

Ecological Applications, 11(4), 2001, pp. 947–960
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A MAMMALIAN PREDATOR-PREY IMBALANCE: GRIZZLY BEAR AND WOLF EXTINCTION AFFECT AVIAN NEOTROPICAL MIGRANTS

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Abstract. Because most large, terrestrial mammalian predators have already been lost from more than 95–99% of the contiguous United States and Mexico, many ecological communities are either missing dominant selective forces or have new ones dependent upon humans. Such large-scale manipulations of a key element of most ecosystems offer unique opportunities to investigate how the loss of large carnivores affects communities, including the extent, if any, of interactions at different trophic levels. Here, we demonstrate a cascade of ecological events that were triggered by the local extinction of grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*) from the southern Greater Yellowstone Ecosystem. These include (1) the demographic eruption of a large, semi-obligate, riparian-dependent herbivore, the moose (*Alces alces*), during the past 150 yr; (2) the subsequent alteration of riparian vegetation structure and density by ungulate herbivory; and (3) the coincident reduction of avian neotropical migrants in the impacted willow communities. We contrasted three sites matched hydrologically and ecologically in Grand Teton National Park, Wyoming, USA, where grizzly bears and wolves had been eliminated 60–75 yr ago and moose densities were about five times higher, with those on national forest lands outside the park, where predation by the two large carnivores has been replaced by human hunting and moose densities were lower. Avian species richness and nesting density varied inversely with moose abundance, and two riparian specialists, Gray Catbirds (*Dumetella carolinensis*) and MacGillivray's Warblers (*Oporornis tolmiei*), were absent from Park riparian systems where moose densities were high. Our findings not only offer empirical support for the top-down effect of large carnivores in terrestrial communities, but also provide a scientific rationale for restoration options to conserve biological diversity. To predict future impacts, whether overt or subtle, of past management, and to restore biodiversity, more must be known about ecological interactions, including the role of large carnivores. Restoration options with respect to the system that we studied in the southern Greater Yellowstone Ecosystem are simple: (1) do nothing and accept the erosion of biological diversity, (2) replace natural carnivores with human predation, or (3) allow continued dispersal of grizzly bears and wolves into previously occupied, but now vacant, habitat. Although additional science is required to further our understanding of this and other terrestrial systems, a larger conservation challenge remains: to develop public support for ecologically rational conservation options.

Key words: biodiversity; conservation; extinction; Grand Teton National Park; Greater Yellowstone Ecosystem; grizzly bears; moose; neotropical migrant birds; restoration ecology; riparian vegetation; trophic cascades; wolves.

INTRODUCTION

Among organisms conspicuously absent from many of this planet's ecological communities are two types of large mammals. In the Neotropics, sites that otherwise appear virtually intact have been referred to as “empty forests” because of the depletion of game

Manuscript received 2 August 1999; revised 21 March 2000; accepted 3 April 2000; final version received 30 August 2000. For reprints of this Invited Feature, see footnote 1, p. 945.

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(Redford 1992). In western North America, many public lands designated as wilderness lack grizzly bears (*Arctos ursus*) and wolves (*Canis lupus*). Although these carnivores still occur across vast tracts of Asian and North American boreal forests and the Arctic, their localized extinction has been both thorough and swift (within the last 100 yr), to the extent that they are currently absent from 95–99% of their former ranges within the contiguous United States and Mexico (Clark et al. 1999). Despite a few well-publicized natural recolonizations, such as wolves into Glacier National Park (Boyd et al. 1994), most ecosystems and nature

reserves are more likely to lose, rather than gain, large carnivores, irrespective of recent highly publicized efforts such as the restoration of wolves in Yellowstone and central Idaho (Phillips and Smith 1996).

The widespread disruption or total cessation of interactions between large mammalian carnivores and prey species has had numerous consequences, including the local irruption of native and domestic herbivores (McCullough 1997, Sinclair 1998), mesocarnivore release (Crete and Desrosiers 1995, Crooks and Soulé 1999, Terborgh et al. 1999), site-specific changes in prey behavior (Berger 1998, 1999), and, perhaps, the facilitation of Lyme disease at the local level (Wilson and Childs 1997). The scale at which such predator-prey disequilibria have occurred provides exceptional opportunities to learn more about ecological processes (Berger and Wehausen 1991), including the long-standing debate over the role of top carnivores in the regulation of prey populations (Terborgh 1987, Wright et al. 1994), and whether top-down or bottom-up effects play a larger role in biological organization (Paine 1966, Polis and Strong 1996). Although most research on trophic cascades has focused on aquatic or marine systems (Power 1992, Estes et al. 1998), and has involved heterotherms and invertebrates (Spiller and Schoener 1994, Carter and Rypstra 1995), the recent localized, but widespread, extinction of large vertebrate carnivores throughout much of their ranges allows us to examine how predation and food can structure terrestrial communities and how species losses can affect the maintenance of biological diversity.

There is a problem, however. Because so many of this planet's terrestrial systems have already been greatly modified, it is often impossible to find appropriate regions where human and nonhuman effects can be disentangled. For instance, although overabundant elephant populations in Botswana affect avian diversity in woodland habitats (Herremans 1995), the degree to which humans have facilitated these elephant populations is unclear (Gibson et al. 1998). In other areas, including both boreal and neotropical systems, humans and nonhuman predators compete for the same mammalian food base (Gasaway et al. 1992, Jorgensen and Redford 1993), although human patterns of selection may have more important demographic effects on the prey themselves (Ginsberg and Milner-Gulland 1994, Berger and Gompper 1999). From an ecological perspective, however, what may be more critical than knowing about predation per se is understanding the community-level consequences of the removal of predation as a selective force.

In many systems, the speed of ecological change has been accelerated with human intervention (Sutherland 1998). A notable example concerns demographic responses of ungulates to the loss of large carnivores which, in turn, through population irruptions, often affects habitat structure through herbivory-related pro-

cesses (Wagner and Kay 1993, Naiman and Rogers 1997). With increasingly dense prey populations, it is now known that vegetation alterations through browsing also change patterns of habitat selection in neotropical migrant birds (McShea et al. 1995, McShea and Rappole 1997). Because habitat structure is often one of the best predictors of avian diversity (MacArthur and MacArthur 1961, Cody 1974, Wiens 1989, Jackson 1992), the possibility that predation by large mammalian carnivores, or its absence, can affect other components of biological diversity, such as birds, presents serious challenges for restoration and conservation biologists alike.

Our intent here is twofold: first, to assess evidence of top-down effects of large carnivores by considering (1) their influences on a semi-obligate riparian specialist, moose (*Alces alces*), (2) herbivory-related effects of moose on willow community structure, and (3) interrelationships between structural modification of habitat and avian species diversity and abundance; and second, to suggest how our results can bear on the outcomes of different conservation options.

BIODIVERSITY AND THE MOOSE–GRIZZLY BEAR–WOLF SYSTEM AS A MODEL

We used the well-understood moose–grizzly bear–wolf system to explore potential interrelationships between human intervention and trophic levels on long-term patterns that connect carnivores and biological organization. Moose have a circumpolar distribution, occurring from Mongolia and the northern Great Basin Desert throughout boreal, subarctic, and Arctic regions of North America, Europe, and Asia (Franzmann and Schwartz 1998). Moose populations are controlled by predation and, in its absence, by food (Messier 1991, Gasaway et al. 1992, Orians et al. 1997), and they achieve states of relative equilibrium that depend on carnivore abundance (Fig. 1A). Where intact carnivore communities exist, such as in Alaska and the Yukon, predation on moose is intense, with up to 90% of the juveniles being killed annually by grizzly bears and wolves (Gasaway et al. 1992, Bowyer et al. 1998). However, after humans remove bears and wolves, moose population growth is near maximum (Orians et al. 1997). In the relatively unique situation on Isle Royale, Michigan, USA, where only moose and wolves interact, the situation differs because of weather and other factors (Peterson 1999).

Moose may have important localized effects on ecosystems (Pastor et al. 1993, Post et al. 1999), partly because they consume large quantities of woody shrubs and young trees including aspen, willow, and cottonwood, and because they achieve high densities (Houston 1968) that, in riparian zones, may exceed 20 individuals/km² (Fig. 2) for up to 5–6 months per year. In Alaska and the Yukon, moose density is affected by

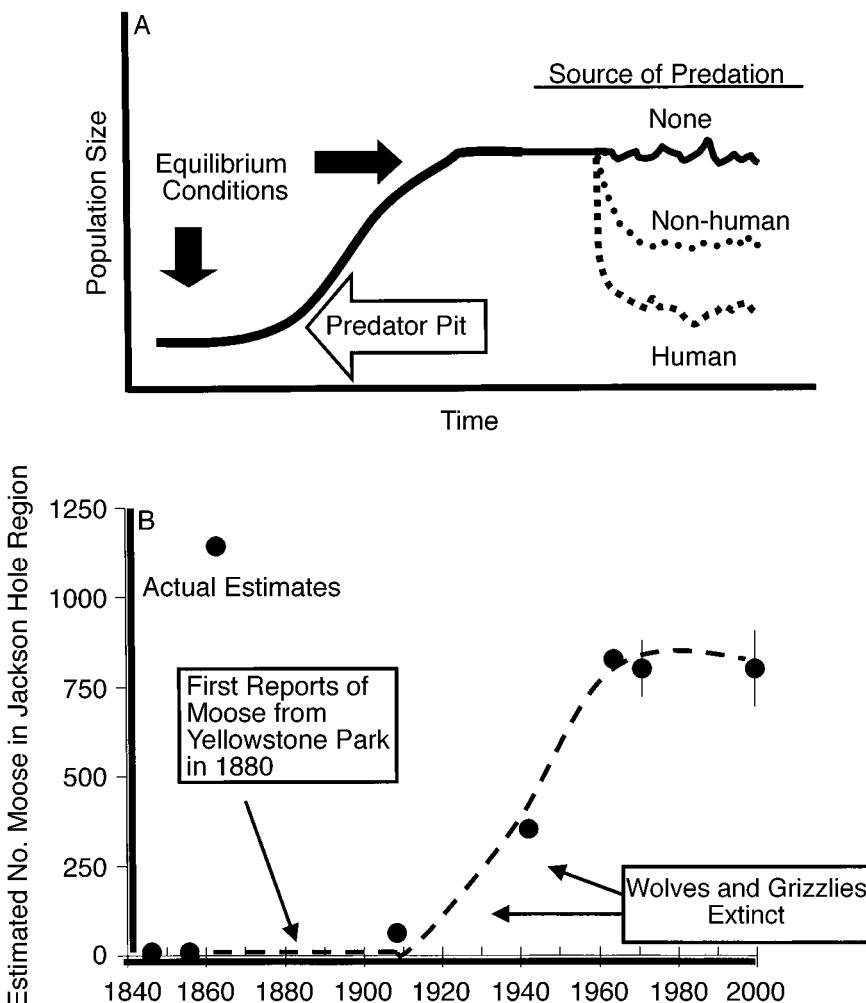


FIG. 1. (A) Conceptualization of moose population states under equilibrium and disequilibrium conditions. Each scenario has been supported empirically (for case studies, see Orians et al. [1997]). (B) Patterns of colonization and general population trends of moose in the Jackson Hole region of the Greater Yellowstone Ecosystem from the 1840s to 1990s in relation to the loss of grizzly bears and wolves. (Source: J. Berger, *unpublished data* from trapper records, historical journals, and Wyoming Department of Game and Fish files. Solid circles reflect estimates from the literature.)

predation (see Fig. 1A), but not in many areas of the Rocky Mountains where large carnivores are extinct.

The moose–grizzly–wolf system has critical advantages that make it useful as a model for exploring issues related to biodiversity and conservation. First, these two predators influence moose populations in the absence of humans (Gasaway et al. 1992), and, thus, their loss has resulted in substantial demographic change (Ballard and Van Ballenberghe 1998). Both species prey on adult and juvenile moose, with the bear being more of a specialist on calves (Gasaway et al. 1992). Although the cessation of Native Americans as major predators (Kay 1994a, b) of moose also corresponds, at a broad level, to the localized extinctions of these two carnivores, from a demographic point of view, moose populations increase when grizzly bears and wolves are reduced or absent (Boertje et al. 1996).

Second, when released from predation pressure (Fig. 1), native species, including cervids other than moose, may achieve extraordinarily high densities (Alverson and Waller 1997, Schmitz and Sinclair 1997). Although domestic species may severely impact sensitive habitats (Knopf and Cannon 1982, Kauffman and Krueger 1984, Belsky et al. 1999), little is known about the effects of colonizing native browsers such as moose. This is a particularly critical issue in riparian systems because, in arid zones like the American West, these areas represent <1% of the total area but may contain up to 80% of the local avian diversity (Ohmart 1994, Stacey 1995, Dobkin et al. 1998). Additionally, at a local scale, abundant herbivores like elk may affect avian diversity through structural effects on vegetation (Jackson 1992). It seems reasonable to expect not only that intense herbivory might affect riparian biodiver-

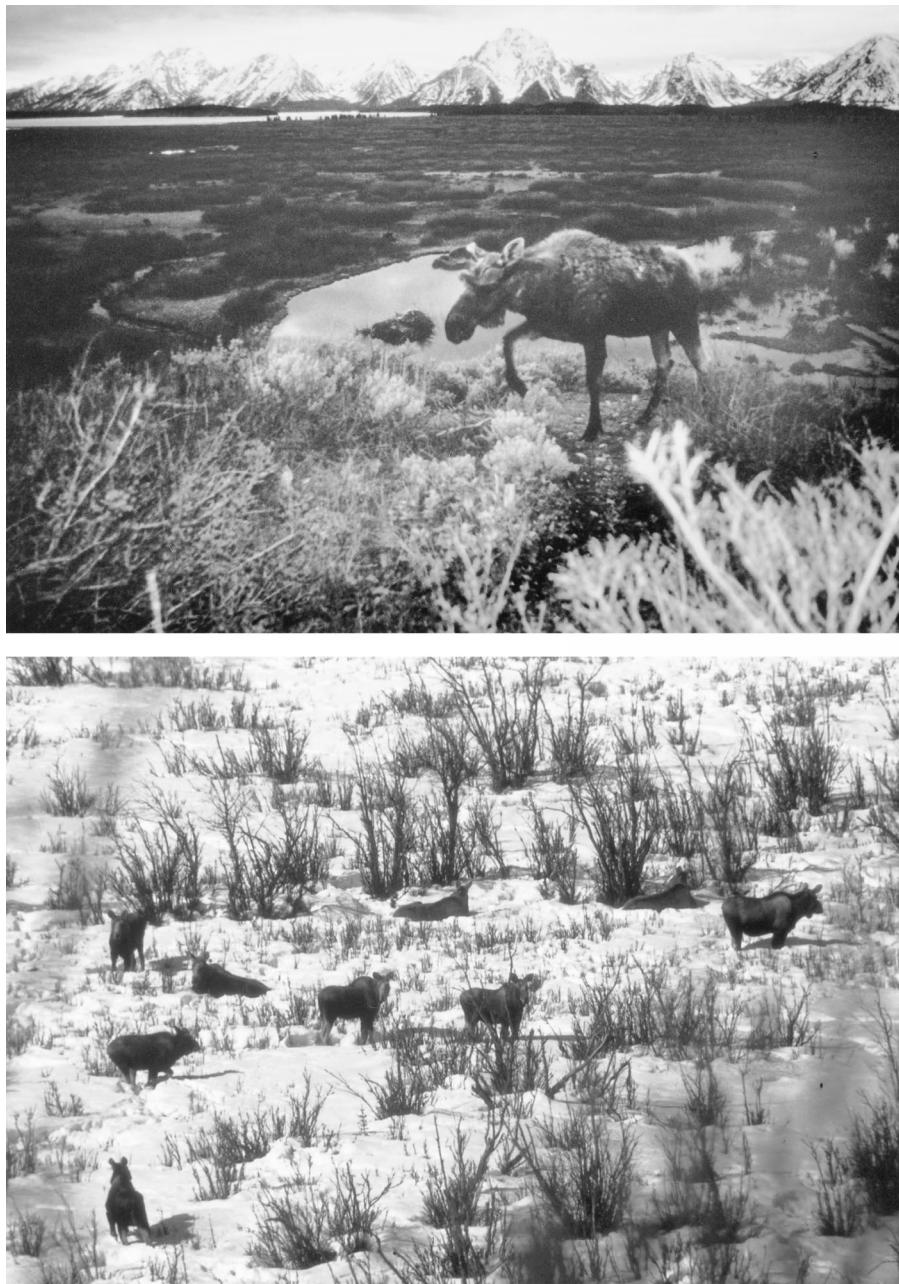


FIG. 2. Top: moose and riparian zones in Grand Teton National Park. Bottom: nine of a group of more than 30 moose in a riparian zone (April 1995).

sity, but also that the moose–grizzly bear–wolf system holds promise to further knowledge about biological organization as it may relate to large carnivores and terrestrial community dynamics.

HISTORY, BACKGROUND, AND STUDY AREA

We studied interactions among moose populations, the structure of their major winter food supply in riparian zones, and avian species diversity in Grand Teton National Park (GTNP) and adjacent public lands

managed by Bridger-Teton National Forest (BTNF) in the Jackson Hole region of Wyoming. Wolves have been extinct in this system since the 1930s (J. Craighead and F. Craighead, *personal communication*), and grizzly bears have not been known at either of our study areas since 1936 or earlier (Hoak et al. 1981).

During the 1800s, moose were rare in much of western North America (Karns 1998), and 150 yr ago they were absent from the Jackson Hole region at the center of the Greater Yellowstone Ecosystem (GYE). Moose

appeared from the north, their existence first being noted in Yellowstone Park in the 1880s (Schullery and Whittlesey 1995). With the reduction of wolves and grizzly bears and the absence of significant predation by Native Americans, moose populations irrupted (Kay 1994b). Based on data from Houston (1968), current local moose densities and population size in the Jackson Hole area appear to have reached a plateau, and have remained relatively stable for about the last 30 yr, a pattern characteristic of populations that reach demographic ceilings (Fig. 1B).

The two primary types of federal lands (GTNP and BTNF) that exist in Jackson Hole are managed very differently. On BTNF lands, moose are subject to human harvest; between 1971 and 1991, >10 800 were killed (Houston 1992). In contrast, GTNP moose are not managed, and this fundamental difference in federal policy has resulted in variation in moose density.

Moose depend upon willow as a primary food source during winter (Peek 1998). If populations in GTNP have reached the point at which food is limiting, then riparian vegetation may be altered more when moose occur at high densities than when they are controlled by predation (whether by humans or natural carnivores). Alternatively, moose may have little, if any, impact on riparian vegetation.

We evaluated these possibilities by contrasting effects of moose herbivory on riparian willow communities, using three areas within GTNP (with no human or natural predation for ~60 yr) and three similar sites in BTNF (where human hunting has replaced that by native carnivores). Moose wintering densities varied by about five times as a consequence of the different management regimes (mean density is 5.2 individuals/km² at GTNP sites and 1.1 individual/km² at BTNF sites). Thus, our treatment was predation (absent or present), with each area containing three replicated riparian communities, all matched with the following characteristics: (1) willow riparian habitat lacking cottonwood, spruce and aspen gallery forests; (2) major willow species being Wolf's (*Salix wolffii*), Geyers (*S. geyeriana*), and Booth's (*S. boothii*); (3) wet meadow species composition dominated by willow spp., sedges, and grass; (4) some standing water with evidence of wetland histosol soils and a lack of rodent burrows and tunnels; (5) situated in different drainages; and (6) watersheds within a 25 km radius of, and flowing into, the Snake River. The specific sites for the "Predation" treatment (all in BTNF), were: Grey's River (43°03.370' N, 110°49.420' W), Fall Creek (43°20.990' N, 110°49.649' W), and Ditch Creek (43°41.502' N, 110°34.814' W). For the "No Predation" treatment (all in GTNP), sites were: Triangle X (43°47.139' N, 110°33.179' W), Pacific Creek (43°52.394' N, 110°29.256' W), and Buffalo Fork (43°50.303' N, 110°29.276' W).

METHODS

Sampling

Vegetation.—Our sampling occurred during spring and summer 1998. At each site we measured vegetation height, volume, and structure using three 100-m transects, ≥200 m apart. Twenty 1 × 1 m plots per transect were selected using a random number table, 10 plots situated on each side of the transect line. Vegetation type, percent cover, height, and vertical structure were recorded at each 1 × 1 m plot. For each vegetation/ground cover type (water, bare ground, grass and sedge, herbs, willows, and other shrubs), percent cover and four height categories (0–0.5 m, 0.5–1 m, 1–2 m, and ≥2 m) were recorded. Canopy volume at each height category was estimated by the "stacked-cube" method (Kus 1998) by placing PVC pipe on the ground to map quadrat boundaries and then by connecting lengths of the PVC to enclose the vertical cover. Willow volume was the product of density and cover. We gauged browsing intensity by recording in each plot the proportion of willow stems >10 mm in diameter that were either browsed or unbrowsed, and either alive or dead.

Birds.—Nesting densities were estimated using spot-mapping techniques (Ralph et al. 1993). Briefly, two observers slowly walked along the vegetation transects and recorded all birds perched or singing within 50 m of the transect line. The location of each bird was recorded on maps, and behaviors were noted, as well as the presence or absence of a second bird or young. Three censuses at each transect were conducted during the breeding season (15 May–1 July) between sunrise and 1100, with a minimum interim of 7 d between sampling.

To derive spatial configurations, convex polygons were drawn around all observations of the same species at the same general location on different dates. A second polygon was then drawn around the mapped locations of all individual species, this area being that which was actually surveyed during the census. The resulting data provided evidence of both presence/absence for each species, and relative density (e.g., three territories within a surveyed area of 1200 m² = 0.25 pairs/100 m²). This approach has been used to estimate avian densities in riparian zones (e.g., Ammon and Stacey 1997), and it enabled us to calculate species diversity (both richness and evenness) within the surveyed regions.

Moose.—Our starting premise, that predation release of moose has occurred with the localized extinction of wolves and grizzly bears, would be untrue if other carnivores prey on moose. Although these two carnivores were absent, both black bears (*Ursus americana*) and pumas (*Felis concolor*) were not, and they are capable of killing moose (Ballard and Van Ballenberghe 1998). If black bears and pumas prey on moose, juvenile recruitment could be affected. Without investigation, this

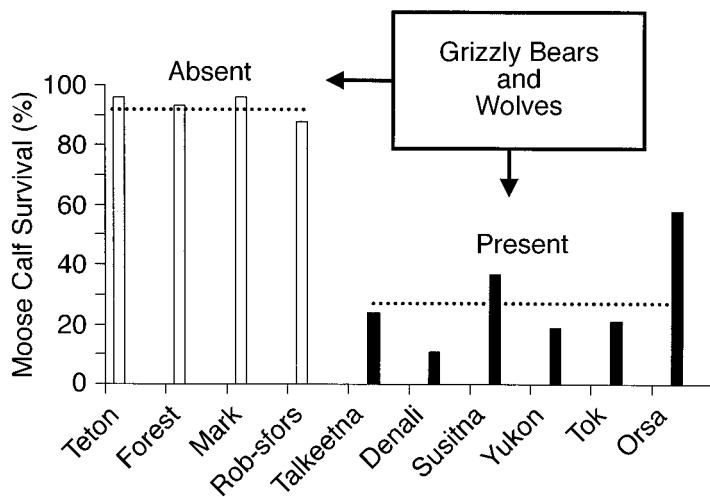


FIG. 3. Contrasting effects of the presence and absence of grizzly bears and wolves on moose calf survival at sites in Alaska, Canada, Norway, and the southern Greater Yellowstone Ecosystem in Wyoming. Dotted lines indicate mean survival. Sources (in order from left to right) are: Berger et al. (1999), Swenson et al. (1999), Testa (1998), Bowyer et al. (1998), Ballard et al. (1991), Larsen et al. (1989), and Gasaway et al. (1992).

would render impossible any conclusions about whether predation had (or had not) been relaxed with the loss of grizzly bears and wolves.

We examined this issue by using two analyses to evaluate whether the local extirpation of wolves and grizzly bears affected juvenile recruitment. First, we contrasted patterns of juvenile survival at sites with and without grizzly bears and wolves. Second, because food and other factors also affect juvenile survival, we assessed pregnancy rates. Pregnancy and other correlates of fecundity are useful indices of food quality and quantity (Franzmann and Schwartz 1985, Gasaway et al. 1996). We relied on fecal metabolites (Montfort et al. 1993) to assess pregnancy in radio-collared moose from 1995 to 1997, and we subsequently followed the fates of neonates from known mothers. This procedure enabled us to assess not only whether a recruitment failure occurred, but also whether it might have arisen as a consequence of reduced pregnancy rates or other factors. Details of laboratory and field protocols are provided in Berger et al. (1999).

Analyses.—Effects of predation treatment on both vegetation and avian parameters were examined by general linear models (Norusis 1997) with transect nested within site (i.e., a repeated measure), or a two-way repeated-measures ANOVA to evaluate two-dimensional vegetation profiles. The number of observations in our data set was 18 (two treatments, three sites for each, and three transects per site), but for all comparisons in this nested design, the degrees of freedom were one (treatment) and four (site). Pairwise posthoc multiple comparisons were conducted with Duncan's Multiple Range Test, with similar groupings denoted by the same letter and contrasting ones ($P < 0.01$) with different letters.

RESULTS

Assumptions and their tests

Prior to interpreting our empirical data from the field, we made two important assumptions about the effects

of large carnivores on moose. First, predation is relaxed after the extinction of wolves and grizzly bears. Second, after release from predation, populations will approach or exceed an ecological food ceiling. If these assumptions are supported, then it seems reasonable to expect that other levels of biological organization may be affected by the loss of these two carnivores.

Predation is relaxed.—Although grizzly bears were not entirely extirpated from Grand Teton National Park, they were highly restricted to northern portions, where densities were extremely low and verified observations averaged less than one every three years (Hoak et al. 1981). Most importantly, they did not occur at our specific study sites. Wolves were extirpated in the 1930s (Fig. 1), and only in 1998 did dispersal from Yellowstone National Park result in some recolonization into the Tetons and other areas of Jackson Hole (J. Berger, *unpublished data*).

If the local extinction of grizzly bears and wolves had an impact on moose, then differences in juvenile survival should have existed between areas where these carnivores were present and absent. If, however, mesocarnivores such as black bears and pumas killed moose at roughly similar rates, or other factors compromised juvenile survival, then it would be difficult to argue that predation has been relaxed. However, the available data support the premise that grizzly bears and wolves have major impacts on neonatal moose survival, and that their loss results in a threefold increase in mean neonate survival (Fig. 3).

In absence of predation, herbivore populations approach or exceed ecological capacity.—Abundant literature supports the idea that ungulate populations experience density dependence, particularly in the absence of predation (Clutton-Brock and Albon 1989, Sinclair 1995). However, because species including moose may respond differently to varied ecological conditions or reduced predator densities (Peterson 1999), it is important to assess the evidence with re-

TABLE 1. Summary of vegetation contrasts involving browsing intensity on willow communities at sites with and without predation on moose.

Willow status	Predation on moose		<i>F</i>	<i>P</i>
	Human	None		
Alive, not browsed	0.53 (0.15)	0.10 (0.11)	18.56	<0.0001
Alive, browsed	0.22 (0.15)	0.59 (0.10)	7.73	<0.0025
Dead, not browsed	0.12 (0.07)	0.01 (0.01)	13.74	<0.0002
Dead, browsed	0.13 (0.08)	0.29 (0.09)	5.04	<0.0128

Note: Mean values (and 1 SD) reflect proportions ($N = 360$).

spect to GTNP moose. Although we cannot directly test whether moose in GTNP are at or above their food supply, pregnancy rates can be used as a surrogate measure that reflects body condition, which, in turn, is directly related to the food supply (Franzmann and Schwartz 1985).

First, we examined changes in pregnancy as a function of time. If food were limiting, then pregnancy rates should decline over time. The evidence is consistent with this interpretation; pregnancy rates dropped as the population apparently stabilized (Fig. 1B), from ~90% in 1966 ($N = 41$; Houston 1968) to 75.5% in 1997 ($N = 49$; Berger et al. 1999), a change that approaches significance ($G_{adj} = 3.36$; $P < 0.10$). Second, populations below a “food ceiling,” that is, in a growth phase, tend to have relative high pregnancy rates. However, the current pregnancy rate (~75%) for GTNP moose is comparatively low, and it ranks in the bottom 85th percentile of North American populations (Berger et al. 1999). Hence, the low pregnancy rates in GTNP may be a consequence of populations released from predation and currently occurring at high densities.

Riparian willow communities and moose density

As previously indicated, moose densities varied, being almost five times higher in the absence of predation (GTNP) than on adjacent forest lands where predation by humans occurred (mean density was 5.2 individuals/km² at GTNP sites and 1.1 individuals/km² at BTNF sites). No details are available on the degree of similarity between willow communities in Grand Teton National Park and adjacent forest lands prior to moose

irruptions. We assumed, however, that because other large-bodied browsers were absent from these riparian systems, willow structure was comparable.

Did vegetation at local sites that varied in moose density also differ? Areas that varied in predation treatments differed significantly in both mean willow height and density ($F_{5,17} = 7.95$, $P < 0.01$; $F_{5,17} = 8.43$, $P < 0.01$, respectively). Where moose densities were limited by humans, willows were taller (2.17 ± 0.32 m, $\bar{x} \pm 1$ SD) and their percentage of volume was greater ($0.72 \pm 0.05\%$) than in areas lacking predation (1.77 ± 0.45 m and $0.63 \pm 0.09\%$, respectively). Additionally, the proportion of willow stems >10 mm that were browsed, and either alive or dead, was also associated with moose density (Table 1). These results substantiate that moose density affected vegetation.

Predation treatment also affected vegetation structure through influences on vegetation height categories, VHC (Tables 2 and 3). At both the ground level, where heavy winter snowfall reduces willow availability, and in the vegetation canopy above which moose regularly feed, differences in the proportion of browsed willow stems were not detectable (Table 3). However, at intermediate vegetation layers, moose densities had dramatic effects on the proportion of browsed willows (Table 3). These data suggest that (1) treatment effects were robust; and that (2) our measures are consistent with predictions about VHC as a bioassay of browsing-related herbivory. Our findings that variation in moose density failed to produce browsing-related differences between treatments for both the ground and top vegetation layers, but not at intermediate sites within the willow canopy, reinforce the idea that moose per se, rather than other factors, were responsible for the observed variation.

TABLE 2. Statistical summary of effects of moose browsing (proportion of stems browsed relative to total available) in riparian willow communities at sites in different drainages within 25 km of the Snake River in northwest Wyoming.

Sources of variation	df	MS	<i>F</i>	<i>P</i>
Predation	1	0.190	23.44	0.0001
Site	4	0.074	9.11	0.0001
VHC	3	2.484	307.09	0.0001
Site \times VHC	3	0.060	7.41	0.0003
Error		0.008		

Note: The table presents results of two-way repeated-measures ANOVA of the effects of predation (present/absent) and study site on vegetation height categories (VHC).

TABLE 3. Duncan's grouping examining the effects of predation (present/absent) on moose browsing at designated vegetation height categories.

Predation	Vegetation height category (m)			
	0–0.5	0.5–1	1–2	2+
Present	a	b	c	e
Absent	a	c	d	e

Note: Different letters indicate significant differences at $P < 0.01$.

TABLE 4. Summary of mean migrant breeding bird densities per 100 × 100 m transect at riparian sites differing in moose densities, with predation on moose as the treatment.

Species	No. bird pairs/ha			
	Human predation on moose	No predation on moose	F	P
Calliope Hummingbird (<i>Stellula calliope</i>)	2.00 (0.87)	0.22 (0.44)	10.67	0.0004
Willow Flycatcher (<i>Empidonax traillii</i>)	0.78 (0.44)	0.55 (0.53)	2.40	0.0994
Gray Catbird (<i>Dumetella carolinensis</i>)	0.88 (0.92)	0.00 (0)	5.12	0.0096
Yellow Warbler (<i>Dendroica petechia</i>)	3.78 (0.97)	2.33 (1.00)	3.21	0.0453
Wilson's Warbler (<i>Wilsonia pusilla</i>)	0.11 (0.33)	0.67 (0.87)	1.86	0.1760
Yellowthroat (<i>Geothlypis trichas</i>)	0.00 (0)	0.11 (0.33)	1.00	0.4582
MacGillivray's Warbler (<i>Oporornis tolmiei</i>)	0.22 (0.44)	0.00 (0)	0.80	0.5705
Black-headed Grosbeak (<i>Pheucticus melanocephalus</i>)	0.77 (0.44)	0.22 (0.44)	3.00	0.0552
Song Sparrow (<i>Melospiza melodia</i>)	1.67 (0.70)	1.11 (0.93)	3.91	0.0245
Fox Sparrow (<i>Passerella iliaca</i>)	0.44 (0.53)	0.11 (0.33)	0.85	0.5405
Lincoln's Sparrow (<i>Melospiza lincolni</i>)	0.22 (0.44)	0.66 (0.71)	0.91	0.5038
White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	0.00 (0)	0.55 (1.13)	0.82	0.5612

Avian species diversity and willows

To determine whether moose density was also associated with the distribution or abundance of the riparian avian community, we used five assessments of avian distribution and abundance (Table 4). All were similarly affected by moose density, with each being statistically greater where moose densities were regulated by predation: (1) species richness of breeding birds ($N = 23$ vs. 18; $F = 14.44$, $P < 0.003$); (2) nesting density ($F = 7.78$, $P < 0.002$); (3) Shannon's diversity index ($F = 13.10$, $P < 0.004$); (4) Hill's Diversity measure 1 ($F = 10.30$; $P < 0.008$); and (5) Hill's Diversity Measure 2 ($F = 7.10$; $P < 0.021$). Where moose densities were high, the nesting density of many migrants including Willow Flycatchers, Calliope Hummingbirds, Yellow Warblers, Fox Sparrows, and Black-headed Grosbeaks was substantially reduced (Table 4). Two other species, Gray Catbirds and MacGillivray's Warblers, were absent. Overall, ~50% of the riparian willow bird species were reduced or absent from sites inside GTNP where moose were protected from predation and thereby attained high local densities. The fact that typical riparian species were present at all sites (e.g., Yellow and Wilson's Warblers; see Table 4 for others) substantiates that the samples were derived from the same ecological pool.

At a more refined scale, we asked whether levels in the willow canopy were differentially affected by moose density and whether they, in turn, influenced either avian richness or density. Thus, these two measures were contrasted between the species guilds that nest primarily near the ground (GR: Gray Catbirds and the four species of sparrows) and those that nest above ground (AG: Calliope Hummingbird, Willow Flycatcher, all warblers, and Black-headed Grosbeak). Because our sample sizes were further subdivided, our results are qualitative only. For AG, mean richness was greater at low than at high moose density (4.0 vs. 2.3 species), as was also the case in all other contrasts (AG density was 7.1 vs. 4.1 pairs/10 000 m², respectively; GR rich-

ness was 2.2 vs. 1.5 species; GR density was 3.2 vs. 2.4 pairs/10 000 m² for low vs. high moose density). Notable, however, is that the apparent magnitude of differences due to moose density was less in ground nesters, as would be expected given the lack of significant herbivory-related effects at ground level relative to higher levels in the canopy (Table 3). Overall, species richness and density were reduced to a greater extent in AG than in GR, patterns that are consistent with the idea that moose browsing at higher densities negatively impacts neotropical migrants.

Although these data suggest that moose browsing shaped avian communities at a microgeographical scale, the link between the structural modification of riparian willows at our sites and avian diversity had been uncertain. A direct relationship between willow volume (mean using the proportion of live willow stems) and avian species diversity (Y) existed, although much variance remains unexplained ($Y = 0.51X + 0.33$, $n = 18$, $r^2 = 0.24$; $P < 0.03$). Nonetheless, it appears that avian species diversity is partially affected through structural modifications of the willow canopy by moose whose densities, in turn, are controlled at our study areas by humans, either by total protection (park) or hunting (national forest lands).

DISCUSSION

Large herbivores and trophic cascades.—Our finding that large herbivores affect both riparian vegetation and associated avian communities is not entirely novel; somewhat similar relationships have been detected at sites grazed by domestic livestock (Dobkin et al. 1998, Sanders and Edge 1998, Skagen et al. 1998). However, what differs about our results is that they are based on the irruption of a native, rather than an introduced, species, a browser, after natural predators were removed from the system. Still, in today's highly modified world, the detection of indirect effects stemming from human actions, including the loss of carnivores, and those of other processes has become increasingly

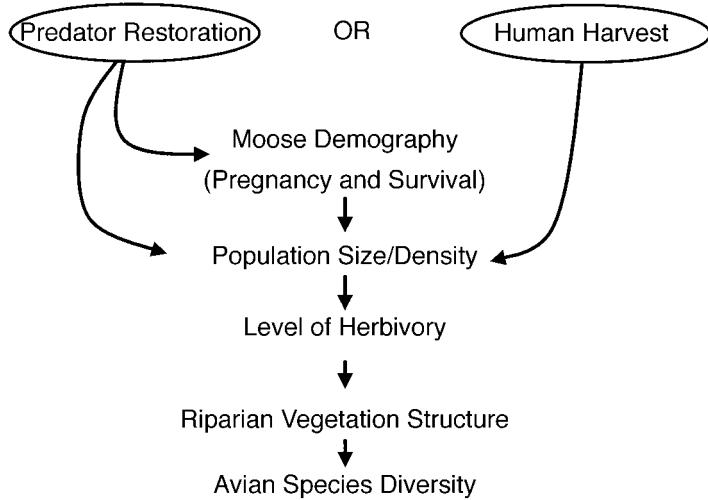


FIG. 4. Overview of conservation options and the linkages among biological tiers of organization in a terrestrial ecosystem with large carnivores.

difficult. For instance, where large, terrestrial carnivores have been extirpated, one consequence has been the release of herbivores, with concomitant habitat alterations (Wagner and Kay 1993, Kay 1994b, McShea and Rappole 1997). However, factors other than the loss of carnivores, such as climatic change and fire, confound straightforward analyses (Houston 1982, Singer et al. 1998, Boyce and Anderson 1999).

Our analyses, which focused exclusively on areas within the Jackson Hole area of the Greater Yellowstone Ecosystem, support the idea that a dynamic chain of interactions involving multiple tiers of biological organization were set in motion some 60–100 yr ago, principally by the removal of large predators (Fig. 4). Among the key events were: (1) human decisions to exterminate large carnivores, especially wolves (Murie 1940, Phillips and Smith 1996), but also grizzly bears (Craighead 1979) in Yellowstone Park per se and in adjacent regions; (2) a resultant growth of an apparent low-density moose population (Fig. 1) that, although it began expanding from 1880 to 1910, irrupted partially due to a dampened effect on juvenile mortality (Fig. 3); (3) increasing herbivory in riparian willow communities at sites lacking predation or hunting (Table 1); (4) structural modification of these communities (Tables 2 and 3); and (5) decreased avian richness and diversity (Table 4).

Although the idea of top-down regulation of communities by carnivores, especially in complex terrestrial ecosystems, has been both attractive and controversial (Polis and Strong 1996), our data offer support for its importance at least in *this* system. In other terrestrial regions, the plausibility of trophic cascades has been noted, as have confounding variables that cloud the interpretation for top-down regulation. For example, jaguars may or may not regulate mammalian herbivores in the Neotropics (Terborgh 1987, Wright et al. 1994), but the nature of comparative evidence from

geographically disparate sites without adequate replication limits broad generalization (Terborgh et al. 1999). In temperate boreal systems, where at least one long-term data set is available, the evidence is stronger, in that wolves affect moose that subsequently limit productivity of fir trees (Post et al. 1999). However, many of the studies that target community regulation by terrestrial carnivores have not considered bottom-up effects (Boyce and Anderson 1999) or questioned the role of potentially confounding variables.

Alternative hypotheses and potential confounding variables.—Although we argue that the loss of large, terrestrial carnivores eventually caused a loss in biodiversity (Fig. 4), other factors may be involved and may account for the differences in the avian communities in riparian areas where there is, or is not, predation on moose.

1. *Climate or local weather conditions could vary between study regions.*—Although explanations along these lines have been used to suggest possible causal links for elk population changes through time in Yellowstone's Lamar Valley or the loss of riparian vegetation (see Krausman 1998), these do not apply to our study system. Our sites were all situated in drainages within a 25 km radius of the Snake River, they were independent of each other at the scale at which we worked, and all have experienced similar edaphic, hydrological, and weather conditions.

2. *Microhabitat variation in willow community structure could exist.*—This is a clear possibility, although we suspect that it is not a strong one, because study areas were matched for additional characteristics including the lack of both conifer and deciduous tree canopies, the amount of edge and adjacent habitats, and a minimum of roads and human disturbances. In addition, all sites shared the same basic suite of riparian bird species. Nevertheless, our data on avian species diversity were based on a single year; additional mul-

tiyear monitoring will be necessary to affirm our initial findings.

We presume, but do not know, that differential use of willows by moose in Grand Teton National Park may have begun around 1950, which is when the Park was expanded to cover areas that included our riparian zone study areas. Although moose populations in Jackson Hole were already in an exponential phase of growth by 1950 (Fig. 1A), human harvesting of moose on adjacent national forest was still occurring. There is no reason to expect that moose density was not in the process of changing between areas of total (park) protection and areas with human hunting. In essence, it seems more likely that variation among willow communities was due to differential herbivory and not microgeographical variation.

3. Predation by humans and predation by nonhumans have different demographic consequences.—There is no doubt truth in this premise, and no reason to expect that moose cannot also be affected. For instance, males and females of sexually dimorphic ungulates (including moose) not only respond differently to types of predation but also select different habitats and may even consume foods that vary in quality (Clutton-Brock et al. 1982, Miquelle et al. 1992). Life history or behavior responses may also vary with predation intensity and degree of past selection (Cheney and Seyfarth 1990, Berger 1991). For example, with the relaxation of predation for ~10 generations, moose no longer responded to Ravens, which typically associate with grizzly bears and wolves. At sites where these predators were not extirpated, however, moose were highly responsive (Berger 1999). Nonetheless, despite notable differences in the age and sex of ungulate prey taken by human vs. nonhuman hunters (Ginsberg and Milner-Gulland 1994), the fact remains that for moose and other species, harvesting by humans results in striking reductions in population density (Crete 1987, Cederlund and Sand 1991).

Three points bear on this issue with respect to moose in the southern Greater Yellowstone Ecosystem. First, wolves and grizzly bears are capable predators of moose (Ballard and Van Ballenberghe 1998), but in the absence of predation (whether by humans or nonhumans), moose populations increase rapidly and attain relatively higher densities (Gasaway et al., 1992, Orians et al. 1997). Second, densities in the Jackson Hole area have been mediated either through total protection (e.g., park) or through human predation (on adjacent national forest lands). Third, as shown in this study, levels of herbivory in riparian zones are affected by moose density.

4. Herbivory-related effects may have been due to ungulates other than moose.—Although this possibility also exists, it is unlikely. First, despite controversy over the effects of elk (*Cervus elaphus*) browsing on willows in Yellowstone National Park (Singer et al. 1994), there

has been little evidence of elk at our GTNP study zones during winter over the last 40 yr (Houston 1968, 1992; J. Bohne and G. Frahlick, *personal communication*), although exceptions exist. For instance, during the five winters from 1995 to 1999, 30–50 elk spent about six weeks in 1997 at one of the GTNP study areas. However, even this number of elk represented <5% of the available ungulate biomass during that winter, and <1% during the other four winters (J. Berger, *unpublished data*). The other major ungulates in the Greater Yellowstone Ecosystem (bison, *Bison bison*; mule deer, *Odocoileus hemionus*; pronghorn, *Antilocapra americana*; and bighorn sheep, *Ovis canadensis*) use different habitats than do moose. Second, feeding grounds provide alternate foods (alfalfa pellets, primarily) during winter, and these concentrate and sustain a large (<15 000–20 000) elk population (Boyce 1989). This type of management by humans has resulted in a de facto release of winter herbivory by elk in the riparian sites that we studied. Thus, we have not observed the competitive displacement of moose by elk that has apparently occurred in Yellowstone National Park when elk densities are sufficiently high (Tyers 1996, Singer et al. 1998). Hence, it is likely that the effects on vegetation and bird communities that we report here were attributable to moose and not to other ungulates.

Conservation options within the context of large carnivores, biodiversity, and public lands.—It is ironic that, in a protected area such as GTNP, where the intent has been to enhance biological diversity through hands-off management, the opposite has occurred. Protection, after the localized extinction of large carnivores, has resulted in the decline of avian taxa within the protected boundaries; in contrast, lands outside the park have involved multiple uses (administered by the USDA Forest Service), where the active management of wildlife has resulted in greater levels of diversity (Table 4). Although grizzly bears and wolves, until very recently, have also been extinct on much of the national forest lands adjacent to Jackson Hole, moose have been controlled in these regions, as is evident by the harvest of >10 000 animals during a 20-yr period (Houston 1992). Upon closer inspection, however, it is probably not uncommon that subtle, but ecologically important, changes in landscapes occur, even after complete protection. National parks in western North America are good examples because, despite protection that can be traced to a century or longer, numerous species extinctions still occur (Newmark 1987) and ecological processes are altered in the absence of management.

Where restoration is an active goal, a hands-off policy may be inadequate. As our data show, a cascade of events triggered by the loss of large carnivores can lead to changes at multiple trophic levels, including a diminution in avian diversity. Nevertheless, in the absence of detailed biological information, options for ecological restoration both in the southern Greater Yellow-

stone Ecosystem and elsewhere (Boyce 1998, Sinclair 1998) will continue to depend largely on guesswork or local politics. This emphasizes the need for administrative support in many parks for the acquisition of baseline data and the performance of credible science (Wagner et al. 1995).

Our data, although specific to a system in the Rocky Mountains, offer a basis to guide future conservation planning and action. Where conservation objectives are to maintain or promote biotic diversity, several options exist (Fig. 4). The first is to reintroduce or to allow continued dispersal of large carnivores into previously occupied, but now vacant, habitat. This currently is occurring in formal recovery areas, for both grizzly bears and wolves, although localized conflicts involving livestock management on public lands complicate the restoration process (Niemeyer et al. 1994, Mattson et al. 1996). On lands outside of U.S. national parks, for instance, hunting for large herbivores by the public entails access to areas where recovering carnivores may inadvertently (or purposefully) be shot. A relationship also exists between carnivore mortality and road density (Mattson et al. 1998). Yet, there is also some promise. In areas of the Canadian Rockies, aspen regeneration may be occurring because of the reduction of elk by wolves (White et al. 1998). Nevertheless, effects of carnivores on abundance of prey species are likely to vary from area to area; what occurs in Canada may not apply to the Greater Yellowstone Ecosystem.

Where wolves and moose co-exist, elk are the primary prey of wolves, but whether wolves or grizzly bears or some synergistic effect of these two large carnivores will ultimately reduce moose population density in GTNP remains unknown. One step in garnering opportunities to examine a longer term role of top carnivores in terrestrial ecosystems, irrespective of locality, will require continually educating the public, both within local regions of carnivore reintroduction and at broader geographical levels (Smith et al. 1999).

A second, and perhaps equally controversial, option for the restoration of naturally functioning ecosystems might be to replace patterns of carnivore predation by human control actions (Fig. 4), a practice that we believe should be directed at a broader spectrum of the prey population and less at trophy males per se. Clearly, this option does nothing to facilitate the restoration of large carnivores, but it does raise a practical means by which to look beyond carnivores per se and to consider instead how carnivores may be represented as major agents of change at a landscape level.

However, the mere suggestion of human harvest is controversial, particularly when a desired vegetation condition can be considered arbitrary (Boyce 1998, Kay 1998). Additionally, humans and carnivores often hunt very differently, particularly with respect to the sex and age of their prey (Ginsberg and Milner-Gulland 1994, Berger and Gompper 1999). If humans are to

simulate the predation practices of nonhuman carnivores, then serious consideration of how prey harvesting by humans should proceed will be necessary. If the goal is merely density reduction of ungulates without regard to juvenile recruitment, population trajectories, or how or where the sexes segregate (Bowyer et al. 1996), then the status quo may be acceptable. We suspect that some intermediate practice between these two strategies will be the most appropriate.

Finally, one can do nothing. If this latter path is preferred, our results suggest that there may be a continued *de facto* erosion of avian diversity due to multiple cascades of the effects of past manipulations at different trophic levels. The extent to which such change may apply to other taxa awaits further investigation.

ACKNOWLEDGMENTS

We thank the following people and agencies for support: J. Bohne and D. Brimeyer (Wyoming Department of Game and Fish), S. Cain and R. Schiller (National Park Service), W. Weber and J. Robinson (Wildlife Conservation Society, WCS), and the Universities of Nevada and New Mexico. Funding was provided by the Denver Zoological Foundation, the National Science Foundation, and WCS. We greatly appreciate the insights and critical comments of J. H. Brown, S. Cain, C. Cunningham, D. Finch, B. Kus, D. Ligon, B. Miller, R. Noss, K. Redford, F. Wagner, and an anonymous reviewer.

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