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Recovery of African wild dogs suppresses prey but does not trigger a trophic cascade

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Abstract. Increasingly, the restoration of large carnivores is proposed as a means through which to restore community structure and ecosystem function via trophic cascades. After a decades-long absence, African wild dogs (*Lycaon pictus*) recolonized the Laikipia Plateau in central Kenya, which we hypothesized would trigger a trophic cascade via suppression of their primary prey (dik-dik, *Madoqua guentheri*) and the subsequent relaxation of browsing pressure on trees. We tested the trophic-cascade hypothesis using (1) a 14-year time series of wild dog abundance; (2) surveys of dik-dik population densities conducted before and after wild dog recovery; and (3) two separate, replicated, herbivore-exclusion experiments initiated before and after wild dog recovery. The dik-dik population declined by 33% following wild dog recovery, which is best explained by wild dog predation. Dik-dik browsing suppressed tree abundance, but the strength of suppression did not differ between before and after wild dog recovery. Despite strong, top-down limitation between adjacent trophic levels (carnivore–herbivore and herbivore–plant), a trophic cascade did not occur, possibly because of a time lag in indirect effects, variation in rainfall, and foraging by herbivores other than dik-dik. Our ability to reject the trophic-cascade hypothesis required two important approaches: (1) temporally replicated herbivore exclusions, separately established before and after wild dog recovery; and (2) evaluating multiple drivers of variation in the abundance of dik-dik and trees. While the restoration of large carnivores is often a conservation priority, our results suggest that indirect effects are mediated by ecological context, and that trophic cascades are not a foregone conclusion of such recoveries.

Key words: Acacia; *African wild dogs* (Lycaon pictus); *antelope; dik-dik* (Madoqua guentheri); *endangered species; food web; indirect effect; large carnivore; rain; savanna; tree cover.*

INTRODUCTION

Carnivores can powerfully shape ecosystems through their direct effect on herbivores, and their resulting indirect effect on plants and abiotic processes such as nutrient cycling, erosion, and fire (e.g., Hairston et al. 1960, Estes et al. 1998, Schmitz et al. 2004, Croll et al. 2005, Estes et al. 2011). The strength of these indirect effects has been used to justify conservation efforts, with the prediction that the restoration of large carnivores will trigger a trophic cascade (Mech 2012, Ripple et al. 2014). Ecologists have struggled to quantify this prediction, and so there remains a number of unresolved questions both about the strength and generality of top-down control as well as the mechanisms by which large carnivores indirectly benefit plants (Kauffman et al. 2010, Kuker and Barrett-Lennard 2010, Estes et al. 2011, Beschta and Ripple 2012, 2013, Mech 2012, Winnie 2012, 2014, Newsome et al. 2013, Beschta et al. 2014, Peterson et al. 2014). Thus, while we know that large carnivores can affect important ecosystem processes in some cases, the question remains: in which ecological contexts do the indirect effects of carnivores exert primacy over other drivers of species abundance?

Terrestrial food webs are embedded within complex and shifting ecological contexts that determine the strength of indirect effects (Schmitz 2010). This context may include the presence of reticulate food chains, donor control, and environmental heterogeneity (Strong 1992, Polis and Strong 1996, Polis et al. 2000). Reticulate food chains encompass multiple species with similar resource requirements within a given trophic

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level (Polis and Strong 1996, Tschanz et al. 2007, Thibault et al. 2010). Following the decline of a single species of consumer, functional or numerical compensation within that trophic level may buffer against a trophic cascade (Finke and Denno 2004). For example, wolves, grizzly bears, and cougars may all contribute to the decline of elk and the release of aspen in the Greater Yellowstone Ecosystem, muddling causation from any single predator (Peterson et al. 2014). Donor control arises when organisms defend themselves (e.g., secondary compounds or defensive armaments) or otherwise impede (e.g., risk-avoidance behavior in animals) the flow of energy to higher trophic levels within food chains (Polis and Strong 1996, van der Stap et al. 2007, Mooney et al. 2010). For example, impala avoid risky areas of the landscape, leading to the suppression of preferred plants and the domination of well-defended plants in safe areas (Ford et al. 2014). Environmental heterogeneity, particularly variation in light, soil nutrients, and rainfall, can limit plant abundance more than herbivory (Leibold 1989, Schmitz 1994). Lack of rainfall can reduce resource availability for herbivores, thereby limiting populations directly (Hopcraft et al. 2010) or increasing the vulnerability of individuals to predation (Sinclair and Arcese 1995). Together, reticulate food chains, donor control, and environmental heterogeneity shape the ecological context in which trophic cascades either emerge or are overridden in terrestrial food webs.

We tested the trophic-cascade hypothesis in Laikipia, Kenya, a 12 000-km^2 region that was naturally recolonized by African wild dogs (*Lycaon pictus*) following a 20-year absence (Woodroffe 2011). About 60% of African wild dog diets are composed of dik-dik (*Madoqua guentheri*; Woodroffe et al. 2007), which is also the most abundant ungulate in this region (Augustine 2010). Previous work in this system indicates that herbivory by small-sized (i.e., dik-dik) and medium-sized (i.e., impala) ungulates limit the biomass of tree communities (Augustine and McNaughton 2004, Goheen et al. 2013, Ford et al. 2014). Given the importance of dik-dik as prey for wild dogs and the potential effect of dik-dik on tree abundance, there is potential that wild dog recovery triggered a density-mediated trophic cascade. However, reticulate food chains, donor control, and environmental heterogeneity are also present in this system: both wild dogs and dik-dik coexist alongside a diverse assemblage of competitors; savanna ecosystems are characterized by unstable variation in rainfall that limits the distribution of tree cover (Sankaran et al. 2005); trees consumed by dik-dik possess chemical and mechanical defenses that can alter the direction of trophic cascades (Ford et al. 2014). Thus, in addition to a trophic cascade, we evaluated multiple sources of causality that may also explain variation in the abundance of dik-dik and trees.

Specifically, we assembled data to test the following predictions: (1) that wild dogs suppress the abundance of dik-dik; (2) that dik-dik are capable of suppressing the abundance of trees; and (3) that the effect of dik-dik on tree abundance was reduced in the presence of wild dogs. To test these predictions, we monitored wild dog and dik-dik populations for 14 years, and used size selective ungulate-exclusion plots to quantify the effect of herbivory by dik-dik. A separate set of exclusion plots was established both before and after wild dog recovery, and therefore enabled us to test whether predation by wild dogs decreased the net effect of herbivory on tree abundance.

Methods

Prediction 1: Wild dogs suppress dik-dik abundance

Since their return to the study area in 2002, we have monitored wild dogs at Mpala Research Centre (MRC) using global positioning system (GPS) telemetry and radio-telemetry to quantify pack-level biomass. We monitored the abundance (i.e., density) of dik-dik using distance sampling methods on a semiannual basis from 1999 to 2002 and again from 2008 to 2014. Details on the study area and methods for monitoring wild dogs and dik-dik are provided in Appendix A.

We evaluated four lines of evidence to assess how wild dogs affected the dik-dik population. First, we compared the density (individuals/km^2) of dik-dik before and after wild dog recovery using a generalized least squares (GLS) analysis. We used a GLS because of non-independence between sequential estimates of density. For this and all subsequent GLS analyses, we tested for serial autocorrelation of residuals using autocorrelation and partial autocorrelation functions. Following Zuur et al. (2009), we incorporated both correlation and variance structures into the model and present coefficient estimates based on restricted maximum likelihood estimation. A summary of these models is provided in Appendix A.

Second, we quantified the effect of the estimated consumption of dik-dik by wild dogs on the population growth rate (r) of dik-dik. We estimated consumption of dik-dik based on the energetic demand of wild dogs combined with the energetic return of an adult dik-dik (Woodroffe et al. 2007). An average-sized wild dog (25.2 kg) that fed hypothetically and exclusively on dik-dik would require the caloric return of 0.61 dik-dik per day; however, because dik-dik account for ~62% of prey biomass of wild dogs at our study site (Woodroffe et al. 2007), the predicted demand of dik-dik for an average-sized wild dog is 0.378 dik-dik per day, or 0.015 dik-dik per day per kilogram of wild dog. Thus, to estimate consumption of dik-dik by wild dogs, we multiplied 0.015 by the estimated biomass of wild dog packs on MRC and by the number of days each pack spent in the area. To quantify the population growth rate of dik-dik, we calculated

$$r = \frac{N_{i+1} - N_i}{t_{i+1} - t_i},$$

where N is the population density estimate of dik-dik from the *i*th survey at time *t*. We then used *r* as the response variable in a GLS regression, and the estimated consumption of dik-dik by wild dogs between t_i and t_{i+1} as a predictor. We assumed the number of dik-dik consumed per kilogram of wild dog has remained constant among all dik-dik population surveys. However, foraging theory suggests that the rate of dik-dik consumption by wild dogs may change with the density of dik-dik (i.e., a Type I, II, or III functional response [Holling 1959]). If the functional response of wild dogs changed, then the estimated consumption of dik-dik by wild dogs would interact with dik-dik population density to affect *r*. We therefore tested an interaction between the estimated consumption of dik-dik by wild dogs and the population density of dik-dik on *r*. We also tested for density dependence in the dik-dik population using N_i as a predictor variable and *r* as the response. If the dik-dik population is experiencing density-dependent growth, then N_i will have a negative effect on *r*; such density dependence could confound the potential effects of wild dog recovery on the dik-dik population. We assessed the effects of wild dog predation, rainfall, and density dependence using an information-theoretic approach, and Akaike information criterion corrected for small sample sizes ($\mathrm{AIC_c}$) to evaluate support for competing models (see Appendix B).

Third, we quantified the effect of the estimated consumption of dik-dik by wild dogs on an index of dik-dik recruitment. Following Augustine (2010), we used the proportion of dik-dik groups consisting of three or more individuals for each population survey as an index of recruitment. Because dik-dik are territorial, monogamous, and females typically give birth to a single offspring, the presence of a group of three is almost always the result of successful reproduction (Kingswood and Kumamoto 1996, Komers 1996). We used a GLS regression to test for the effect of consumption by wild dogs on the recruitment index.

Fourth, a wild dog den was established midway through a series of line-transect surveys conducted in 2011–2012, and we quantified short-term responses of dik-dik to this event. The den was established in December 2011, occupied by 31 individuals (19 adults, 12 pups), and was abandoned after the pups were fully weaned in late January 2012. While denning, wild dogs typically increase their consumption of dik-dik by 10% (Woodroffe et al. 2007) and forage almost exclusively within 3 km of the den site (i.e., the denning home range; Appendix B: Fig. B1). This shift in the diet and movements associated with wild-dog denning allowed us to investigate responses of dik-dik to a short-term pulse of intense predation. Our 2011–2012 surveys were conducted in addition to the surveys used to estimate dik-dik density across MRC and were focused on a subsection of the study area. We quantified encounter rates (number of dik-dik/km) with dik-dik along a 14-km road transect before (pre-denning, November 2011), during (active denning, January 2012), and after (post-denning, March 2012) this den was used by wild dogs. Because dik-dik are territorial, we do not expect that short-term changes in abundance would be caused by emigration of dik-dik from the denning home range. We compared dik-dik encounter rates in the denning home range to a 17-km transect in a nearby control area where wild dogs did not forage as frequently while the den was active (Appendix B: Fig. B1). The control area consisted of similar habitat and climate as the denning home range, and was accessible to wild dogs based on our telemetry study. To quantify encounter rates, we drove 10 km/h with two dedicated observers and one driver to locate dik-dik. Typically, distance sampling methods are preferred to encounter rates because the former provides an estimate of variance and accounts for non-detection. However, due to lack of temporal replication of transects within each pre-, active-, and post-denning survey period, density estimates could not be derived from these surveys. We validated the relationship between encounter rates and density in our study area using the 16 population surveys conducted across MRC (i.e., excluding the surveys conducted in the control and denning areas in 2011–2012) between 1999 and 2013 ($r^2 = 0.873$, $P < 0.0001$), indicating that encounter rates provide an accurate index of dik-dik density. We used an exact test with a Poisson distribution to evaluate the null hypothesis that the encounter rate during the active-denning period did not differ from that of the pre-denning or post-denning periods. We performed separate exact tests for the denning home range and the control area. In addition to encounter rates, we also compared the recruitment index in the denning and control areas among pre-, active-, and post-denning survey periods using a proportion test. This test evaluates the null hypothesis that recruitment does not change with the denning activity of wild dogs. We performed separate proportion tests for the denning home range and the control area.

Other potential drivers of dik-dik abundance

We considered three possible alternatives to wild dog recovery that may explain variation in dik-dik density. First, we evaluated whether populations of other large carnivores had increased along with wild dogs, thereby contributing to the suppression of dik-dik and confounding the effect of wild dog recovery. We focused on species of carnivore likely to consume a significant number of dik-dik (i.e., leopards [*Panthera pardus*] and black-backed jackals [*Canis mesomelas*] [Estes 1991]) and compared the number of detections from a camera-trapping survey conducted before wild dog recovery (2000–2002; 7364 trap hours at 19 sites) with a survey conducted after wild dog recovery (2011; 48 513 trap hours at 97 sites). We placed camera traps in random sites throughout the study area. We used a lag time of 6 minutes between sequential camera images to identify unique camera trap events. We used an exact test with a Poisson distribution to evaluate if detection rates (i.e., images per trap hour) of leopards and jackals had changed between these two periods. Following wild dog recovery, an increase in the number of leopard or jackal detections could obfuscate an effect of predation by wild dogs per se on dik-dik abundance.

Second, to evaluate the potential influence of rainfall on the dik-dik population, we first calculated the cumulative rainfall (mm) over a 6-month period preceding each dik-dik population survey (which represents the average inter-birth period; Kingswood and Kumamoto 1996). We regressed rainfall against r using a GLS analysis, and compared this with models involving the estimated consumption of dik-dik by wild dogs. We also compared the total rainfall per month before and after wild dog recovery using a GLS. A significant, positive effect of rainfall on the population growth rate of dik-dik, combined with an overall decrease in rainfall after wild dog recovery, confounds any negative effect of predation by wild dogs on dik-dik abundance.

Third, we evaluated if dik-dik were more difficult to detect following wild dog recovery. Dik-dik are thought to rely on crypsis to evade predators (Estes 1991, Brashares et al. 2000). If wild dogs reduced the conspicuousness of dik-dik, this could create the perception of reduced abundance. Under this scenario, and following wild dog recovery, the detection distance (i.e., the effective strip width based on distance sampling methodology) should decrease as dik-dik become less conspicuous.

Prediction 2: Dik-dik suppress tree abundance

We assessed the effect of dik-dik browsing on three abundant species of tree: *Acacia etbaica*, *Acacia mellifera*, and *Grewia* spp., which comprised approximately 40%, 5–10%, and 8% of tree cover in our study area, respectively (Young et al. 1995). These species are present among all experimental treatments in the before and after wild dog exclusion experiments (see *Prediction 3*). We also measured the response of the aggregate tree community to dik-dik browsing by pooling the abundances of all tree species (32 species). We measured the effect of browsing by dik-dik per se on tree abundance, using replicated ungulate exclusions that are part of the UHURU (ungulate herbivory under rainfall uncertainty) experiment (Goheen et al. 2013). The UHURU experiment was initiated in 2009 and consists of 36 1-ha fenced areas distributed among three sites that are spread across a spatial gradient in rainfall (Goheen et al. 2013). At each site, there are three 4-ha blocks each consisting of 1-ha treatments that exclude (1) all ungulates (TOTAL); (2) all ungulates $\geq$40 kg and $\geq$1.2 m tall, thereby allowing dik-dik (MESO); (3) elephant and giraffes (MEGA); (4) no ungulates (OPEN). Within each 1-ha treatment, we recorded the number of woody plants in the 1.0–2.0 m height class in 2009 and in 2012. We did not include the northern and most arid plots from the UHURU experiment to maintain consistency with the study area from the before wild dog exclosure experiment (see *Prediction 3*).

To analyze the effect of dik-dik on tree abundance, we calculated the net difference in density of trees in the 1.0–2.0 m height class (individuals$\cdot$100 $\text{m}^{-2}\cdot\text{yr}^{-1}$) between 2009 and 2012 as the response variable, with treatment (i.e., MESO vs. TOTAL) as the predictor variable, and used a GLS analysis. We then ran a Fisher's combined probability test with a weighted-Z approach for the three species-level GLS models (Whitlock 2005). If dik-dik exerted top-down control on trees, then we expected to see a greater increase in stem density in TOTAL plots (i.e., excludes all ungulates) relative to MESO plots (i.e., those accessible to dik-dik, but not larger than dik-dik).

Prediction 3: The effect of dik-dik on tree abundance is reduced in the presence of wild dogs

While Prediction 2 addresses whether dik-dik in isolation have the potential to suppress *A. etbaica*, *A. mellifera*, *Grewia* spp., or the aggregate tree community over a three-year period, Prediction 3 addresses the effect of browsing by all ungulates before and after wild-dog recovery. If wild dog recovery alters the plant community via suppression of dik-dik, then a reduction in browsing by dik-dik should be evident in the presence of other ungulates.

We first measured the effect of ungulate exclusion on tree abundance in 1999–2002, just prior to wild dog recovery (Augustine and McNaughton 2004). This exclusion experiment consisted of three 0.5-ha electrified fenced areas that excluded all ungulates (TOTAL plots), and were paired with 0.5-ha unfenced control areas (OPEN plots). To quantify the effect of ungulate exclusion on tree abundance after wild dog recovery, we compared the TOTAL and OPEN plots from the UHURU experiment (2009–2012).

The trophic cascade hypothesis predicts that differences in tree abundance between OPEN and TOTAL plots should be greater in the before wild dog exclusion experiment than in the after wild dog exclusion experiment; i.e., all else equal, browsing pressure should be reduced in the presence of wild dogs. We tested this prediction using a GLS analysis, with the net difference in the density of trees in the 1.0–2.0 m height class (individuals$\cdot$100 $\text{m}^{-2}\cdot\text{yr}^{-1}$) as the response variable, and an interaction between treatment (OPEN vs. TOTAL plots) and the status of wild dog recovery (before vs. after; hereafter "recovery status") as predictor variables. We included a structured variance term to stabilize heteroscedasticity in residuals. We conducted separate analyses for *A. etbaica*, *A. mellifera*, *Grewia* spp., and the tree community in aggregate, each fit using maximum likelihood to facilitate model selection and selected the best-fitting model using AIC_c. If the best-fitting model(s) include the interaction term between treatment and recovery status, this may (depending on the direction of the interaction) indicate that wild dogs suppressed the effect of dik-dik on tree abundance. Thus, if models containing the interaction term had a $\Delta AIC_c < 2.0$, we proceeded to refit the model using restricted maximum likelihood estimation, and compared pairwise differences for each combination of treatment and recovery status using a Tukey's honestly significant difference test. In addition, we compared the mean difference in tree abundance (d) for each ungulate exclusion experiment ($d_s = \mathrm{TOTAL}_s - \mathrm{OPEN}_s$) where s indicates recovery status (before vs. after wild dog recovery) at the time of the experiment. We used a pooled standard error to quantify uncertainty in grouped means (Quinn and Keough 2002). The trophic-cascade hypothesis predicts $d_{\mathrm{before}} > d_{\mathrm{after}}$; however, if mean differences are similar, it indicates that the effect of herbivory has not changed appreciably following the recovery of wild dogs.

Other potential drivers of tree abundance

In addition to the indirect effect of wild dogs, we considered two alternative drivers of tree abundance. First, we evaluated whether the abundance of browsers other than dik-dik (e.g., impala, giraffe, and elephants) had changed along with wild dog recovery. We compared the energetic demand of all non-dik-dik browsers before (2000–2002) and after wild dog recovery (2008–2011). Population densities of these browsers were quantified while performing the dik-dik population surveys in 2000–2002 (Augustine 2010) and 2008–2011 (T. G. O'Brien and M. F. Kinnaird, *unpublished data*; see Appendix B: Table B3). Biomass was estimated using the mean adult body size of each browser multiplied by species density. To estimate energetic demand of all browsers, we calculated the mass-specific field metabolic rates as $\mathrm{FMR} = \sum_{j=1}^{n} 4.82 M_j^{0.734}$, where M is the mean biomass density (g/km^{-2}) of species j and FMR is the energetic demand in kJ/d (Ernest and Brown 2001, Nagy 2005). If the biomass density or energetic demand of browsers (besides dik-dik) has increased with wild dog recovery, it may negate any indirect effect of wild dogs on tree abundance. Likewise, if the density of browsers (besides dik-dik) had decreased with wild dog recovery, it would confound our ability to ascribe increased tree abundance to the suppression of dik-dik alone.

We also considered the possibility that rainfall covaried with the recovery status of wild dogs. Higher rainfall after wild dog recovery could enhance tree survival, growth, and reproduction, and thus confound the indirect effect of wild dogs on tree abundance. Our methods for analyzing rainfall are described in *Prediction 1: Wild dogs suppress dik-dik abundance*.

RESULTS

Prediction 1: Wild dogs suppress dik-dik abundance

The biomass density of wild dogs on Mpala Research Center peaked between June 2007 and January 2008 at 3938 kg·d^{-1}·km^{-2}, with a mean biomass density of 1600 ± 266 kg· d^{-1}·km^{-2} (mean ± SE) since recovery in 2002. Dik-dik density was 145 ± 4 individuals/km^2 before wild dog recovery (1999–2002) and 97 ± 7 individuals/km^2 since 2008, corresponding to a ~33% decline in dik-dik abundance ($F_{1,14} = 27.9$, $P < 0.001$; Fig. 1a). The best-fitting model for r (the population growth rate of dik-dik) consisted only of the main effect for the energetic demand of wild dogs ($\beta = -0.78 \pm 0.19$, $F_{1,\,13} = 16.0$, $P = 0.002$), which far outperformed the next best-fitting model ($\Delta AIC_c > 6$; Appendix B: Table B1).The recruitment index declined by 41%, from 0.17 ± 0.02 (1999–2002) to 0.10 ± 0.01 (2008–2013), and decreased with increasing energetic demand of wild dogs (Fig. 1b). Relative to the pre-denning period, encounter rates with dik-dik decreased by 42% in the denning home range while the den was active (Fig. 1c; Poisson rate parameter, λ [95% CI] = 0.525 [0.36–0.74], $P < 0.001$). The encounter rate in the control area did not change over the same period of time ($\lambda = 1.01$ [0.82–1.25], $P = 0.916$]). Two months after den abandonment by wild dogs, the proportionate difference in encounter rates compared to their respective pre-denning period was similar near the den (22%) and in the control area (19%; Fig. 1c). During the active denning phase, the recruitment index declined by 20% within the denning home range, while there was a fivefold increase in the recruitment index over the same period in the control area (Fig. 1d; $\chi^2 = 5.75$, $P = 0.008$). Thus, over both expansive (82 km^2, 14 years) and localized (31 km, 33 days) spatiotemporal scales, the energetic demand of wild dogs was correlated negatively with abundance and recruitment of dik-dik.

Other potential drivers of dik-dik abundance

The decline in the dik-dik population following wild dog recovery could not be explained by an increase in the abundance of other predators, lower rainfall (resource availability), or reduced detectability of dik-dik. Compared to before wild dog recovery, the relative abundance of carnivores most likely to consume dik-dik was either the same (leopard, $\lambda = 1.13$ [0.265, 10.260], $P \geq 0.999$) or significantly less (black-backed jackal, $\lambda = 0.13$ [0.041,0.419], $P < 0.001$) following wild dog recovery.

The observed decline in dik-dik abundance was likely not caused by declining resource availability. On average, 23% more monthly rainfall occurred after wild dog recovery (58.3 ± 4.5 mm, 2003–2013) compared to before wild dog recovery (47.3 ± 6.2 mm, 1999–2002), but this difference was not statistically significant ($t_{2,\,187} = 1.12$, $P = 0.264$; Appendix B: Fig. B2). Moreover, we did not find support for an effect of rainfall on population growth of dik-dik (Appendix B: Table B1).

We did not observe a change in the effective strip width of dik-dik during population surveys conducted before (22.7 ± 0.4 m) and after wild dog recovery (24.4 ± 0.5 m). Thus, it is unlikely that the decline in the

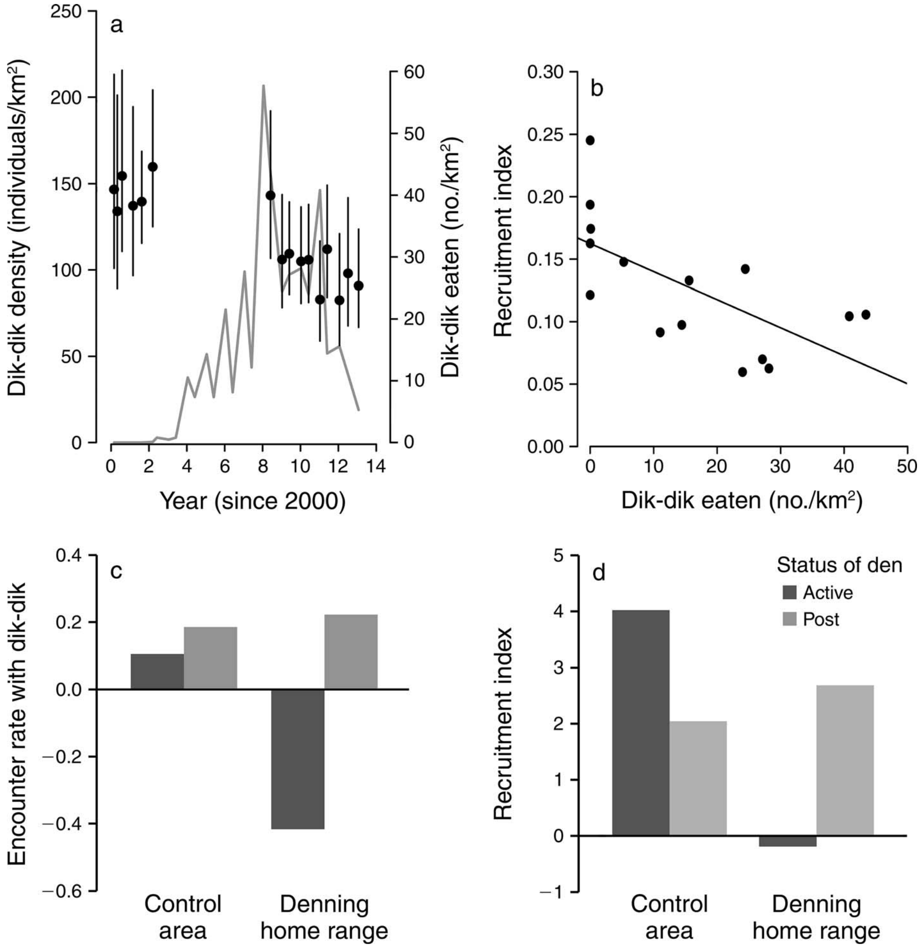

FIG. 1. Changes in dik-dik abundance over 14 years in an 82-km^2 area, shown as (a) dik-dik density (black) and the estimated number of dik-dik eaten by wild dogs between dik-dik population surveys (gray). Consumption of dik-dik accounts for energetic content of dik-dik, and the diet composition, total biomass, and days of occupancy by wild dogs in our study area. Error bars show 95% CI. (b) The estimated number of dik-dik eaten by wild dogs was negatively correlated with the recruitment index of dik-dik ($F_{1,14} = 9.75$, $P = 0.008$). Over a finer spatiotemporal scale (34 km, 33 days), suppression of dik-dik by wild dogs was evident on (c) the proportionate difference in encounter rates (dik-dik/km) from the pre-denning period, which decreased by 42% in the denning home range but increased by 10% in a nearby control area where wild dogs foraged much less frequently during the same period (Appendix B: Fig. B1); and on (d) the recruitment index, which decreased near the den but increased in the control area during the same time. Responses during the active- and post-denning periods are equal to the pre-denning period at a value of 0.

abundance of dik-dik was an artifact of heightened crypsis following wild dog recovery.

Prediction 2: Dik-dik suppress tree abundance

By themselves, dik-dik significantly reduced the abundance of *A. mellifera* but their effect on the abundance of *A. etbaica*, *Grewia* spp., and the aggregate tree community was not statistically detectable (Fig. 2). Over a three-year period, the abundance of *A. mellifera* in TOTAL plots (excluded dik-dik and other ungulates) increased by 84% relative to MESO plots (allowed dik-dik, excluded other ungulates; $t_{1,10} = 2.88$, $P = 0.016$). The abundance of *A. etbaica*, *Grewia* spp., and the aggregate tree community increased by 54% ($t_{1,10} = 1.37$, $P = 0.201$), 52% ($t_{1,10} = 1.49$, $P = 0.167$), and 40% ($t_{1,10} = 0.96$, $P = 0.360$), respectively, in TOTAL plots relative to MESO plots (Fig. 2). This result indicates that dik-dik had a tendency to exert top-down control on these species. A Fisher's combined probability test (Whitlock 2005) of *A. mellifera*, *A. etbaica*, and *Grewia* spp. indicated that this collective difference was statistically significant ($P = 0.011$). Thus, between 2009 and 2012, dik-dik alone contributed to the suppression of three tree species and the aggregate tree community, with *A. mellifera* being the most sensitive species to variation in herbivory by dik-dik (Fig. 2).

Prediction 3: The effect of dik-dik on tree abundance is reduced in the presence of wild dogs

Generally, tree abundance increased at a faster rate after wild dog recovery than before wild dog recovery.

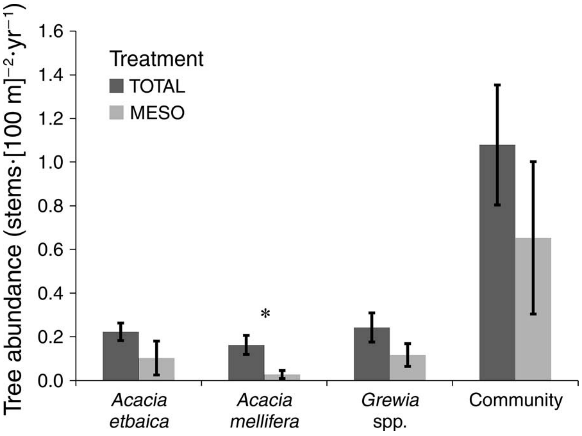

FIG. 2. Top-down regulation of dik-dik on tree abundance, shown as the net rate of change in tree density between 2009 and 2012 for individuals in the 1.0–2.0 m height class. TOTAL plots excluded dik-dik and all other browsers, while MESO plots permitted access by dik-dik (5 kg), but not larger browsers. Error bars indicate ±SE; asterisk indicates significance ($P < 0.05$) for a generalized least squares analysis.

For example, there was a significant increase in stem abundance for the aggregate tree community in OPEN plots after wild dog recovery compared to OPEN plots before wild dog recovery ($t_{1,9} = -2.96$, $P = 0.021$; Appendix B: Fig. B3). This effect was in the same direction, but was not significant for *A. mellifera* ($t_{1,9} = -1.67$, $P = 0.138$), *A. etbaica* ($t_{1,9} = -2.05$, $P = 0.080$), and *Grewia* spp. ($t_{1,9} = -1.45$, $P = 0.190$). A Fisher's combined probability test (Whitlock 2005) of *A. mellifera*, *A. etbaica*, and *Grewia* spp. indicated that this collective difference was statistically significant ($P = 0.026$). Superficially, the positive relationship between the recovery of wild dogs and increased tree abundance in OPEN plots is consistent with the trophic-cascade hypothesis.

Critically, however, the net effect of herbivory, as measured by comparing tree abundance in OPEN vs. TOTAL plots, was not reduced in the presence of wild dogs. None of the best-fitting ($\Delta AIC_c < 2$) models for the effect of ungulate exclusion on any tree species included an interaction of treatment and recovery status (Appendix B: Table B2). By itself, ungulate exclusion was included in the best-fitting models for all three tree species, showing that browsing has an important effect on tree abundance. The status of wild dog recovery was present in the best-fitting models for *A. etbaica*, *A. mellifera*, and *Grewia* spp. (Appendix B: Table B2); however, the direction of this effect was negative, in contrast to the central prediction of the trophic-cascade hypothesis (Fig. 3). These results indicate that the effect of herbivory by the entire community of browsing ungulates is either unchanged or has intensified following wild dog recovery: in other words, we did not find evidence for a trophic cascade.

Other potential drivers of tree abundance

A slight increase in the abundance of other browsers and variation in rainfall may explain why the effect of herbivory was not reduced by wild dog recovery. The total biomass density of browsing ungulates (excluding dik-dik) increased slightly from 4129 kg/km^2 before wild dog recovery to 4178 kg/km^2 after wild dog recovery (Appendix B: Table B3), and the energetic demand of non-dik-dik browsers increased slightly by 7%, from 450 MJ/km^2 to 480 MJ/km^2, following wild dog recovery. In addition, there was a statistically nonsignificant 36% increase in mean monthly rainfall from before (44.8 ± 6.7 mm [1999–2002]) to after wild dog recovery (60.9 ± 7.6 mm [2009–2012]; $F_{1,94} = 1.19$, $P = 0.278$).

DISCUSSION

We did not find support for a trophic cascade following the recovery of African wild dogs, in spite of (1) the suppression of the dik-dik population by wild dogs, (2) dik-dik's suppression of tree abundance, and (3) the positive correlation between tree and wild dog abundance. Trophic cascades arise when plant abundance is increased by the alteration of top-down forces through at least two sequential trophic levels. These forces must be demonstrably stronger than other factors that regulate species abundance. We evaluated a number of potentially limiting factors for dik-dik populations and could find no explanation more parsimonious than predation by wild dogs. Consistent with Augustine and McNaughton (2004), we also demonstrated that dik-dik by themselves suppress the abundance of at least some

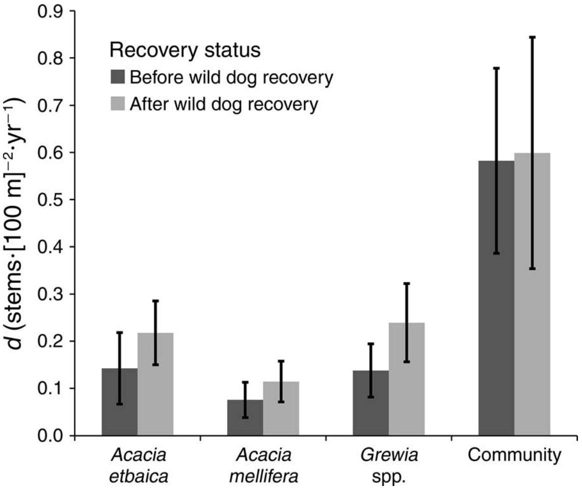

FIG. 3. The effect of browsing on tree abundance before (1999–2002) and after (2009–2012) recovery of wild dogs, where $d = \text{TOTAL} - \text{OPEN}$, i.e., the difference between the mean tree abundance of TOTAL plots (excludes all ungulates) and OPEN (accessible to all ungulates) plots over a three-year period for individuals in the 1.0–2.0 m height class. Tree abundances for each combination of treatment (TOTAL vs. OPEN) and experiment (before vs. after wild dog recovery) are shown in Appendix B: Fig. B3. Error bars indicate ±SE.

tree species. Although top-down forces are strong within this ecosystem, the recovery of wild dogs did not counteract intense browsing pressure. Below, we discuss potential mechanisms that may have prevented us from detecting the cascading effects of wild dogs, and highlight the implications of our findings for the restoration of large carnivores in savanna ecosystems.

A lingering question from our study is why wild dogs, in spite of their demonstrably strong effect on the population of the most abundant browser in this system, did not generate a detectable trophic cascade. One explanation, rooted in food web theory (Yodzis 1988), suggests that indirect effects take longer to manifest than direct effects (but see Menge 1997). In our study, the 20-year absence of wild dogs prior to their recovery, coupled with the seven-year difference between the initiation of our two herbivore exclusion experiments, may not have been long enough to detect a change in the abundance of long-lived plants like *Acacia* spp., *Grewia* spp., and other trees in this community. A second explanation is that the 36% increase in mean monthly rainfall following the recovery of wild dogs may have overridden any signal of reduced browsing by dik-dik. Across African savannas, tree abundance is limited by rainfall below a mean annual precipitation (MAP) of 650 mm, and more so by herbivores and fire above a MAP of 650 mm (Sankaran et al. 2005). During the before-recovery exclosure experiment, MAP was below this threshold (537 ± 100 mm) but exceeded it following wild dog recovery (730 ± 146 mm). Because of increased rainfall, and in spite of declining dik-dik abundance, the per capita (i.e., per individual herbivore) effect of browsing on tree abundance may have increased following the recovery of wild dogs (but see Louthan et al. 2013). A third and perhaps more promising explanation is that this community of browsing ungulates constitutes a reticulate food web that dampened the strength of indirect effects resulting from wild dog recovery (Polis and Strong 1996), such that forage that would have otherwise been released by the suppression of dik-dik may have been consumed by other species.

Correlative studies and natural experimentation often are the only means through which to investigate trophic cascades at scales commensurate with the movements and lifespans of large mammals and their prey. Our results highlight the advantages of incorporating manipulative approaches to explicitly quantify the constituent interactions that create trophic cascades. Trophic cascades require that top-down limitation, by way of at least two direct interactions (e.g., carnivore–herbivore, herbivore–plant), give rise to an indirect interaction (e.g., carnivore–plant). A strong inferential approach to the study of trophic cascades would therefore (1) directly quantify each of the three interactions hypothesized to comprise the cascade (Schmitz 2010) and (2) evaluate alternative explanations that can produce patterns similar to trophic cascades (Estes et al. 1998, Post et al. 1999, Hebblewhite et al. 2005, Peterson et al. 2014). A number of studies, most of which were conducted in temperate biomes, have interpreted a positive correlation between the biomass of plants and large carnivores as evidence of a trophic cascade (e.g., Ripple et al. 2001, Callan et al. 2013, Kuijper et al. 2013). This approach addresses patterns consistent with indirect effects, but quantifies neither the response of herbivores to carnivores, nor the response of plants to herbivores. Consequently, and because of the absence of a demonstrated mechanism, some of these studies have generated lively debate centered on the standards of evidence needed to demonstrate causation in the trophic-cascade hypothesis (Mech 2012, Winnie 2012, 2014, Allen et al. 2013, Kauffman et al. 2013, Beschta et al. 2014). In the few studies to manipulate predation by large carnivores through removal experiments, trophic cascades did not occur even though carnivore–herbivore and herbivore–plant interactions were strong (Sinclair et al. 2000, Maron and Pearson 2011). In our study, wild dogs suppressed dik-dik, dik-dik suppressed trees, and tree abundance outside of herbivore exclusion plots increased following wild dog recovery, a pattern that would otherwise suggest a trophic cascade. However, counter to the predictions of the trophic-cascade hypothesis, we found that the effect of herbivory on tree abundance was not reduced following wild dog recovery. Consequently, the claim that trophic cascades are a universal property of ecosystems (sensu Terborgh et al. 2010) may be premature without evidence from a greater number of ecological communities, combined with more concerted efforts to evaluate alternative hypotheses, especially in systems where experiments often are not used to test predictions.

Across savannas, tree cover is a key determinant of both ecosystem dynamics and rural livelihoods, as it affects nutrient cycles (Belsky 1994, Treydte et al. 2007), surface water retention (Scholes and Archer 1997, Smit and Rethman 2000), forage for both wild and domestic herbivores (Odadi et al. 2009, 2011), and household fuel availability in many areas (Chambers and Longhurst 1986). Factors influencing tree cover are therefore an important consideration for ecological and conservation-related research. Rainfall, soils, natural disturbance, and herbivory are widely recognized drivers of tree cover in African savannas (Sankaran et al. 2005, Bond 2008, Lehmann et al. 2014). If large carnivores also contribute to the regulation of tree cover via trophic cascades, it could have profound impacts on the livelihoods of people and ecosystem function (Estes et al. 2011, Ripple et al. 2014). Although indirect effects are an important process in some food webs (Terborgh et al. 2010), further study is needed to understand the ecological contexts in which the restoration of large carnivores will trigger trophic cascades in African savannas.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A and B are available online: http://dx.doi.org/10.1890/14-2056.1.sm