

January 2008

esa

Volume 89 No. 1

ECOLOGY

A PUBLICATION OF THE ECOLOGICAL SOCIETY OF AMERICA



Reports

Hydrology and grazing jointly control a large-river food web

Longevity can buffer plant and animal populations against changing climatic variability

Elephants as agents of habitat creation for small vertebrates at the patch scale

Articles

Herbivore-induced "rent rise" in the host plant may drive a diet breadth enlargement in the tenant

A nearly neutral model of biodiversity

ELEPHANTS AS AGENTS OF HABITAT CREATION FOR SMALL VERTEBRATES AT THE PATCH SCALE

ROBERT M. PRINGLE¹

Department of Biological Sciences, Stanford University, Stanford, California 94305 USA

Abstract. Ecologists increasingly recognize the ability of certain species to influence ecological processes by engineering the physical environment, but efforts to develop a predictive understanding of this phenomenon are in their early stages. While many believe that the landscape-scale effects of ecosystem engineers will be to increase habitat diversity and therefore the abundance and richness of other species, few generalities exist about the effects of engineering at the scale of the engineered patch. According to one hypothesis, activities that increase structural habitat complexity within engineered patches will have positive effects on the abundance or diversity of other organisms. Here I show that, by damaging trees and increasing their structural complexity, browsing elephants create refuges used by a common arboreal lizard. Observational surveys and a lizard transplant experiment revealed that lizards preferentially occupy trees with real or simulated elephant damage. A second experiment showed that lizards vacate trees when elephant-engineered refuges are removed. Furthermore, local lizard densities increased with (and may be constrained by) local densities of elephant-damaged trees. This facilitative effect of elephants upon lizards via patch-scale habitat modification runs contrary to previously documented negative effects of the entire ungulate guild on lizards at the landscape scale, suggesting that net indirect effects of large herbivores comprise opposing trophic and engineering interactions operating at different spatial scales. Such powerful megaherbivore-initiated interactions suggest that anthropogenic changes in large-mammal densities will have important cascading consequences for ecological communities.

Key words: *allogenic ecosystem engineers; disturbance; geckos; habitat facilitation; herbivory; Kenyan Acacia savannas; keystone species; Loxodonta africana; Lygodactylus keniensis; positive interactions; quantile regression; trait-mediated indirect effects.*

INTRODUCTION

Ecosystem engineers are organisms that control the availability of resources to other species by modifying the physical environment (Jones et al. 1994). Since its formal introduction 14 years ago, this concept has generated much interest, a growing number of reviews and conceptual explorations (e.g., Crain and Bertness 2006, Wright and Jones 2006), and some controversy (e.g., Jones et al. 1997a, Power 1997, Reichman and Seabloom 2002, Wilby 2002).

Critics of the concept have alleged that the phenomenon is so widespread that the term has limited utility (Reichman and Seabloom 2002), and that authors have been overly quick to apply the ecosystem-engineering label to any process that involves habitat modification (Power 1997). Others have countered that the ubiquity of the phenomenon does not detract from the utility of the concept (Wright and Jones 2006). Nonetheless, even the staunchest proponents of the idea evince concern that, in the absence of more encompassing theory, the

ecosystem-engineering literature might collapse into a heap of “just-so” stories (Jones et al. 1994, Wilby 2002).

Recent work has therefore emphasized the need for a predictive understanding of how ecosystem engineers affect the abundance and diversity of sympatric species (Wright and Jones 2004), and of how these effects are contingent upon scale (Hastings et al. 2007). Jones et al. (1997b) proposed that physical ecosystem engineering should have positive effects on organismal abundance and diversity at large spatial scales, but that there is no reason to assume these effects to be positive at local scales (the scale of the engineered patch, *sensu* Wright and Jones 2004). Later, Crooks (2002) drew on a large literature documenting positive relationships between habitat complexity and biotic abundance and diversity (e.g., MacArthur and MacArthur 1961) to suggest that ecosystem engineers that increased structural habitat complexity should buttress abundance and diversity, regardless of scale. Crooks’s (2002) review, however, yielded only partial support for this hypothesis, necessitating further studies that simulate ecosystem engineering by manipulating habitat structure.

Elephants are among the more obvious examples of ecosystem engineers (Wright and Jones 2006) and have complex scale-dependent effects on habitat structure. Savanna elephants are perhaps best known for their role in maintaining open wooded grasslands (i.e., reduced

Manuscript received 10 May 2007; revised 10 September 2007; accepted 13 September 2007. Corresponding Editor: R. J. Marquis.

¹ E-mail: pringle@stanford.edu



PLATE 1. Elephants browsing on *Acacia nilotica* at Mpala Research Centre, Kenya. The young elephant is stripping bark from a twig, and several larger broken limbs are visible. Photo credit: Nathan Gregory.

habitat complexity: Laws 1970, Dublin et al. 1990); much of the literature about elephants as agents of habitat change revolves around concerns that elephant overabundance in protected areas will cause habitat degradation (Caughley 1976, van Aarde and Jackson 2007). Less well appreciated is the role of elephants in increasing habitat complexity at restricted spatial and temporal scales by modifying woody-plant architecture and increasing exposed woody surface area (see Fig. 1A, B). According to the habitat complexity hypothesis advanced by Crooks (2002), elephant damage to trees might therefore be expected to augment the abundance of smaller animals.

Here, I describe a positive interaction linking elephants (*Loxodonta africana* Blumenbach) with an arboreal gecko (*Lygodactylus keniensis* Parker) in an African savanna. By breaking tree limbs and stripping bark while browsing, elephants create crevices that lizards use as refuges (see Plate 1). Lizards' preference for elephant-damaged trees is so strong that local lizard density appears to be regulated largely by the local density of elephant-damaged trees. This positive patch-scale effect of elephants on lizards via engineering counteracts net negative landscape-scale effects of all large herbivores on lizards via reduced prey and habitat availability (Pringle et al. 2007), reemphasizing the need

to integrate the trophic and engineering effects of herbivores (Wilby et al. 2001).

METHODS

Study site and organisms

I conducted this study between June 2004 and March 2007 at Mpala Research Centre (0°20' N, 36°53' E, 1650 m elevation) in the Laikipia District of central Kenya. Rainfall averages 500 mm in a weakly tri-modal annual pattern, with rainfall peaking during April–May, August, and October, and a consistent dry season occurring from January–March. The study area is underlain by friable sandy loams derived from metamorphic basement rocks (Augustine and McNaughton 2004). The dominant trees in this community are *Acacia etbaica* Schweinf and *A. mellifera* (Vahl) Benth. Elephants, which are predominantly browsers, have the greatest biomass density of any wildlife species in this system (29 kg/ha: Augustine and McNaughton 2004).

Lygodactylus keniensis (syn. *L. picturatus*) is the dominant lizard in this area, accounting for >90% of all individuals (Pringle et al. 2007); with densities approaching 200 individuals/ha, it is also perhaps the most abundant vertebrate in the system. This species is strictly arboreal, small (~3 cm snout–vent length, ~1 g), diurnal, and preys on a variety of non-ant arthropods

3–30 mm long (Greer 1967), especially beetles (Hardy and Crnkovic 2006, Pringle et al. 2007). Males are strongly territorial (maximum of one individual per tree), whereas females are less so and frequently cohabit trees (Greer 1967). In the absence of any disturbance, lizards apparently remain on individual trees for extended periods (Greer 1967; *personal observation*).

*Elephant damage and the local distribution and abundance of *L. keniensis**

From June–September in 2004 and 2005, I censused *L. keniensis* in twelve 25 × 25 m plots spread across a study area spanning 12 km north-to-south. In each census, I visited the plot on three consecutive days and marked lizards with a visit-specific color of diluted water-based paint; I then used the sighting histories to estimate local population densities (Pringle et al. 2007: Methods). Each time a new lizard was marked, I recorded the height and degree of elephant damage of the tree on which it was found. Elephant browsing is easily diagnosed by the presence of stripped bark, roughly broken stems, or damage to the entire plant (Fig. 1A; Augustine and McNaughton 2004). Such damage occasionally kills mature *A. etbaica* and *A. mellifera*, but more commonly causes nonlethal architectural modifications. Wood decays slowly in this semiarid area, so these modifications last for years (*personal observation*) and probably decades, creating an extended legacy (*sensu* Hastings et al. 2007) of elephant activity. For this study, I categorized elephant damage as either none-to-minor (frayed shoot tips or broken twigs, hereafter “undamaged”) or moderate-to-severe (bark stripping or ≥1 large broken limb, hereafter “damaged”).

I assumed that in the absence of any lizard preference for elephant-damaged trees, the observed frequency of lizards occupying elephant-damaged trees would equal the overall frequency of elephant-damaged trees in the plot. I then compared these observed and expected frequencies using Pearson chi-square tests. I used least-squares regression to test the hypothesis that estimated local lizard density increases with the local density of elephant-damaged trees. Data were square-root transformed to meet assumptions of least-squares regression. Because lizard density is likely to be a function of several determinants, I also used quantile regression to test the hypothesis that the density of elephant-damaged trees constrains the upper limits of local lizard density (Cade and Noon 2003). I calculated the 0.90 conditional quantile using the “quantreg” library of the R statistical software program (*available online*)² and tested the null hypothesis that the slope of the regression line was indistinguishable from zero using bootstrapped standard errors of the regression coefficient (Knight and Ackerly 2002).

Assessing the mechanisms underlying lizard habitat preference

Because the observational data suggested that lizards strongly preferred elephant-damaged trees (see *Results*), I performed two experiments to elucidate the mechanisms that produced this pattern. I hypothesized four reasons why this pattern might occur. First, bark stripping and branch splintering by elephants often creates crevices large enough to serve as refuges for *L. keniensis* (Fig. 1B). Second, elephant damage often opens the canopy and produces one or more exposed horizontal perches, which are otherwise rare on the shrublike *A. etbaica* and *A. mellifera*. Many arboreal lizards use such perches for thermoregulation and vigilance, both of which are potentially important needs for *L. keniensis*. Third, elephant damage might increase the abundance of invertebrates (i.e., lizard prey), either by creating dead wood and crevices or by promoting palatable leafy regrowth (Musgrave and Compton 1997). Fourth, elephants and lizards might each prefer similar types of trees for their own reasons, resulting in a coincidental association.

I investigated these hypothesized drivers of lizard habitat preference using a lizard-transplant experiment in a factorial randomized-block design. At each of 10 blocks along a 2-km transect, I chose four *A. etbaica* trees ~3 m tall and assigned them randomly to each of four treatment combinations of perch/refuge addition. I created perch + refuge trees by pulling down a large vertical stem until it was approximately horizontal; the resulting fractures created crevices similar to those that elephants create (Fig. 1C). I created perch-only trees by pulling down a large vertical stem and subsequently plugging all resulting crevices with window caulk. I created refuge-only trees by collecting abandoned ant domatia from the myrmecophilous tree *Acacia drepanolobium* Sjøstedt, which is rare at the study sites but abundant in heavy-clay vertisol soils nearby (Palmer et al. 2000); I have observed *Lygodactylus keniensis* sheltering in these domatia where *A. drepanolobium* is present. Using fishing line, I lashed six of these domatia to the main stems of refuge-only trees (Fig. 1D). Control trees were left untouched.

I performed these manipulations in September 2006. In January 2007, I collected 40 adult male lizards and kept them in a laboratory overnight. (I used males because they hold and defend stricter territories than females in this species.) The following day, I allocated these lizards randomly to the 40 experimental units. Lizards were marked and released at the base of trees and allowed to climb up the main stem. Two to four observers monitored each of these trees daily. When a tree was noted as vacant during a given survey, I confirmed that it was again vacant on the following day, after which I omitted it from subsequent surveys. (Because lizards remain on “territory trees” for extended periods, I interpreted absence for 48 h to mean that they had forsaken the tree to establish territory on a “better”

² (<http://cran.r-project.org/>)



FIG. 1. (A) Elephant-damaged *Acacia mellifera* with multiple damaged stems. (B) Close-up of recent elephant damage illustrating crevices, with a Bic mechanical pencil for scale. (C) Artificial “elephant damage” created for lizard transplant experiment, with pencil for scale. (D) Abandoned ant domatium lashed to *Acacia etbaica* to provide artificial refuge in lizard transplant experiment. Photo credits: R. M. Pringle.

tree elsewhere.) I terminated the experiment and censored the data after seven days, at which point only four of the 40 experimental units remained occupied. I analyzed these times-to-vacancy using a Cox proportional-hazards regression model (Fox 2001) with block, refuge, perch, and the refuge \times perch interaction as effects.

I estimated prey availability on each of the 40 experimental trees in February 2007 by nailing two 8×13 cm yellow cardboard sticky traps (Olson Products, Medina, Ohio, USA) to the main stem of each tree at 0.5 m from the ground (where I have often observed lizards foraging) and leaving them for 72 h. I identified arthropods ($N = 2534$) to order, excluding insects ≤ 1 mm or >30 mm in length and all ants. I summed data from the two sticky traps on each tree and analyzed square-root-transformed abundances using analysis of variance (ANOVA) with block, refuge, perch, and perch \times refuge as effects, to parallel the proportional-hazards model used for the lizards.

The role of refuges in driving the elephant–lizard interaction

Because the experiment described previously indicated that refuge availability most strongly influenced lizard

habitat preference (see *Results*), I conducted another experiment to test the hypothesis that refuge removal would increase rates of emigration (or mortality) from occupied trees. In February 2007, I selected 20 elephant-damaged *A. mellifera* that had been occupied by adult lizards on three consecutive days, suggesting that these were territory trees. I randomly allocated 10 of these trees to a refuge-removal treatment and 10 to a sham-manipulation treatment. Tree height did not differ between these two treatments (2.8 ± 0.2 m and 2.8 ± 0.1 m, respectively, means \pm SE), and neither did the initial number of lizard inhabitants, which in most cases consisted of a male–female pair (1.8 ± 0.2 and 1.8 ± 0.1 individuals, respectively, means \pm SE). On refuge-removal trees, I removed loose bark and plugged crevices with window caulk and duct tape, taking care to avoid other disturbances to the tree. On sham-manipulation trees, I removed a smaller amount of bark and added similar amounts of caulk and tape without obscuring crevices. Three observers monitored each tree daily as described previously. I terminated the experiment after seven days; trees still occupied by one or more lizards at that time were treated as censored data points. I analyzed times-to-vacancy by treatment using a proportional-hazards model with the treatment as the

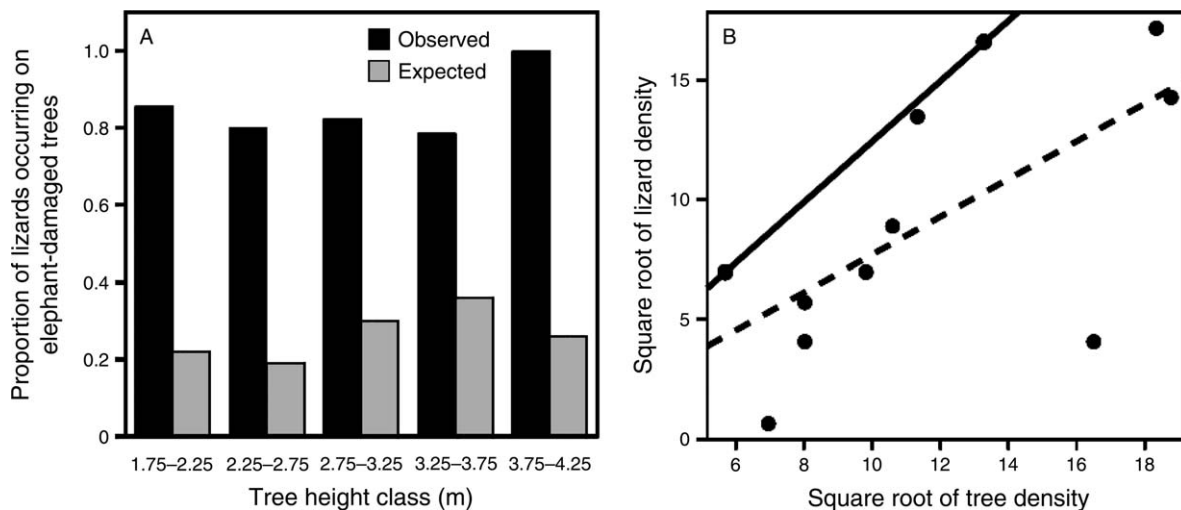


FIG. 2. Results from lizard censuses. (A) Observed vs. expected proportions of lizards occurring on elephant-damaged trees within 0.5-m height classes (Pearson chi-square tests, all $P < 0.001$). (B) Relationship between estimated local lizard density (no. lizards/ha) and density of elephant-damaged trees (no. trees/ha), with least-squares (dashed line; $r^2 = 0.43$, $F_{1,10} = 7.6$, $P = 0.02$) and 90th quantile (solid line; coefficient = 1.3, $t = 2.3$, $df = 11$, $P = 0.04$) regression lines.

main effect and the initial number of lizard inhabitants as a covariate.

After the termination of this experiment, I estimated prey availability in two ways. First, I used the methods described previously to estimate prey availability on the main stem of each refuge-removal and sham-manipulation tree, along with 10 undamaged *A. mellifera* of similar size. I analyzed the untransformed abundances of arthropods ($N = 1953$) among these three groups using one-way ANOVA. Second, I placed one sticky trap on the ground near the base of each of these same trees for 72 h (cf. Roughgarden and Fuentes 1977). I again analyzed untransformed arthropod abundances ($N = 1499$) using one-way ANOVA.

RESULTS

Elephant regulation of L. keniensis distribution and local abundance

Across the 12 sites, roughly a quarter of the trees exhibited moderate-to-severe elephant damage (109 of 430), yet 84% of all observed lizards occurred on these trees (54 individuals, with 10 individuals on undamaged trees; $\chi^2_1 = 118.2$, $P < 0.0001$). Because the mean height of lizard-occupied trees was greater than the population mean (3.4 ± 0.2 vs. 2.4 ± 0.05 m, mean \pm SE; Wilcoxon $Z_{43,386} = 5.4$, $P < 0.0001$), and because older, larger trees were more likely to have sustained elephant damage (3.0 ± 0.1 vs. 2.4 ± 0.1 m; $Z_{109,320} = 4.1$, $P < 0.0001$), I verified that the association between lizard occurrence and elephant damage still existed when the analysis was controlled for tree size (Fig. 2A).

Local lizard density increased with the local density of elephant-damaged trees (Fig. 2B). Moreover, the 90th linear quantile of lizard density increased with a

significantly nonzero slope ($P = 0.04$; Fig. 2B), suggesting that the density of elephant-damaged trees might constrain the maximum local density of lizards. Using a larger data set of lizard densities, Pringle et al. (2007) showed that lizard density increased with total tree density across habitat types at the landscape scale. Therefore note that in the present data set, which comprises only one habitat type, no consistent relationship existed between total tree density and lizard density ($r = 0.18$, $F_{1,10} = 0.4$, $P = 0.6$) or between total tree density and the density of damaged trees ($r = 0.46$, $F_{1,10} = 2.6$, $P > 0.1$).

Factors influencing lizard habitat choice

Lizards transplanted onto trees with experimentally added refuges remained on those trees three times longer on average than lizards transplanted onto trees without refuges (2.3 ± 0.6 vs. 0.8 ± 0.3 days, mean \pm SE), and all of the trees that retained their lizard transplants at the termination of the experiment ($N = 4$) contained added refuges. In contrast, lizards transplanted onto trees with experimentally added perches remained on those trees an average of 1.1 ± 0.5 days, as opposed to 1.9 ± 0.6 days for trees without perches. The presence or absence of refuges was the only statistically significant effect in the proportional-hazards model ($\chi^2_1 = 4.8$, $P < 0.03$). The perch and block terms were nonsignificant ($P > 0.1$ and > 0.2 , respectively), and there was only a hint that the refuge \times perch interaction increased the length of time that lizards remained on trees ($\chi^2_1 = 2.9$, $P = 0.09$). None of the treatment combinations had a detectable effect on arthropod abundance (ANOVA, $F_{12,27} = 0.8$, $P = 0.6$; $P > 0.15$ for all individual effect tests).

The importance of refuges

The experimental removal of refuges from elephant-damaged trees produced a dramatic effect on lizard-occupancy patterns: within five days, seven of 10 refuge-removal trees were completely vacant, compared with 0 of 10 sham-manipulated trees (proportional-hazards $\chi_1^2 = 12.0$, $P = 0.0005$; Fig. 3). Of the three refuge-removal trees that remained occupied at the termination of the experiment, one had lost two of its three original inhabitants, while none of the sham-manipulated trees lost a single individual. The initial number of lizard inhabitants had no detectable effect on the outcome of the experiment ($\chi_1^2 = 1.7$, $P = 0.2$). There were also no detectable differences in arthropod abundance between refuge-removal, sham-manipulated, or undamaged trees, either on the trees themselves (ANOVA, $F_{2,27} = 0.4$, $P > 0.6$) or on the ground beneath the trees ($F_{2,27} = 1.7$, $P > 0.2$).

DISCUSSION

These results show that elephant-engineered habitat heterogeneity strongly regulates habitat selection by a common arboreal lizard (Figs. 2A and 3), and that local lizard population density increases with, and may be constrained by, the number of elephant-damaged trees in an area (Fig. 2B). Thus, this interaction represents an indirect effect initiated by elephants, transmitted by trees, and received by lizards (terminology sensu Abrams et al. 1996). To date, most studies of indirect effects have focused on trophic cascades and other interactions initiated by predators (e.g., Schmitz 1998, Borer et al. 2005). Several recent studies have shown that herbivores, too, initiate powerful trophic indirect effects (Gomez and Gonzalez-Megias 2002, Ohgushi 2005), as well as effects resulting from engineering (Wright et al. 2002, Lill and Marquis 2003, Bailey and Whitham 2006, Marquis and Lill 2007). This study, together with previous work in this system (Pringle et al. 2007), shows that herbivores can simultaneously precipitate both types of effects.

The experimental data showed that the engineering interaction described here is driven by elephants' creation of crevices used by lizards. None of the alternative hypotheses was supported. Transplanted lizards showed no affinity for trees with added perches, and three bouts of intensive arthropod sampling failed to reveal significant differences in prey abundance between undamaged trees, elephant-damaged trees, or experimentally damaged trees. That experimentally adding and removing refuges altered lizards' behavior likewise rejects the possibility that the observational associations were a coincidental outcome of independent preferences by the two animal species.

Although I only quantified responses of *L. keniensis*, I found several nocturnal geckos (*Hemidactylus brookii* Gray) beneath partially stripped bark on damaged trees, suggesting that elephant-engineered refuges may affect lizards other than *L. keniensis*. In northern Kenya, *L.*

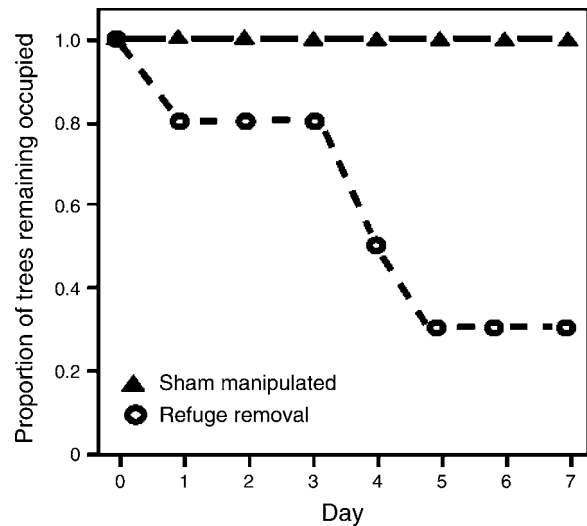


FIG. 3. Temporal-persistence curves for lizards on refuge-removal and sham-manipulated trees during seven days of monitoring following the experimental manipulation (proportional-hazards regression coefficient = -8.4 , $\chi_1^2 = 12.0$, $P = 0.0005$).

keniensis and *L. somalicus* occur sympatrically with similar natural histories (Greer 1967), again suggesting possible lizard-community responses to elephant activity. Small mammals may also derive shelter from elephant damage, which often creates dense thorny tangles at ground level.

There are at least three nonexclusive reasons why elephant-engineered refuges might be critical to lizards' habitat selection. One is that lizards utilize crevices to reduce predation risk—a common explanation for secondary use of engineered shelters by various taxa (Fukui 2001, Norkko et al. 2006). Alternatively, habitat selection might be driven by microclimatic factors. Sheltering in ectotherms often serves thermoregulatory needs (Huey et al. 1989, Pringle et al. 2003), and occupation of engineered constructs has been shown to reduce desiccation risk in leaf-tying caterpillars and other invertebrates (Hunter and Willmer 1989, Marquis and Lill 2007). Finally, it is possible that damaged trees constitute good territories because engineered crevices make good nest sites (Lill and Marquis 2004, Machicote et al. 2004); indeed, I uncovered several sets of *L. keniensis* eggs beneath partially stripped bark while conducting this work. Further experiments in controlled settings that examine microhabitat selection by sex while simultaneously manipulating predator presence and microclimate might be used to evaluate these possibilities.

Using a large-mammal exclusion experiment at Mpala Research Centre, Pringle et al. (2007) showed that the ungulate community as a whole depressed lizard densities by directly reducing tree density and indirectly reducing arthropod density. Thus, it appears that the net effect of ungulates (collectively) on lizards comprises

opposing indirect effects, and that the suppressive effect of ungulates in general outweighs the facilitative effect of elephants in particular. Wilby et al. (2001), using case studies of crested porcupines and harvester ants in the Negev desert, separated trophic impacts from engineering effects on plant communities and showed that in both cases, engineering effects outweighed trophic ones. The present study confirms that herbivores can produce indirect effects by acting simultaneously along two functional axes (consumer and engineer), although it is difficult to compare the strength of these effects directly because elephants cannot be excluded without excluding other members of the ungulate community, namely giraffes.

It seems likely the precise balance between these positive and negative effects at the scale of the landscape (as opposed to the habitat patch) will depend on elephant density. At high densities, elephants contribute to the maintenance of open grassland (Dublin et al. 1990) and perhaps to the suppression of arthropods, which would have negative consequences for this arboreal insectivore. At low elephant densities, few engineered microhabitats would exist. Thus, while patch-scale lizard density increases linearly with the density of elephant-damaged trees (Fig. 2B), landscape-scale lizard density might be greatest at intermediate elephant densities (see Marquis and Lill 2007 for a similar idea applied to plant-based arthropod communities).

More fundamentally, this study illustrates that indirect effects initiated by diverse guilds such as “ungulates” or “carnivores” may often comprise diverse components stemming from the varied activities of individual species. Thus, relatively blunt experimental methods like guild-level exclusion may reveal net effects without exposing the full suite of mechanisms that produce them.

Because lizards were virtually absent from undamaged trees in this study, how is it that lizards are ~60% more abundant in ungulate-exclusion plots (Pringle et al. 2007), where trees bearing elephant damage predating enclosure establishment are comparatively rare (~8% of all trees)? I surmise that in the total absence of ungulates, other community changes enable lizards to thrive. Plant and litter densities increase in the absence of ungulates in these nutrient-poor soils (Sankaran and Augustine 2004), which might offer whatever combination of predation refuge, microclimate, prey abundance, and/or nest-site availability ultimately limit lizard abundance. In other words, the importance of engineered refuges to *L. keniensis* appears to be contingent upon the presence of a robust large-herbivore community.

Along similar lines, the importance of this engineering effect may be diminished in habitats where refuges are abundant even in the absence of engineers. As mentioned in the *Methods*, lizards frequently shelter in abandoned ant domatia on *Acacia drepanolobium*. Several surveys in vertisol-soil habitats dominated by this tree failed to

reveal a strong effect of elephant damage on lizard habitat selection (R. M. Pringle, *unpublished data*), which is consistent with this hypothesis.

ACKNOWLEDGMENTS

I am grateful to Mohamud Mohamed and Samson Kurkura for field assistance and to Geoff Trussell, Todd Palmer, Jake Goheen, Truman Young, Lauren McGeoch, and Doug McCauley for discussion. Thoughtful comments from two anonymous reviewers improved the manuscript immensely. This work was supported by the Stanford Graduate Fellowships, NSF D-DIG DEB-0709880, and a grant from the Sherwood Family Foundation to Gretchen Daily.

LITERATURE CITED

- Abrams, P. A., B. A. Menge, G. G. Mittelbach, D. A. Spiller, and P. Yodzis. 1996. The role of indirect effects in food webs. Pages 371–395 in G. A. Polis and K. O. Winemiller, editors. *Food webs: integration of patterns and dynamics*. Chapman and Hall, New York, New York, USA.
- Augustine, D. J., and S. J. McNaughton. 2004. Regulation of shrub dynamics by native browsing ungulates on East African rangeland. *Journal of Applied Ecology* 41:45–58.
- Bailey, J. K., and T. G. Whitham. 2006. Interactions between cottonwood and beavers positively affect sawfly abundance. *Ecological Entomology* 31:294–297.
- Borer, E. T., E. W. Seabloom, J. B. Shurin, K. E. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2005. What determines the strength of a trophic cascade? *Ecology* 86:528–537.
- Cade, B. S., and B. R. Noon. 2003. A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment* 1:412–420.
- Caughley, G. 1976. The elephant problem: an alternative hypothesis. *East African Wildlife Journal* 14:265–283.
- Crain, C. M., and M. D. Bertness. 2006. Ecosystem engineering across environmental gradients: implications for conservation and management. *BioScience* 56:211–218.
- Crooks, J. A. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* 97:153–166.
- Dublin, H. T., A. R. E. Sinclair, and J. McGlade. 1990. Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *Journal of Animal Ecology* 59:1147–1164.
- Fox, G. A. 2001. Failure-time analysis: studying times to events and rates at which events occur. Pages 253–289 in S. M. Scheiner and J. Gurevitch, editors. *Design and analysis of ecological experiments*. Oxford University Press, New York, New York, USA.
- Fukui, A. 2001. Indirect interactions mediated by leaf shelters in animal-plant communities. *Population Ecology* 43:31–40.
- Gomez, J. M., and A. Gonzalez-Megias. 2002. Asymmetrical interactions between ungulates and phytophagous insects: being different matters. *Ecology* 83:203–211.
- Greer, A. E. 1967. The ecology and behavior of two sympatric *Lygodactylus* geckos. *Breviora* 268:1–16.
- Hardy, L. M., and A. C. Crnkovic. 2006. Diet of amphibians and reptiles from the Engare Ondare River region of central Kenya, during the dry season. *African Journal of Herpetology* 55:143–159.
- Hastings, A., J. E. Byers, J. A. Crooks, K. Cuddington, C. G. Jones, J. G. Lambrinos, T. S. Talley, and W. G. Wilson. 2007. Ecosystem engineering in space and time. *Ecology Letters* 10:153–164.
- Huey, R. B., C. R. Peterson, S. J. Arnold, and W. P. Porter. 1989. Hot rocks and not-so-hot rocks: retreat-site selection by garter snakes and its thermal consequences. *Ecology* 70:931–944.

- Hunter, M. D., and P. G. Willmer. 1989. The potential for interspecific competition between two abundant defoliators on oak: leaf damage and habitat quality. *Ecological Entomology* 14:267–277.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* 69:373–386.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1997a. Ecosystem engineering by organisms: why semantics matters. *Trends in Ecology and Evolution* 12:275.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1997b. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78:1946–1957.
- Knight, C. A., and D. D. Ackerly. 2002. Variation in nuclear DNA content across environmental gradients: a quantile regression analysis. *Ecology Letters* 5:66–76.
- Laws, R. M. 1970. Elephants as agents of habitat and landscape change in East Africa. *Oikos* 21:1–15.
- Lill, J. T., and R. J. Marquis. 2003. Ecosystem engineering by caterpillars increases insect herbivore diversity on white oak. *Ecology* 84:682–690.
- Lill, J. T., and R. J. Marquis. 2004. Leaf ties as colonization sites for forest arthropods: an experimental study. *Ecological Entomology* 29:300–308.
- MacArthur, R., and J. W. MacArthur. 1961. On bird species diversity. *Ecology* 42:594–598.
- Machicote, M., L. C. Branch, and D. Villarreal. 2004. Burrowing owls and burrowing mammals: are ecosystem engineers interchangeable as facilitators? *Oikos* 106:527–535.
- Marquis, R. J., and J. T. Lill. 2007. Effects of arthropods as physical ecosystem engineers on plant-based trophic interaction webs. Pages 246–274 in T. Ohgushi, T. P. Craig, and P. W. Price, editors. *Ecological communities: plant mediation in indirect interaction webs*. Cambridge University Press, Cambridge, UK.
- Musgrave, M. K., and S. G. Compton. 1997. Effects of elephant damage to vegetation on the abundance of phytophagous insects. *African Journal of Ecology* 35:370–373.
- Norkko, A., J. E. Hewitt, S. F. Thrush, and G. A. Funnell. 2006. Conditional outcomes of facilitation by a habitat-modifying subtidal bivalve. *Ecology* 87:226–234.
- Ohgushi, T. 2005. Indirect interaction webs: herbivore-induced effects through trait change in plants. *Annual Review of Ecology, Evolution, and Systematics* 36:81–105.
- Palmer, T. M., T. P. Young, M. L. Stanton, and E. Wenk. 2000. Short-term dynamics of an acacia ant community in Laikipia, Kenya. *Oecologia* 123:425–435.
- Power, M. 1997. Ecosystem engineering by organisms: why semantics matters, reply. *Trends in Ecology and Evolution* 12:275–276.
- Pringle, R. M., J. K. Webb, and R. Shine. 2003. Canopy structure, microclimate, and habitat selection by a nocturnal snake, *Hoplocephalus bungaroides*. *Ecology* 84:2668–2679.
- Pringle, R. M., T. P. Young, D. I. Rubenstein, and D. J. McCauley. 2007. Herbivore-initiated interaction cascades and their modulation by productivity in an African savanna. *Proceedings of the National Academy of Sciences (USA)* 104:193–197.
- Reichman, O. J., and E. W. Seabloom. 2002. Ecosystem engineering: a trivialized concept? Response. *Trends in Ecology and Evolution* 17:308.
- Roughgarden, J. D., and E. Fuentes. 1977. Environmental determinants of size in solitary populations of West-Indian *Anolis* lizards. *Oikos* 29:44–51.
- Sankaran, M., and D. J. Augustine. 2004. Large herbivores suppress decomposer abundance in a semiarid grazing ecosystem. *Ecology* 85:1052–1061.
- Schmitz, O. J. 1998. Direct and indirect effects of predation and predation risk in old-field interaction webs. *American Naturalist* 151:327–342.
- van Aarde, R. J., and T. P. Jackson. 2007. Megaparks for metapopulations: addressing the causes of locally high elephant numbers in southern Africa. *Biological Conservation* 134:289–297.
- Wilby, A. 2002. Ecosystem engineering: a trivialized concept? *Trends in Ecology and Evolution* 17:307.
- Wilby, A., M. Shachak, and B. Boeken. 2001. Integration of ecosystem engineering and trophic effects of herbivores. *Oikos* 92:436–444.
- Wright, J. P., and C. G. Jones. 2004. Predicting effects of ecosystem engineers on patch-scale species richness from primary productivity. *Ecology* 85:2071–2081.
- Wright, J. P., and C. G. Jones. 2006. The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges. *BioScience* 56:203–209.
- Wright, J. P., C. G. Jones, and A. S. Flecker. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia* 132:96–101.