarity of these descriptions does not represent their infrequency in natural systems and we expect that with increased attention from ecologists, more such examples will become apparent.

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