

Impacts of large herbivorous mammals on bird diversity and abundance in an African savanna

D. L. Ogada · M. E. Gadd · R. S. Ostfeld · T. P. Young · F. Keesing

Received: 27 February 2007 / Accepted: 31 January 2008
© Springer-Verlag 2008

Abstract Large native mammals are declining dramatically in abundance across Africa, with strong impacts on both plant and animal community dynamics. However, the net effects of this large-scale loss in megafauna are poorly understood because responses by several ecologically important groups have not been assessed. We used a large-scale, replicated exclusion experiment in Kenya to investigate the impacts of different guilds of native and domestic large herbivores on the diversity and abundance of birds over a 2-year period. The exclusion of large herbivorous native mammals, including zebras (*Equus burchelli*), giraffes (*Giraffa camelopardalis*), elephants (*Loxodonta*

africana), and buffalos (*Syncerus caffer*), increased the diversity of birds by 30%. Most of this effect was attributable to the absence of elephants and giraffes; these megaherbivores reduced both the canopy area of subdominant woody vegetation and the biomass of ground-dwelling arthropods, and both of these factors were good predictors of the diversity of birds. The canopy area of subdominant trees was positively correlated with the diversity of granivorous birds. The biomass of ground-dwelling arthropods was positively correlated with the diversity of insectivorous birds. Our results suggest that most native large herbivores are compatible with an abundant and diverse bird fauna, as are cattle if they are at a relatively low stocking rate. Future research should focus on determining the spatial arrangements and densities of megaherbivores that will optimize both megaherbivore abundance and bird diversity.

Communicated by Scott Robinson.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-008-0994-1) contains supplementary material, which is available to authorized users.

D. L. Ogada
Ornithology Section, National Museums of Kenya,
Nairobi, Kenya

M. E. Gadd
Division of International Conservation,
U.S. Fish and Wildlife Service, 4401 N. Fairfax Drive,
ARLSQ 730, Arlington, VA 22203, USA

R. S. Ostfeld
Institute of Ecosystem Studies, Box AB,
Millbrook, NY 12545, USA

T. P. Young
Department of Plant Sciences,
University of California, Davis, CA 95616, USA

F. Keesing (✉)
Bard College, Box 5000, Annandale, NY 12504, USA
e-mail: keesing@bard.edu

Keywords Bird diversity · Cattle · Indirect effects · Kenya · Livestock · Megaherbivore

Introduction

Birds play important functional roles in many ecosystems. Granivorous birds can decrease seed survival (Marone et al. 1998; Kelt et al. 2004), while insectivores can reduce the abundance of herbivorous arthropods (Strong et al. 2000; Sanz 2001; Hooks et al. 2003; Van Bael et al. 2003), and frugivorous birds can be important agents of seed dispersal (Herrera et al. 1994; Tabarelli and Peres 2002; Ingle 2003). Consequently, birds can influence the survival and reproduction of herbaceous and woody plants both directly, through seed predation, and indirectly, by reducing the abundance of herbivorous insects (Strong et al. 2000; Van Bael et al. 2003) or by dispersing seeds to more favorable

germination sites (Nogales et al. 1998). Birds are also important prey for other avian and mammalian predators (e.g., Rosalino and Santos-Reis 2002; Hounscome and Delahay 2005; Tornberg et al. 2005) and may exert bottom-up effects on higher trophic levels. Therefore, factors influencing the abundance and diversity of birds could have important indirect effects on community structure and function.

Most of the research carried out on factors influencing local bird diversity has focused either on the effects of vegetation structure (e.g. MacArthur and MacArthur 1961) or the effects of human-induced habitat changes, such as habitat fragmentation and conversion (Dranzo 2001; Tellería et al. 2003; Donnelly and Marzluff 2004). Donnelly and Marzluff (2004), for example, examined bird species richness and evenness in urban, suburban, and exurban nature reserves of varying sizes and within varying matrix types in the Seattle metropolitan area of the northwestern USA. They found that species richness declined with decreasing reserve size, as predicted by theory, and that species evenness increased.

In some ecosystems, large mammals can affect vegetation structure and composition directly, with potential indirect effects on birds. Cattle generally have negative effects on bird diversity and abundance (Bock et al. 1984; Taylor 1986; Temple et al. 1999; Gonnet 2001; Soderstrom et al. 2001; but see Knopf 1996). However, little research is devoted to understanding how large wild mammals influence birds, either directly or indirectly. In one study, McShea and Rappole (2000) found that white-tailed deer (*Odocoileus virginianus*) did not affect bird diversity at sites in eastern North America, although the deer did depress bird abundance through their effects on understory vegetation. In Africa, elephants (*Loxodonta africana*) have been found to reduce bird abundance and diversity in sites with high levels of elephant impact (Herremans 1995; Cumming et al. 1997). To our knowledge, however, no study has compared the effects of different guilds of large herbivores on bird communities.

We investigated how a diverse assemblage of large herbivorous mammals in an African savanna ecosystem influenced bird diversity and abundance by experimentally manipulating the presence and absence of megaherbivores (giraffes and elephants), other large native herbivorous mammals, and domestic cattle. To explore the underlying mechanisms of potential interactions between birds and large herbivores, we simultaneously investigated the effects of large herbivores on vegetation and arthropod biomass. Because the numbers of native large herbivores throughout African savannas are declining while cattle populations are increasing (duToit and Cumming 1999; Ottichilo et al. 2000), an understanding of the nature and strength of the impacts of large herbivorous mammals on bird communities should both provide basic information about the

functioning of these complex ecosystems and guide conservation and management decisions.

Methods

Study site

The study was conducted from February 2001 to February 2003 at the Mpala Research Center, located in the Laikipia District in the highlands of central Kenya. The study area consists of wooded grassland with ‘black cotton’ soils characterized by a heavy-clay content (60%) with impeded drainage (Young et al. 1998). These soils support some of the most productive rangelands in East Africa. In the study area, one tree species, *Acacia drepanolobium*, represents >97% of the overstory cover (Young et al. 1998); the remaining woody vegetation includes important food plants for wild herbivores. The five most common subdominant trees are (in order from most common to least) *Cadaba farinosa*, *Balanites aegyptica*, *Acacia mellifera*, *Lycium europaeum*, and *Rhus natalensis* (Gadd 2003). Five species of grasses predominate in the black cotton soils: *Lintonia nutans*, *Brachiaria lachnantha*, *Themeda triandra*, *Pennisetum mezianum*, and *P. stramineum*. The dominant native forbs are *Aerva lanata*, *Rhinacanthus ndorensis*, *Dyschoriste radicans*, and *Commelina* spp. (Young et al. 1997).

The climate is semi-arid with a pronounced dry season from December through mid-March. Rainfall averages 500–600 mm per year, although it does show considerable spatial and temporal heterogeneity. The first 2 months of data collection for this study coincided with the end of an intense 2-year drought. In contrast, November 2001 was exceptionally wet, with almost half of that year’s rainfall falling during that 1 month (M. Ogada, unpublished data).

Ungulates in this ecosystem include elephants (*Loxodonta africana*), reticulated giraffes, (*Giraffa camelopardalis*), Grevy’s zebras (*Equus grevyi*), Burchell’s zebras (*E. burchelli*), Grant’s gazelles (*Gazella granti*), Jackson’s hartebeests (*Alcelaphus buselaphus*), elands (*Taurotragus oryx*), Beisa oryx (*Oryx beisa*), steinbucks (*Rhaphicercus campestris*), cape buffalos (*Syncerus caffer*), and domestic cattle and sheep.

The avian fauna known to occur in the area during this study comprises approximately 75 species, of which nine are seasonal migrants. The most common species include rattling cisticolas (*Cisticola chiniana*), superb starlings (*Lamprotornis superbus*), ring-necked doves (*Streptopelia capicola somalica*), taita fiscals (*Lanius dorsalis*), Speke’s weavers (*Ploceus spekei*), yellow-bellied eremomelas (*Eremomela icteropygialis abdominalis*), and pied wheatears (*Oenanthe p. pleschanka*), which are seasonal migrants.

The two dominant diurnal raptors are the black-shouldered kite (*Elanus c. caeruleus*) and the common kestrel (*Falco tinnunculus*), a seasonal migrant.

Large herbivore enclosures

This research was conducted within a long-term herbivore exclusion experiment (the Kenya Long-term Exclusion Experiment, or KLEE) that was established at the Mpala Research Centre in 1995 (Young et al. 1998). The KLEE consists of a randomized block design, with three replicates of six treatments. The six treatments exclude different combinations of wild and domestic large-herbivore species, and each treatment is 200 × 200 m, or 4 ha (Table 1).

Exclusion treatments are maintained through a combination of fencing and controlled access by cattle. We excluded all large herbivores with a 2.3-m-tall fence composed of 11 strands of wire, with every other strand electrified at 6000–7000 V. Fencing to exclude megaherbivores consists of a single live wire 2 m off the ground and two ground wires: one ground wire is located above the live wire; the other runs along the ground. Single wires run along the live wire; these hang down (length 50 cm) from the live wire at 50-cm intervals. The presence of cattle is regulated by the KLEE staff, which conducts timed 2-h cattle runs consisting of 120 *Bos indicus* cows in each of the treatment plots used in this study four to eight times per year; these were designed to reflect a ranch stocking rate of 0.1–0.2 cattle/ha per year (see Young et al. 2005).

While we did not determine the density of large wild herbivores in the specific study site during our study, mean densities of megaherbivores and other large wild herbivores in Laikipia District are 0.004 + 0.002 and 0.05 + 0.01 animals/ha, respectively, based on aerial sample surveys conducted between 1985 and 2005 (Georgiadis et al., 2001, 2003). These densities are characterized by wide spatial and

temporal variations but are generally higher in properties that are more accommodative to wildlife, such as Mpala Ranch where our study site was located (Georgiadis et al., 2001, 2003). For details of the KLEE experiment, see Young et al. (1998).

Bird surveys

Bird surveys were conducted using a point-count method at the center of each of the eighteen 4-ha plots. Surveys were conducted twice per month during the first year (February 2001–March 2002) and every 3 months during the second year (June, September, December 2002, and February 2003). All 18 plots were surveyed within 48 h of one another, except in November 2001, when surveys were suspended due to heavy rainfall and were completed during the first week of December 2001. During the surveys, each plot was observed for 30 min in both the early morning (0700–0900 hours) and late afternoon (1600–1800 hours). Birds were recorded only if they perched or were actively foraging in the plot. Birds flying overhead but not landing in the plot were not recorded. Aerial feeders—swallows and swifts—were not recorded due to the difficulty of distinguishing foraging flights from local movements. In addition, birds that were heard but not seen were not recorded due to the errors associated when observers use only an auditory cue (Cresswell et al. 1997). Birds that could not be positively identified—6% of sightings—were recorded as ‘unknown’ and used in analyses of bird abundance but not of bird diversity.

Arthropod surveys

Arthropods were sampled once per month during the first year of the study (March–September 2001, December 2001–January 2002) and every 3 months during the second year of the study (June, September, December 2002, February 2003), with the exception of October and November 2001 when sampling was suspended due to heavy rainfall. At each sampling session, ground arthropods were sampled using pitfall traps. An array (spacing 2 m) of four traps (8 cm diameter × 12 cm deep) was placed in the same relative position on each of the 18 treatments, for a total of 72 traps. Traps were half-filled with a solution of water and laundry detergent and were opened for 3 days per month, and then all arthropods were collected.

Arthropods located in the grass layer were sampled by sweep-netting. Samples were collected in the morning between 0800 and 1000 hours using a sweep net with a diameter of 37.5 cm. A total of 100 sweeps per plot were made by walking the perimeter of the inner hectare of each plot. After 50 sweeps, the net contents were transferred to a Ziploc bag and another 50 sweeps were made. Data from

Table 1 The six treatments of the Kenya Long-term Exclusion Experiment (KLEE) in which each treatment allows access (+) to a different combination of large herbivores

Treatment	Megaherbivores	Other wildlife	Cattle
0	–	–	–
C	–	–	+
W	–	+	–
WC	–	+	+
MW	+	+	–
MWC	+	+	+

M, Megaherbivores (giraffes and elephants); W, other native wildlife; C, cattle. Other wildlife includes large herbivores, such as zebras and buffaloes

Each treatment area is 200 × 200 m, or 4 ha, and there are three blocks of these six treatments in KLEE

the two sweeps were pooled for analysis. All arthropods were sorted to order, counted, dried, and weighed. Biomass and diversity estimates of arthropods excluded ants because of the tendency of ants to follow each other along pheromone trails, resulting in potentially non-random sampling.

Woody plant surveys

Because subdominant trees responded quickly to the exclusion of large mammals, we measured the canopy areas of subdominant trees during October–November 2001 for a sample of trees located within a 50 × 50-m central quadrat in each 200 × 200-m KLEE treatment. Canopy area was determined by measuring the widest diameter of the tree canopy and its corresponding perpendicular diameter and then calculating the area of an ellipse. Tree height was measured to the nearest centimeter using a graduated measuring pole. *Acacia drepanolobium* trees were not measured because their densities, heights, and canopy areas were not significantly affected by the removal of large herbivores at the time of this study (B. Okello, T.P. Young, unpublished data).

Analyses of variance

We first tested for block effects for all dependent variables. Because no significant effects were found, we omitted block as an independent variable from the analyses. Levene's test was used to ensure all analyses of variance (ANOVAs) did not violate the assumption of equal variances. All dependent variables were transformed if necessary to meet the assumptions of normality. Unless otherwise indicated, statistical tests were conducted using SYSTAT ver. 10 (SPSS 2000).

We compared mean bird abundance, species richness, and the Shannon diversity index among the six treatments using two-way ANOVAs, with two levels of cattle (presence, absence) and three levels of wildlife (no wildlife, all wildlife, all wildlife except megaherbivores) as factors. If those tests revealed no significant effect of cattle but a significant effect of wildlife, we then pooled data from the cattle treatments with the corresponding treatments without cattle (e.g. treatments with no large mammals were treated the same as treatments with only cattle). We then conducted a one-way ANOVA with three levels of wildlife (no wildlife, all wildlife, all wildlife except megaherbivores) and used Fisher least significant difference (LSD) post-hoc tests to differentiate the effects of megaherbivores from those of other wildlife. We conducted repeated measures ANOVAs on bird diversity, species richness, and abundance as well, with time (17 sampling occasions) and treatment (the six large-mammal treatments) as factors.

We chose to use the Shannon index of diversity, which is more sensitive to differences in species richness than

species evenness (Magurran 1988), to minimize the impact on our diversity index of the presence of two seasonally abundant, gregarious species—Speke's weavers (*Ploceus spekei*) and red-billed queleas (*Quelea quelea aethiopica*).

Birds were categorized for diet (granivore, insectivore, other) and foraging guild (ground-forager, foliage-gleaner, bark-gleaner, hawk) using information from a combination of field observations and published data (Feare 1984; Mackworth-Praed and Grant 1952, 1955; Zimmerman et al. 1996). Birds were also categorized for habitat preference (savanna, open woodland) based on descriptions in Zimmerman et al. (1996, Appendix 1). Birds that occupied only "savanna" or both "savanna" and "brush" habitats were classified as "savanna" species; birds that occupied "woodland" or "woodland" and "brush" habitats were classified as "woodland" species. For each category (dietary guild, foraging guild, habitat preference), we calculated mean bird abundance and the Shannon diversity index. These values were then used as dependent variables in six multivariate ANOVAs (MANOVAs), each with two factors: cattle (presence, absence) and wildlife (no wildlife, all wildlife, all wildlife except megaherbivores). When those tests revealed no significant effect of cattle but a significant effect of wildlife, we pooled data from the cattle treatments with the corresponding treatments without cattle and conducted a one-way MANOVA with three levels of wildlife (no wildlife, all wildlife, all wildlife except megaherbivores). We conducted post-hoc tests using Fisher LSD tests to differentiate the effects of megaherbivores from those of other wildlife. All MANOVAs were performed with STATISTICA ver. 6.1 (StatSoft 2001).

We analyzed the relationship between large herbivorous mammals and (1) biomass of arthropods caught in pitfall traps, (2) biomass of arthropods caught in sweep sampling, (3) Shannon diversity index of all arthropods, (4) both mean and total canopy area of subdominant trees (trees other than *Acacia drepanolobium*), as a measure of habitat diversity, and (5) coefficient of variation in the height of subdominant trees as a measure of habitat structural complexity. We used two-way ANOVAs, with two levels of cattle (presence, absence) and three levels of wildlife (no wildlife, all wildlife, all wildlife except megaherbivores) as factors. If the tests revealed no significant effect of cattle but a significant effect of wildlife, we pooled data from the cattle treatments with the corresponding treatments without cattle to increase our sample size. We then conducted a one-way ANOVA with three levels of wildlife (no wildlife, all wildlife, all wildlife except megaherbivores) and used Bonferroni post-hoc tests to differentiate the effects of megaherbivores from those of other wildlife. We also conducted repeated measures ANOVAs on these same dependent variables, with time (17 sampling occasions) and treatment (six large-mammal treatments) as factors.

Regression analyses

For dependent variables that showed a significant response to the exclusion of large herbivores, we evaluated potential predictors using multiple regression analyses. We performed a series of forward stepwise multiple regression tests, with $\alpha = 0.05$ for inclusion. Independent variables in these tests were both individual mean and total canopy area of subdominant trees, the coefficient of variation of the height of subdominant trees, and the biomass of arthropods caught by pitfall traps and by sweep-net sampling.

Results

From February 2001 through February 2003, we observed 6369 birds of 61 different species [Electronic Supplementary Material (ESM), Appendix A]; of these, nine were Palearctic migrants seen only between late-September and March. The rattling cisticola (*Cisticola chiniana*) was the most abundant solitary resident, representing 19% of all sightings. Speke's weavers (*Ploceus spekei*) and red-billed queleas (*Quelea quelea aethiopica*) were seasonally abundant residents.

Effects of large mammals on birds

Treatments allowing access to all native large herbivores had the lowest mean levels of bird diversity over the 2-year study period, and treatments excluding all large wild and domestic herbivores had the highest mean levels of bird diversity. Of a total of 61 different bird species observed on all plots, 45 were recorded in treatments without large herbivorous mammals, and 33 were recorded in the plots allowing access to native large herbivorous mammals, including megaherbivores.

Native large herbivores (hereafter NLH), but not cattle, significantly reduced mean bird species richness (NLH $P_{2,12} = 0.007$; cattle $P_{1,12} = 0.882$; cattle \times NLH $P_{2,12} = 0.859$; Fig. 2). Due to the lack of a significant cattle effect, we treated treatments with native large herbivores the same as their corresponding treatments that included cattle (Table 1) in order to differentiate the effects of megaherbivores (see Methods for details). On the basis of this analysis, megaherbivores appeared to have been responsible for the effect of large herbivores on bird species richness (one-way ANOVA $P_{2,15} = 0.002$; Fig. 1). The presence of NLH also significantly decreased the Shannon diversity index of birds, but cattle had no effect, nor was there an interaction between cattle and native large herbivores (Fig. 1; NLH $P_{2,12} = 0.007$; cattle $P_{1,12} = 0.604$; Cattle \times NLH $P_{2,12} = 0.612$). Based on one-way ANOVA, bird diversity was significantly lower on plots with megaherbivores than on plots

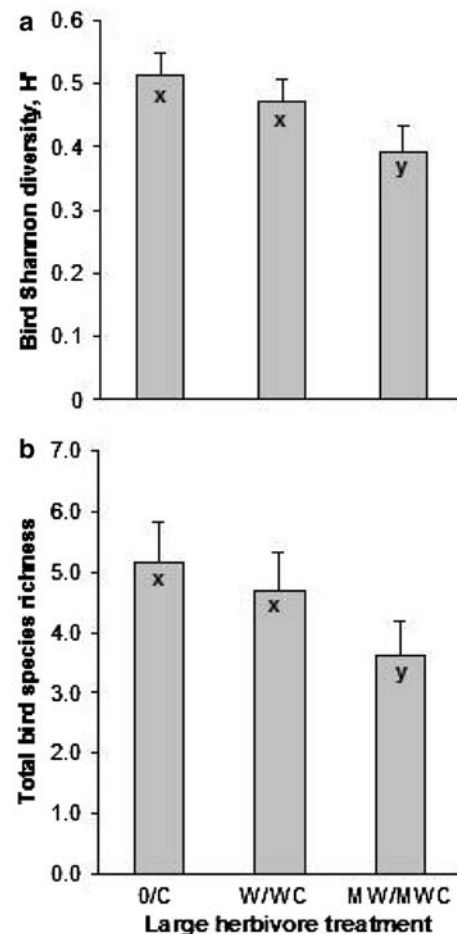


Fig. 1 Effects of six large herbivore treatments on the Shannon diversity index, H' (a) and total bird species richness (b) over the entire study period, 2001–2003 (means + SE). Herbivore treatments are no large herbivores (O), cattle (C), megaherbivores (M), and other large wild herbivores (W); see Table 1 for treatment descriptions. Corresponding treatments with and without cattle were pooled (see Methods for details). Lowercase letters inside bars indicate significant differences (ANOVA, $\alpha = 0.05$)

without (one-way ANOVA $P_{2,15} = 0.003$; Fig. 1). There were no significant effects of large-herbivore treatment on bird abundance (NLH $P_{2,12} = 0.189$; cattle $P_{1,12} = 0.753$; cattle \times NLH $P_{2,12} = 0.785$). No individual bird species was more abundant on sites with megaherbivores than on sites without (ESM, Appendix B).

Bird abundance, species richness, and the Shannon diversity index all varied significantly with time, with the lowest diversity and abundance occurring during dry season sampling (December–January). Diversity was significantly lower in plots to which megaherbivores had access (repeated measures ANOVA; Table 2). The effect of treatment on species richness was not significant in the repeated measures ANOVA ($P = 0.056$; Table 2), and there were no significant time \times treatment interactions (Table 2).

Table 2 Repeated measures ANOVA of the effect of large herbivorous mammals (treatment) on bird abundance and diversity through time

	SS	df	MS	F	P
Bird diversity (H')					
Between subjects					
Treatment	0.85	5	0.17	3.38	0.04*
Error	0.60	12	0.05		
Within subjects					
Time	2.20	16	0.14	2.94	<0.001*
Time \times treatment	4.31	80	0.05	1.15	0.22
Error	8.97	192	0.05		
Bird species richness					
Between subjects					
Treatment	130.03	5	26.00	2.98	0.056
Error	104.82	12	8.74		
Within subjects					
Time	472.00	16	29.50	5.39	<0.001*
Time \times treatment	415.14	80	5.2	0.95	0.60
Error	1050.51	192	5.47		
Bird abundance					
Between subjects					
Treatment	7629.94	5	1526.00	0.78	0.57
Error	22932.04	12	1911.00		
Within subjects					
Time	72471.05	16	4529.44	3.23	<0.001*
Time \times treatment	112460.01	80	1405.75	1.00	0.49
Error	269277.29	192	1402.49		

* $P \leq 0.05$

Bird diversity, abundance, and species richness all varied significantly through time. The presence of large herbivores significantly reduced the Shannon diversity index for birds

The Shannon diversity index of birds was positively correlated ($R^2 = 0.76$) with both mean canopy area of subdominant trees ($P = 0.001$, Fig. 2a) and the biomass of arthropods captured in pitfall traps ($P < 0.02$; Fig. 2b). Total bird species richness was positively correlated with the biomass of insects captured in pitfall traps ($R^2 = 0.65$; $P < 0.01$).

Dietary guild

Of the birds observed, 69% were insectivorous and 25% were granivorous; 6% fed on foods other than insects or seeds and were not included in analyses based on feeding behavior. The MANOVA revealed that the presence of native large herbivores, but not cattle, significantly reduced the abundance of both insectivorous and granivorous birds (NLH $P_{2,11} = 0.05$; cattle $P_{2,11} = 0.31$; cattle \times NLH $P_{4,22} = 0.62$). Based on a subsequent one-way MANOVA ($P_{2,4} = 0.03$), both insectivorous and granivorous birds

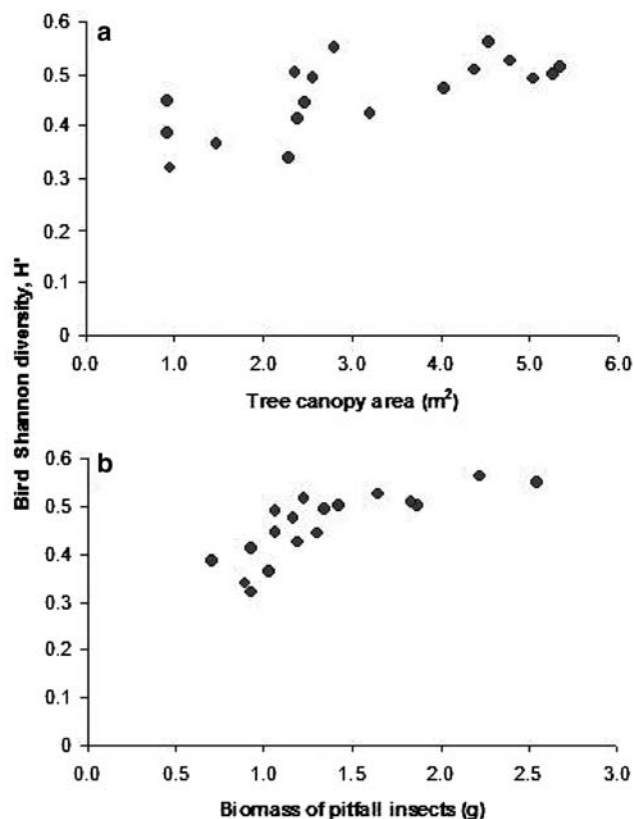


Fig. 2 Relationship between the Shannon diversity (H') of birds and canopy area of subdominant trees(a) and biomass of pitfall insects per sampling session (means shown) (b)

were less abundant on plots with megaherbivores (Table 3; Fig. 3a). The diversity of birds categorized by dietary guild was also significantly reduced by the presence of native large herbivores (NLH $P_{2,11} = 0.03$; cattle $P_{2,11} = 0.85$; cattle \times NLH $P_{4,22} = 0.83$), and a subsequent one-way MANOVA revealed that megaherbivores were also responsible for this effect ($P_{2,4} = 0.01$; Table 3; Fig. 3b).

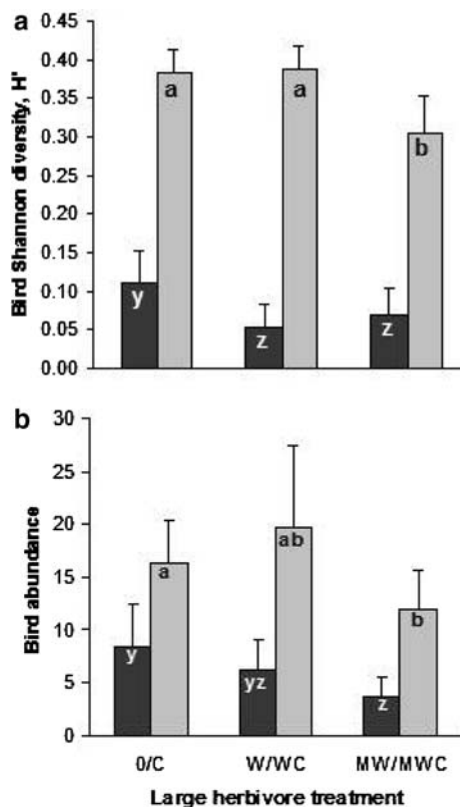
Multiple regression analysis of dietary guilds revealed that both the diversity and abundance of insectivorous birds were positively correlated with the biomass of insects captured in pitfall traps (diversity: $R^2 = 0.39$, $P < 0.01$; abundance: $R^2 = 0.45$, $P < 0.01$), while the diversity and abundance of granivorous birds were positively correlated with the mean canopy area of subdominant trees (diversity: $R^2 = 0.55$, $P < 0.01$; abundance: $R^2 = 0.45$; $P < 0.02$).

Foraging guild

Of all the birds observed in the plots, 74% were ground-feeders, 15% were foliage gleaners, 6% were hawkers, and 5% were bark gleaners. Based on the MANOVA, there were no significant effects of the presence of large herbivores on either the diversity or the abundance of birds categorized by foraging guild.

Table 3 Multivariate analysis of variance (MANOVA) of the presence of large herbivorous mammals on the abundance of birds categorized by dietary guild (insectivore, granivore)

	<i>F</i>	Effect <i>df</i>	Error <i>df</i>	<i>P</i>
Bird abundance				
Intercept	703.76	2	11	<0.01*
Cattle	1.31	2	11	0.31
Wildlife	2.85	4	22	0.05*
Cattle × wildlife	0.67	4	22	0.62
Bird diversity (<i>H'</i>)				
Intercept	980.85	2	11	<0.01*
Cattle	0.17	2	11	0.85
Wildlife	3.38	4	22	0.02*
Cattle × wildlife	0.37	4	22	0.83

* $P \leq 0.05$ **Fig. 3** Effects of large herbivore treatment on the Shannon diversity index (a) and abundance (b) of granivorous (dark gray) and insectivorous (light gray) birds (mean + SE). Herbivore treatments are no large herbivores (O), cattle (C), megaherbivores (M), and other large wild herbivores (W); see Table 1 for treatment descriptions. In this analysis, corresponding treatments with and without cattle were pooled (see Methods for details). Lowercase letters inside bars indicate significant differences (ANOVA, $\alpha = 0.05$)

Habitat preference

Thirty-eight percent of the birds observed are typically savanna residents, while 18% are most commonly residents

of open woodland habitats; the remaining 44% are habitat generalists (occupying savanna, brush, and woodland habitats) and were not considered in subsequent analyses of habitat preference. Large herbivores had no significant effect on either the diversity or the abundance of birds categorized by habitat preference (diversity: NLH $P_{2,11} = 0.15$; cattle $P_{2,11} = 0.99$; cattle × NLH $P_{4,22} = 0.29$; abundance: NLH $P_{2,11} = 0.11$; cattle $P_{2,11} = 0.36$; cattle × NLH $P_{4,22} = 0.50$).

Effects of large herbivores on arthropods

The biomass of arthropods captured in pitfall traps was not significantly affected by the presence of large herbivores (NLH $P_{2,12} = 0.069$; cattle $P_{1,12} = 0.835$; cattle × NLH $P_{2,12} = 0.372$). When data were pooled regardless of the presence or absence of cattle, plots with megaherbivores had a lower biomass of pitfall arthropods than those without (Fig. 4a; $P_{2,15} = 0.05$). In contrast, the biomass of arthropods captured through sweep-netting was unaffected by the presence of native large herbivores, but it was significantly reduced by the presence of cattle (NLH $P_{2,12} = 0.753$; cattle $P_{1,12} = 0.014$; cattle × NLH $P_{2,12} = 0.835$; Fig. 4b). Neither native large herbivores nor cattle affected the diversity of arthropods captured through pitfall or sweep sampling, nor did they affect the pooled diversity of arthropods captured through either method. Using repeated measures ANOVAs, we found no significant effects of the presence of large herbivores on either the biomass or abundance of insects captured in pitfall traps or with sweep nets. Insect abundance and biomass were significantly affected by time (Table 4), but there were no significant time × treatment interactions.

Effects of large herbivores on subdominant trees

After 6 years of fencing, the mean canopy area per subdominant tree was significantly smaller on plots with any native large herbivores (Fig. 5; NLH $P_{2,12} = 0.001$; cattle $P_{1,12} = 0.537$; cattle × NLH $P_{2,12} = 0.684$). The total canopy area of subdominant trees per plot was also smaller on plots with native large herbivores (NLH $P_{2,12} = 0.013$; cattle $P_{1,12} = 0.856$; cattle × NLH $P_{2,12} = 0.717$). There were no significant effects of either native large herbivores or cattle on the number of subdominant trees in the plots.

Discussion

The presence of native large herbivores reduced overall bird diversity and species richness by approximately 30%, but it did not significantly affect overall bird abundance. Most of the effects of native large herbivores were caused by megaherbivores, which appear to affect birds in two

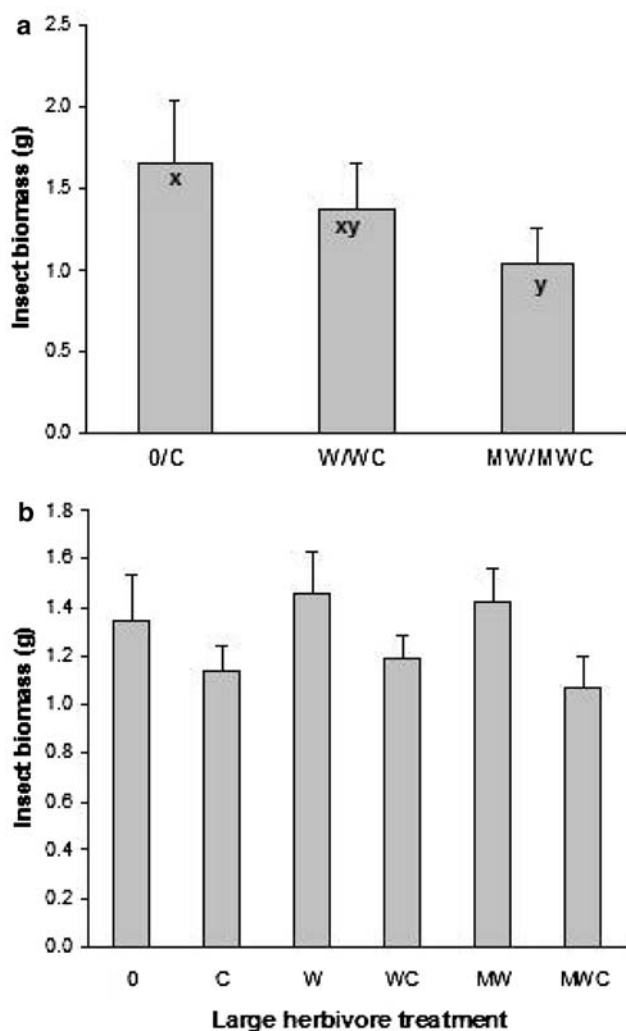


Fig. 4 Effects of large herbivore treatments on the biomass of insects captured in pitfall traps (a) and sweep nets (mean + SE) (b). Herbivore treatments are no large herbivores (O), cattle (C), megaherbivores (M), and other large wild herbivores (W); see Table 1 and the text for treatment descriptions. In panel a, corresponding treatments with and without cattle were pooled (see Methods for details). Lowercase letters inside bars indicate significant differences (ANOVA, $\alpha = 0.05$)

major ways. First, they browse tree canopies; in the presence of megaherbivores, both the mean canopy area and the total canopy area of subdominant trees were lower. Other native large herbivores also significantly reduced the canopy area of those trees, presumably through browsing. In plots where the mean canopy area of subdominant trees was smaller, there was significantly lower bird diversity, and the mean canopy area of subdominant trees was the best predictor of the diversity of granivorous birds. Second, megaherbivores reduced the biomass of ground-dwelling arthropods captured in pitfall traps. The biomass of arthropods was a significant positive predictor of overall bird diversity and species richness and of the diversity of insectivorous birds.

Table 4 Repeated measures analysis of variance of insect abundance and biomass

	SS	df	MS	F	P
Insect abundance (pitfall-collected)					
Between subjects					
Treatment	51404.5	5	10280.9	1.2	0.37
Error	102755.1	12	8562.9		
Within subjects					
Time	456016.8	7	65145.3	16.2	<0.001*
Time \times treatment	123817.7	35	3537.6	0.8	0.66
Error	338372.9	84	4028.2		
Insect abundance (sweep-netted)					
Between subjects					
Treatment	36949.9	5	7389.9	0.3	0.92
Error	316615.1	12	26384.6		
Within subjects					
Time	2329068.5	11	211733.5	30.4	<0.001*
Time \times treatment	294107.1	55	5347.4	0.8	0.87
Error	919948.9	132	6969.3		
Insect biomass (pitfall-collected)					
Between subjects					
Treatment	76.4	5	15.3	2.4	0.1
Error	76.0	12	6.3		
Within subjects					
Time	231.0	7	33.0	3.6	0.002*
Time \times treatment	190.4	35	5.4	0.6	0.96
Error	777.5	84	9.3		
Insect biomass (sweep-netted)					
Between subjects					
Treatment	5.7	5	1.2	1.7	0.22
Error	8.3	12	0.7		
Within subjects					
Time	43.4	11	3.9	10.6	<0.001*
Time \times treatment	19.7	55	0.4	1.0	0.55
Error	48.9	132	0.4		

* $P \leq 0.05$

The total number of subdominant trees did not differ between the large-herbivore treatments, but the mean canopy area did, resulting in an effect of treatment on the total canopy area available to birds. Thus, the strong effects of reductions in the canopy area of trees on birds were likely due to differences in the mean canopy area of each tree, or to differences in the total amount of canopy area available. Birds may be sensitive to canopy area for several reasons. First, reductions in canopy area reduce the number of available perching sites, both overall and on each individual tree. Canopies also provide protection from aerial predators, such as sparrowhawks, eagles, and falcons, which were seen occasionally in the study area. Finally, canopies may influence birds by affecting food availability; for

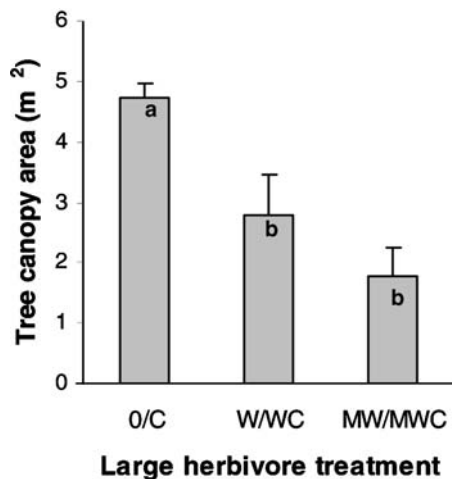


Fig. 5 Effects of large herbivore treatments on canopy area of trees other than *Acacia drepanolobium* (mean + SE). Herbivore treatments are no large herbivores (O), cattle (C), megaherbivores (M), and other large wild herbivores (W); see Table 1 and the text for treatment descriptions. In this analysis, corresponding treatments with and without cattle were pooled (see Methods for details). Lowercase letters inside bars indicate significant differences (ANOVA, $\alpha = 0.05$)

example, aerial insects may be less abundant in and around small tree canopies than in large tree canopies, which could affect the abundance or diversity of insectivorous birds. Preliminary data from this site suggest that aerial insect abundance varies both seasonally and from one tree type to another (D. Ogada, unpublished data); whether abundance varies with canopy area is not yet known.

The mechanisms by which megaherbivores reduce the biomass of ground-dwelling arthropods are not well understood, although trampling and consumption of herbaceous vegetation are likely candidates. The effects of trampling are expected to be immediate and short-term, whereas those of vegetation removal are more likely to persist. Moreover, the presence of megaherbivores reduces the abundance of insectivorous small mammals, such as shrews (Keesing 2000), which would be expected to result in a positive net effect on ground-dwelling arthropods. In this instance, the direct, negative effect of megaherbivores appears to outweigh any potentially positive indirect effects mediated by the suppression of other consumers.

Each of the 4-ha treatment areas was relatively small in comparison to the size of bird territories and home ranges, so that birds observed in this study may have utilized more than one treatment area. Our results demonstrate that bird activity was higher in sites without megaherbivores, whether or not all of the birds observed resided in those plots. Future studies should investigate whether results from this study scale up to larger areas. This study used the largest feasible replicated, controlled experimental design. Studies over larger areas would likely utilize sites that vary

naturally in large-mammal abundance, raising the possibility that underlying differences in bird diversity between the sites could be caused by variation in some factor simultaneously influencing both birds and large mammals.

The density of native large herbivores in KLEE is regulated only by fencing; therefore, there is the potential for the presence of certain species to affect the abundances of others. For example, the presence of elephants could affect the behavior of other smaller herbivores (e.g., buffalos) such that the latter become less abundant on plots with elephants than on plots without elephants. Young et al. (2005) examined this effect at KLEE and found that the density of zebras was 44% higher on plots with no cattle (based on dung counts) than on plots with cattle but that zebras were equally abundant on plots with and without megaherbivores. Dung piles for species other than zebras were not numerous enough for a similar analysis. In principle, the effects of megaherbivores on the birds that we observed could have been caused by the indirect effect of megaherbivores on large herbivores other than zebras.

Similarly, our study design does not enable us to distinguish the effects of giraffes from those of elephants. Both giraffes and elephants browse tree canopies and could have caused the effects we observed on canopy areas of woody vegetation. Both also could have affected ground-dwelling arthropods directly through trampling or indirectly through soil compaction. Giraffes are exclusively browsers and do not eat herbaceous vegetation, but elephants consume significant quantities of understory forbs and grasses (Lindsay 1982; McKnight 1995; but see Cerling et al. 1999). Young et al. (2005) found that megaherbivores reduced grass cover at this site by 8% and forb cover by 33%. Thus, elephants could have affected ground-dwelling arthropods indirectly by consuming herbaceous vegetation.

Previous comparative studies have found that elephants affect bird abundance and diversity (Herremans 1995). In Botswana, elephants reduced the abundance of birds that are canopy specialists (Herremans 1995). In Zimbabwe, bird species richness was lower in woodlands with elephants than in those without. In both studies, elephant densities in the impacted areas were $>0.5/\text{km}^2$. Georgiadis et al. (2003) estimated elephant abundance across the district in which KLEE is located as $0.42/\text{km}^2$. At these densities, elephants appear to suppress site-level bird diversity and abundance.

We found no significant effects of native large herbivores other than megaherbivores on bird diversity or abundance. The diverse ungulate fauna at our site includes zebras, hartebeests, elands, gazelles, and oryx, among others. Our results suggest that their presence is compatible with an abundant and diverse bird fauna. Likewise, bird diversity and abundance were not affected by the presence of cattle, despite the potential for cattle to significantly

reduce grass cover and to reduce the biomass of arthropods caught in sweep nets. This lack of effect may largely be due to rotational grazing and low stocking rates within KLEE. Results from other studies indicate that cattle generally have an adverse effect on bird diversity, with grazed areas supporting fewer bird species (Bock et al. 1984; Gonnet 2001; Taylor 1986; Temple et al. 1999).

Our study and others demonstrate that there is a potential tradeoff between the conservation of elephants and the conservation of other species, including birds. The idea that conservation focused on one species, elephants, for example, may be to the detriment of other species of importance is not new (e.g. Simon et al. 2001; Gadd 2002; Roemer and Wayne 2003; Gangoso et al. 2005), and the resolution of such conflicts may require innovative strategies. The increased bird diversity we found in 4-ha experimental units from which megaherbivores had been excluded indicates that elephant-free zones could be relatively small and still serve as bird refugia.

Our results demonstrate that the presence of megaherbivores reduces local diversity of birds in this East African savanna habitat. Given the potential importance of birds in ecological systems, future research should address the ecological consequences of changes in bird diversity brought about by megaherbivores.

Acknowledgments We gratefully acknowledge the support and cooperation of the Ministry of Education of the Republic of Kenya and Kenyatta University. This research was supported by a National Science Foundation grant (DEB CAREER 0196177) to FK and by grants from the American Society of Mammalogists and the University at Albany Graduate Student Organization to DO. The KLEE plots were built and maintained with grants from the James Smithson Fund of the Smithsonian Institution (to Alan Smith), the National Geographic Society (4691-91), the National Science Foundation (BSR-97-07477 & BSR-03-16402), and the African Elephant Program of the U.S. Fish and Wildlife Service (98210-0G563) (to TPY). Logistical support was provided by the Mpala Research Centre, Mordecai Ogada, Kerry Outram, Nick Georgiadis, Heather Wallington and Bard College. Roy Snelling provided insect identification training. Field and laboratory assistance were provided by Frederick Erii, John Lochukuya, Lynne Gadd, Abdi Kadir Ali Hassan, James Ponoto, Kadir Age, Francis Ewaton and University Research Expeditions Program volunteers. The manuscript was improved by comments from Scott Robinson and two anonymous reviewers.

References

- Bock CE, Bock JH, Kenney WR, Hawthorne VM (1984) Responses of birds, rodents, and vegetation to livestock enclosure in a semidesert grassland site. *J Range Manage* 37:239–242
- Cerling TE, Harris JM, Leakey MG (1999) Browsing and grazing in elephants: the isotope record of modern and fossil proboscideans. *Oecologia* 120:364–374
- Cresswell W, Irwin M, Jensen M, Mee A, Mellanby R, McKean M, Milne L (1997) Population estimates and distribution changes of landbirds on Silhouette Island, Seychelles. *Ostrich* 68:50–57
- Cumming DH, Fenton MB, Rautenbach IL, Taylor RD, Cumming GS, Cumming MS, Dunlop JM, Ford AG, Hovorka MD, Johnston DS, Kalcounis M, Mahlangu Z, Portfors CVR (1997) Elephants, woodlands and biodiversity in southern Africa. *South Afr J Sci* 93:231–236
- Donnelly R, Marzluff JM (2004) Importance of reserve size and landscape context to urban bird conservation. *Conserv Biol* 18:733–745
- Dranzoa C (2001) Breeding birds in the tropical rain forests of Kibale National Park, Uganda. *Afr J Ecol* 39:74–82
- du Toit JT, Cumming DHM (1999) Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. *Biodivers Conserv* 8:1643–1661
- Feare C (1984) *The starling*. Oxford University Press, Oxford
- Gadd ME (2002) The impact of elephants on the marula tree, *Sclerocarya birrea*. *Afr J Ecol* 40:328–336
- Gadd ME (2003) Elephant ecology and conservation in African rangelands. PhD thesis. University of California, Davis
- Gangoso L, Donázar J, Scholz S, Palacios CJ, Hiraldo F (2005) Contradiction in conservation of island ecosystems: plants, introduced herbivores and avian scavengers in the Canary Islands. *Biodivers Conserv* 15:2231–2248
- Georgiadis N, Ojwang G (2001) Numbers and distributions of large herbivores in Laikipia, Samburu, and Isiolo Districts sample count, January 22 to March 07, 2001 for The Laikipia Wildlife Forum. Mpala Research Centre, Kenya
- Georgiadis N, Olwero N, Ojwang G (2003) Numbers and distributions of large herbivores in Laikipia District, Leroghi, and Lewa Conservancy. Mpala Research Centre, Kenya
- Gonnet JM (2001) Influence of cattle grazing on population density and species richness of granivorous birds (Emberizidae) in the arid plain of the Monte, Argentina. *J Arid Environ* 48:569–579
- Herremans M (1995) Effects of woodland modification by African elephant *Loxodonta africana* on bird diversity in northern Botswana. *Ecography* 18:440–454
- Herrera CM, Jordano P, Lopez-Soria L, Amat JA (1994) Recruitment of a mast-fruited, bird-dispersed tree: bridging frugivore activity and seedling establishment. *Ecol Monogr* 64:312–344
- Hooks CRR, Pandey RR, Johnson MW (2003) Impact of avian and arthropod predation on lepidopteran caterpillar densities and plant productivity in an ephemeral agroecosystem. *Ecol Entomol* 28:5–522
- Hounscome T, Delahay R (2005) Birds in the diet of the Eurasian badger *Meles meles*: a review and meta-analysis. *Mammal Rev* 35:199–209
- Ingle N (2003) Seed dispersal by wind, birds, and bats between Philippine montane rainforest and successional vegetation. *Oecologia* 134:251–261
- Keesing F (2000) Cryptic consumers and the ecology of an African savanna. *BioScience* 50:205–215
- Kelt DA, Meserve PL, Gutiérrez JR (2004) Seed removal by small mammals, birds and ants in semi-arid Chile, and comparison with other systems. *J Biogeogr* 31:931–942
- Knopf F (1996) Prairie Legacies—birds. In: Samson FB, Knopf FL (eds) *Prairie conservation: preserving North America's most endangered ecosystem*. Island Press, Covelo, pp 135–148
- Lindsay WK (1982) Habitat selection and social group dynamics of African elephants in Amboseli, Kenya. M.Sc. thesis. University of British Columbia, Vancouver, B.C., Canada
- Macarthur R, Macarthur J (1961) On bird species diversity. *Ecology* 42:594–598
- Mackworth-Praed CW, Grant CCHB (1952) *Birds of Eastern and North Eastern Africa*. Longmans, Green and Co., London
- Mackworth-Praed CW, Grant CCHB (1955) *Birds of Eastern and North Eastern Africa*. Longmans, Green and Co., London
- Magurran AE (1988) *Ecological diversity and its measurement*. Cambridge University Press, Cambridge

- Marone L, Ross BE, Lopez J, Casenave DE (1998) Granivore impact on soil-seed reserves in the central Monte desert, Argentina. *Funct Ecol* 12:640–645
- McKnight BL (1995) Behavioral ecology of hand-reared African elephants (*Loxodonta africana* (Blumenbach) in Tsavo East National Park, Kenya. *Afr J Ecol* 33:242–256
- McShea WJ, Rappole JH (2000) Managing the abundance and diversity of breeding bird populations through manipulation of deer populations. *Conserv Biol* 14:1161–1170
- Nogales M, Delgado JD, Medina FM (1998) Shrikes, lizards and *Lycium intricatum* (Solanaceae) fruits: a case of indirect seed dispersal on an oceanic island (Alegranza, Canary Islands). *J Ecol* 86:866–871
- Ottichilo WK, DeLeeuw J, Skidmore AK, Prins HHT, Said MY (2000) Population trends of large non-migratory wild herbivores and livestock in the Masai Mara ecosystem, Kenya, between 1977 and 1997. *Afr J Ecol* 38:202–216
- Roemer G, Wayne R (2003) Conservation in conflict: the tale of two endangered species. *Conserv Biol* 17:1251–1260
- Rosalino LM, Santos-Reis M (2002) Feeding habits of the common genet *Genetta genetta* (Carnivora: Viverridae) in a semi-natural landscape of central Portugal. *Mammalia* 65:195–205
- Sanz JJ (2001) Experimentally increased insectivorous bird density results in a reduction of caterpillar density and leaf damage to Pyrenean oak. *Ecol Res* 16:387–394
- Simon J, Bosch M, Molero J, Blanche C (2001) Conservation biology of the Pyrenean larkspur (*Delphinium montanum*): a case of conflict of plant versus animal conservation? *Biol Conserv* 98:305–314
- Soderstrom B, Part T, Linnarsson E (2001) Grazing effects on between-year variation of farmland bird communities. *Ecol Appl* 11:1141–1150
- SPSS (2000) SPSS FOR WINDOWS version 10.0. SPSS, Chicago
- StatSoft (2001) STATISTICA 6.1, StatSoft, Tulsa
- Strong AM, Sherry TW, Holmes RT (2000) Bird predation on herbivorous insects: indirect effects on sugar maple saplings. *Oecologia* 125:370–379
- Tabarelli M, Peres CA (2002) Abiotic and vertebrate seed dispersal in the Brazilian Atlantic forest: implications for forest regeneration. *Biol Conserv* 106:165–176
- Taylor DM (1986) Effects of cattle grazing on passerine birds nesting in riparian habitat. *J Range Manage* 39:254–258
- Telleria JL, Baquero R, Santos T (2003) Effects of forest fragmentation on European birds: implications of regional differences in species richness. *J Biogeogr* 30:621–628
- Temple S A, Brick MF, Paine L, Undersander KDJ, Sample DW (1999) Nesting birds and grazing cattle: accommodating both on midwestern pastures. *Stud Avian Biol* 19:196–202
- Tornberg R, Korpimäki E, Jungell S, Reif V (2005) Delayed numerical response of goshawks to population fluctuations of forest grouse. *Oikos* 111:408–415
- Van Bael SA, Brawn JD, Robinson SK (2003) Birds defend trees from herbivores in a neotropical forest canopy. *Proc Natl Acad Sci USA* 100:8304–8307
- Young TP, Stubblefield CH, Isbell LA (1997) Ants on swollen-thorn acacias: species coexistence in a simple system. *Oecologia* 109:98–107
- Young TP, Okello BD, Kinyua D, Palmer TM (1998) KLEE: a long-term multi-species herbivore exclusion experiment in Laikipia, Kenya. *Afr J Range Forage Sci* 14:94–102
- Young TP, Palmer TM, Gadd ME (2005) Competition and compensation among cattle, zebras, and elephants in a semi-arid savanna in Laikipia, Kenya. *Biol Conserv* 122:351–359
- Zimmerman DA, Turner DA, Pearson DJ (1996) Birds of Kenya and northern Tanzania. Princeton University Press, Princeton