

## COMPETITIVE RELEASE IN DIETS OF OCELOT (*LEOPARDUS PARDALIS*) AND PUMA (*PUMA CONCOLOR*) AFTER JAGUAR (*PANTHERA ONCA*) DECLINE

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We used fecal analyses to document the diet of ocelots (*Leopardus pardalis*) and puma (*Puma concolor*) at 2 sites in central Panama. We detected puma on Barro Colorado Island (BCI) nearly every month during the study but never found evidence of jaguars (*Panthera onca*) at either site. Both ocelots and puma fed predominantly on mammalian prey, but consumed a diversity of species. Collared peccaries (*Pecari tajacu*) and Central American red brocket (*Mazama temama*) were the most important food items for puma, whereas Central American agoutis (*Dasyprocta punctata*) and sloths (*Choloepus hoffmanni* and *Bradypus variegatus*) were the most important for ocelots. Considerable overlap in diet was found between populations and species, but the diet of puma on BCI was significantly different from the 2 ocelot populations in containing more large prey, suggesting that dietary differences between these predator species are chiefly related to their relative body size. Comparing across larger scales, both populations of ocelots in our study ate larger prey than elsewhere in their range, suggesting that their fundamental niche includes more medium-sized prey than their realized niche in other sites. Puma on BCI ate proportionally more peccaries and deer than in most other populations. These unusual diets in the wake of a recent decline or local extinction of jaguars are consistent with a prey shift in response to competitive release.

Key words: Barro Colorado Island, Carnivora, competitive release, diet, felid, predation

Recent research has focused on identifying effects of the local extinction of predators on the remaining natural community. The complete absence of mammalian predators has resulted in such drastic ecological changes on islands isolated in Venezuela's Lago Guri that the system has been described as "ecological meltdown" (Terborgh et al. 2001). Regions that have lost only part of their large predator community face less dramatic, but still important, ecological changes in the remaining species, which increase in density or change behavior after being "released" from competition or predation from the newly absent species (e.g., Berger et al. 2001; Courchamp et al. 1999; Crooks and Soulé 1999; Gehrt and Clark 2003; Henke and Bryant 1999).

More specifically, theory predicts that competitive release would allow a predator to expand its niche in the absence of a larger competitor (Brown and Wilson 1956). This effect was

found in 2 communities of insectivorous mammals, where smaller species fed on larger prey after the experimental removal of a larger competitor (Dickman 1988). However, no similar phenomenon has been documented for larger vertebrate predators. No change was found in the diet of Virginia opossums (*Didelphis virginiana*) after the experimental removal of raccoons (*Procyon lotor*—Kasparian et al. 2002). Woodroffe and Ginsberg (2005) compared the diet of African wild dog (*Lycaon pictus*) and leopards (*Panthera pardus*) in pairs of sites with and without top predators but found no evidence of competitive release in those populations. In an even larger comparison of 98 dietary studies of British and Irish mustelid communities, McDonald (2002) also found no evidence of dietary shifts in the absence of larger carnivores. These results are surprising given that most carnivores' diets are typically described as flexible and opportunistic (Gittleman 1985), and that character displacement has been documented in morphological characters linked to diet (Dayan and Simberloff 1994; Van Valkenburgh and Wayne 1994). These results also are alarming, suggesting that the niche of large predators may remain empty in their absence, thus

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amplifying the ecological effect of their extinction on the local ecosystem.

However, the above studies only scratch the surface of possible scenarios where dietary shifts may reveal competition between carnivores. With >40% of the species in the mammalian order Carnivora considered at risk, the potential for ecological release after local extinction of a predator abounds. Documenting competitive release requires data on the diet of predators from a variety of localities, time periods, or both, and biologists are just now quantifying this type of variation. Here we contribute to this effort by documenting the diet of 2 predators from 2 nearby sites in central Panama from which the top predator, the jaguar (*Panthera onca*), is very rare or locally extinct, and comparing that with the diet of other populations where jaguars are present.

The 8- to 18-kg ocelot (*Leopardus pardalis*) and 22- to 80-kg puma (*Puma concolor*) are sympatric carnivores inhabiting a wide variety of ecosystems throughout the tropical Americas (Kitchener 1991; Sunquist and Sunquist 2002). Because of their large space needs, predaceous habits, and charisma, large felids are often considered important species (e.g., keystone, flagship, etc.) for the conservation of entire ecosystems in the region (Eisenberg 1980; Miller and Rabinowitz 2002; Sander-son et al. 2002). Previous studies of diets of ocelots and puma suggest that both are adaptable hunters with respect to the availability of prey (reviewed by Sunquist and Sunquist 2002). Puma are known to kill and eat prey ranging in size from mice to moose, but this appears to vary with latitude (Iriarte et al. 1990). Puma typically prey on large animals (mostly deer) in temperate zones, but focus mostly on animals that weigh less than half their own weight in tropical areas (Sunquist and Sunquist 2002). Studies of ocelots have found a more consistent prey choice of small mammals weighing <1 kg, and thus <10% of their own body weight (reviewed by Sunquist and Sunquist 2002). No studies have quantified diets of ocelots or puma in Panama or from any tropical site from which jaguars have been extirpated.

Information on the ecology of predators on Barro Colorado Island (BCI) is of special interest because this site has been a focal point of an on-going discussion about the importance of top predators to tropical ecosystems (Leigh 1999; Terborgh 1990, 1992; Wright et al. 1994, 1999). Specifically, some authors have speculated that the island is too small to support a resident large felid such as puma or jaguars, causing prey populations to be higher than normal (Terborgh 1990, 1992). Although most of the apparently high mammal densities on BCI have since been shown to reflect their greater habituation toward humans (Wright et al. 1994), the status of predators on the island remains an important and unsettled question.

Here we document the diet of ocelots and puma in the absence of jaguar populations in central Panama through fecal analyses. We describe seasonal and species differences in prey consumption, compare the diet of ocelots on BCI and a mainland site, and compare these data to the diet of puma and ocelot populations with extant jaguars.

## MATERIALS AND METHODS

*Study area.*—We collected feces from 2 sites in the Panama Canal watershed. On the mainland, within the 220-km<sup>2</sup> Soberanía National Park, our scat collection centered along the 6.5-km Plantation Road trail (9°05'N, 79°40'W). The terrain is mostly flat, with a few rolling hills rising 45–300 m above sea level (Asociación Nacional por la Conservación de la Naturaleza 1995). The 2nd study site, BCI (1,500 ha; 9°9'N, 79°51'W), is part of the Barro Colorado Nature Monument (5,500 ha total—Leigh 1999). BCI is a hilltop that was isolated from the mainland in 1914 when the Chagres River was dammed to create Lake Gatun as part of the Panama Canal. The minimum distance between the island and the mainland is 200 m, although small islands break up this gap in some places. The habitat at both sites is moist tropical forest (Leigh 1999; Tosi 1971), and annual precipitation is approximately 2,600 mm, with a pronounced dry season (Windsor 1990). For this paper we divided the year into dry (January–May) and wet (June–December) seasons. Although the 2 preserves are adjacent, the areas of scat collection were separated by about 30 km. BCI has been virtually free of hunting since 1980. Although the Plantation Road trail area is not near any human habitation, it is regularly visited by poachers and was ranked as the 4th-worst site for poaching in a comparison of 8 central Panamanian sites (Wright et al. 2000). Mammal sightings per 1-km survey were uniformly scarcer on Plantation Road trail than on BCI, reflecting lower densities and fewer habituated animals (Wright et al. 2000). Other than hunting, neither site has substantial human-related habitat disturbance, and the old Plantation Road has been overgrown enough to make it only a footpath now.

*Diet data.*—We quantified the diet of ocelots and puma through analysis of their scat. On BCI we searched for felid scats along all trails on the research site and at known latrine sites several times a week from the 1999 rainy season to the 2003 dry season. Such frequent searches are important in this wet habitat where scats decompose quickly, but it is more comprehensive than found in most fecal-based studies. In Soberanía National Park we conducted weekly searches for scats at 1 latrine and along a 6.5-km trail during 1999.

We identified the species of mammal responsible for each scat according to their size, odor, nearby footprints, and the collection location. Most (~90%) ocelot scats were collected at 9 latrines, each of which was used by many different individuals (Moreno and Giacalone, in press). In the absence of accompanying tracks, scats collected off trails were classified as puma if their diameter was greater than 2.8 cm (Farrell et al. 2000). All smaller felid scats were classified as ocelot. Although we cannot estimate the total numbers of individual ocelots we sampled, livetrapping, radiotracking by some of us (RSM and RWK), as well as cameras at latrine sites (Moreno and Giacalone, in press) suggest that at least 15 ocelots were present per year on BCI. No similar data are available for puma or Soberanía National Park, although the smaller collection area suggests we were sampling fewer individuals. We considered it unlikely that the smaller feces found on trails were made by other small felids, because trailside camera traps commonly photograph ocelots but almost never detect other small felids along the trails or at latrines (J. Giacalone, pers. comm.). Each sample was washed, dried, and dissected to separate contents (Emmons 1987; Ludlow and Sunquist 1987). The bone and hair remains within each scat were identified using a stereoscopic microscope and the specimen collection of the Vertebrate Museum at the University of Panama.

To describe the diet of each species, we used both the frequency of appearance (number of detections of an item divided by the total number of items detected) as well as the percentage of occurrence (number of scats containing an item divided by the total number scats).

**TABLE 1.**—Specific identity and relative frequency of items found in scats of ocelots and puma from 2 sites in central Panama. Values per scat do not add up to 100 because many scats had more than 1 prey item. Samples come from Barro Colorado Island (BCI) and the Plantation Road trail of Soberanía National Park (Mainland).

| Order or group             | Species                        | BCI puma                |                        | BCI ocelot              |                         | Mainland ocelot        |                        |
|----------------------------|--------------------------------|-------------------------|------------------------|-------------------------|-------------------------|------------------------|------------------------|
|                            |                                | % of items<br>(n = 121) | % of scats<br>(n = 88) | % of items<br>(n = 250) | % of scats<br>(n = 190) | % of items<br>(n = 66) | % of scats<br>(n = 49) |
| Unidentified small mammals |                                | 1.65                    | 2.3                    | 1.5                     | 2.1                     | 5.8                    | 8.2                    |
| Chiroptera                 | Unidentified bat               | 0.0                     | 0.0                    | 0.0                     | 0.0                     | 1.4                    | 2.0                    |
| Rodentia                   | <i>Proechimys semispinosus</i> | 7.4                     | 10.2                   | 15.4                    | 21.1                    | 4.3                    | 6.1                    |
|                            | <i>Dasyprocta punctata</i>     | 20.6                    | 28.4                   | 16.2                    | 22.1                    | 13.0                   | 18.4                   |
|                            | <i>Agouti paca</i>             | 10.7                    | 14.8                   | 0.4                     | 0.5                     | 0.0                    | 0.0                    |
|                            | Unidentified mice              | 1.7                     | 2.3                    | 9.7                     | 13.2                    | 4.3                    | 6.1                    |
|                            | <i>Coendou rothschildi</i>     | 0.0                     | 0.0                    | 1.2                     | 1.6                     | 0.0                    | 0.0                    |
|                            | <i>Sciurus granatensis</i>     | 0.8                     | 1.1                    | 3.1                     | 4.2                     | 2.9                    | 4.1                    |
|                            | Total rodents                  | 41.3                    | 56.8                   | 45.9                    | 62.6                    | 24.6                   | 34.7                   |
| Lagomorpha                 | <i>Sylvilagus brasiliensis</i> | 0.0                     | 0.0                    | 0.4                     | 0.5                     | 7.2                    | 10.2                   |
| Xenarthra                  | <i>Tamandua mexicana</i>       | 1.7                     | 2.3                    | 1.5                     | 2.1                     | 0.0                    | 0.0                    |
|                            | <i>Choloepus hoffmanni</i>     | 9.9                     | 13.6                   | 8.1                     | 11.1                    | 1.4                    | 2.0                    |
|                            | <i>Bradypus variegatus</i>     | 5.8                     | 8.0                    | 8.5                     | 11.6                    | 18.8                   | 26.5                   |
|                            | <i>Cyclopes didactylus</i>     | 0.0                     | 0.0                    | 0.4                     | 0.5                     | 1.4                    | 2.0                    |
|                            | <i>Dasyurus novemcinctus</i>   | 1.7                     | 2.3                    | 1.9                     | 2.6                     | 8.7                    | 12.2                   |
|                            | Total xenarthrans              | 19.0                    | 26.1                   | 20.5                    | 27.9                    | 30.4                   | 42.8                   |
|                            | Carnivora                      | <i>Procyon</i> sp.      | 0.0                    | 0.0                     | 0.0                     | 0.0                    | 1.4                    |
|                            | <i>Nasua narica</i>            | 3.3                     | 4.5                    | 5.0                     | 6.8                     | 7.2                    | 10.2                   |
|                            | Total carnivores               | 3.3                     | 4.5                    | 5.0                     | 6.8                     | 8.7                    | 12.2                   |
| Artiodactyla               | <i>Mazama temama</i>           | 9.9                     | 13.6                   | 0.4                     | 0.5                     | 0.0                    | 0.0                    |
|                            | <i>Pecari tajacu</i>           | 10.7                    | 14.8                   | 0.4                     | 0.5                     | 0.0                    | 0.0                    |
|                            | Total artiodactyls             | 20.7                    | 28.4                   | 0.8                     | 1.1                     | 0.0                    | 0.0                    |
| Didelphimorphia            | <i>Didelphis marsupialis</i>   | 0.8                     | 1.1                    | 1.5                     | 2.1                     | 4.3                    | 6.1                    |
|                            | <i>Philander opossum</i>       | 1.7                     | 2.3                    | 0.8                     | 1.1                     | 2.9                    | 4.1                    |
|                            | <i>Caluromys derbianus</i>     | 0.0                     | 0.0                    | 0.0                     | 0.0                     | 1.4                    | 2.0                    |
|                            | Total didelphimorphs           | 2.5                     | 3.4                    | 2.3                     | 3.2                     | 8.7                    | 12.2                   |
| Primates                   | <i>Cebus capucinus</i>         | 5.0                     | 6.8                    | 5.0                     | 6.8                     | 0.0                    | 0.0                    |
| Mammals                    | Total mammals                  | 93.4                    | 128.4                  | 81.5                    | 111.0                   | 87.0                   | 122.4                  |
| Reptiles                   | Small lizards                  | 0.0                     | 0.0                    | 0.4                     | 0.5                     | 0.0                    | 0.0                    |
|                            | Snakes                         | 1.7                     | 2.3                    | 5.8                     | 7.9                     | 1.4                    | 2.0                    |
|                            | <i>Iguana iguana</i>           | 0.8                     | 1.1                    | 7.7                     | 10.5                    | 8.7                    | 12.2                   |
|                            | Turtles                        | 0.0                     | 0.0                    | 0.4                     | 0.0                     | 0.0                    | 0.0                    |
|                            | Total reptiles                 | 2.5                     | 3.4                    | 14.3                    | 18.9                    | 10.1                   | 14.3                   |
| Aves                       | Unidentified birds             | 0.8                     | 1.1                    | 0.0                     | 0.0                     | 1.4                    | 2.0                    |
| Plants                     | Cyperaceae                     | 3.3                     | 4.5                    | 4.6                     | 6.3                     | 1.4                    | 2.0                    |

We used contingency tables to compare differences between the species, sites, and seasons (Sokal and Rohlf 1995). Frequency of appearance was used to calculate the relative biomass of prey as a quantitative alternative to raw frequency data (Ackerman et al. 1994). Although these biomass conversions are based on calibration data for North American prey species, they give a better measure of relative importance than raw frequency measures and have been used in other studies of tropical felids (Farrell et al. 2000; Meza et al. 2002). We used the Pianka index to calculate dietary overlap among species, site, and season (Pianka 1973). This overlap matrix was used to build a cluster diagram with an unweighted pair-group average linking rule in STATISTICA 5.1 (StatSoft, Inc. 1997).

## RESULTS

We collected and analyzed 239 ocelot scats and 88 puma scats between 1999 and 2003 (Table 1). Of the ocelot scats, 190 were collected on BCI and 49 on the mainland; all puma scats were collected on BCI. Most (~90%) of the ocelot scats were collected from latrines, with fewer found along trails. We

found puma scat only along trails on BCI, typically with obvious tracks in the mud nearby. We found at least 1 puma scat per month on BCI from 1999 to 2003 except in some of the wettest months (e.g., October and November; Fig. 1), when scats decompose more quickly.

Comparing the overlap between the 3 populations of predators, the diet of BCI ocelots was similar to both mainland ocelots and BCI puma (Pianka's overlap = 0.721 and 0.720, respectively), whereas the overlap between BCI puma and mainland ocelot was less (0.530). These overlap results are similar when season variation is included, with each population being more similar to itself between the wet and dry seasons than to the other 2 populations (Fig. 2). The diet of puma and ocelots was most similar in the wet season, when all 3 study populations frequently ate Central American agoutis (*Dasyprocta punctata*).

The prey eaten by ocelots on BCI and the mainland did not differ significantly in their use of the forest layers or in their body mass (Table 2). Both populations of ocelots preyed

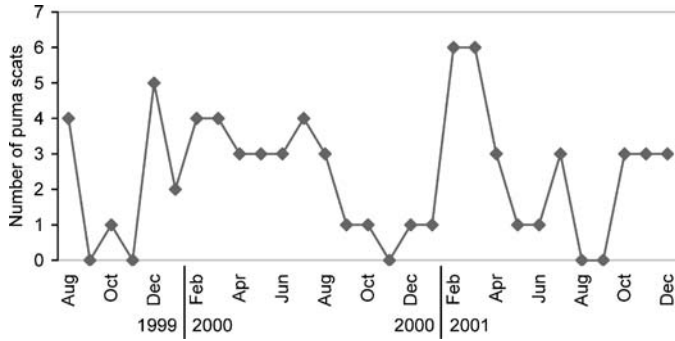


FIG. 1.—The number of puma scats found on Barro Colorado Island, Panama, each month over 4 years (monthly mean = 2.4).

mostly on small (<500-g) and medium-sized (2.0- to 4.9-kg) prey with roughly equal terrestrial compared to arboreal tendencies. In contrast, the diet of puma was significantly different from ocelots in both having more large prey (>10 kg), less small prey (<500 g), and more terrestrial prey.

More differences between the 3 populations are revealed by the specific identity of prey eaten by each population (Table 1). BCI and mainland ocelots frequently ate sloths, agoutis, and iguanas (*Iguana iguana*). Ocelots on the mainland preyed more on tapeti (*Sylvilagus brasiliensis*) and brown-throated 3-toed sloths (*Bradypus variegatus*), whereas ocelots on BCI ate more Hoffmann’s 2-toed sloths (*Choloepus hoffmanni*) and Tome’s spiny rats (*Proechimys semispinosus*). Puma also frequently preyed on agouti and sloths, but differed from ocelots in regularly preying on larger species such as pacas (*Agouti paca*), Central American red brocket (*Mazama temama*), and collared peccaries (*Pecari tajacu*). The relative importance of these prey items as food for these predators is best evaluated by adjusting for the body mass of the prey; in this case, these adjustments further emphasize the importance of large prey for puma, and medium to large prey for ocelots (Fig. 3).

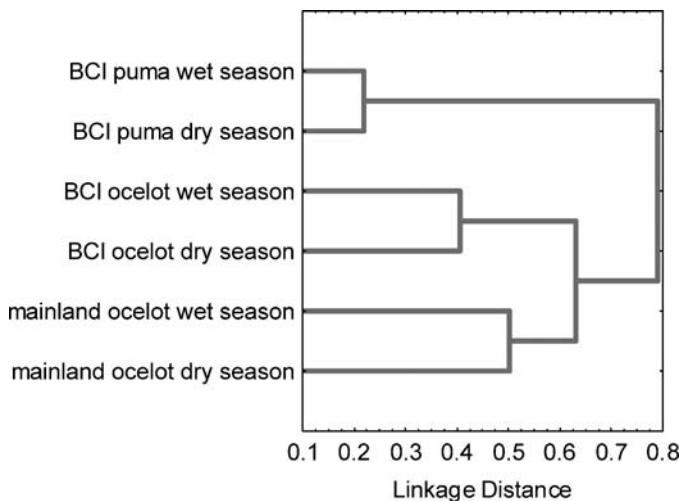


FIG. 2.—Results from a cluster analysis (unweighted pair-group average) of dietary overlap between ocelots and puma by study site and season (wet or dry) on the mainland and on Barro Colorado Island (BCI) in Panama.

TABLE 2.—The relative frequency of prey (per item) found in puma and ocelot scat according to average prey weight and component of the forest used by prey. Samples come from Barro Colorado Island (BCI) and the Plantation Road trail of Soberanía National Park (Mainland), Panama. These values were statistically compared using raw frequency of items with *d.f.* = 4 for prey weight and *d.f.* = 2 for prey use of forest. The prey weights were significantly different when comparing BCI puma with BCI ocelots ( $\chi^2 = 51.6, P < 0.001$ ) or with mainland ocelots ( $\chi^2 = 18.56, P < 0.001$ ), but not between BCI and mainland ocelots ( $\chi^2 = 0.97, P = 0.616$ ). Likewise, prey use of forest was significantly different when comparing BCI puma with BCI ocelots ( $\chi^2 = 16.0, P < 0.001$ ) or mainland ocelots ( $\chi^2 = 10.5, P < 0.01$ ) but not when comparing BCI and mainland ocelots ( $\chi^2 = 0.65, P = 0.72$ ).

|                    | BCI puma | BCI ocelots | Mainland ocelots |
|--------------------|----------|-------------|------------------|
| Prey weight        |          |             |                  |
| <1 kg              | 18.1     | 39.3        | 35.3             |
| 1–10 kg            | 61.9     | 59.9        | 64.7             |
| >10 kg             | 20.0     | 0.8         | 0.0              |
| Prey use of forest |          |             |                  |
| Terrestrial        | 44.63    | 33.20       | 28.99            |
| Scansorial         | 7.44     | 15.83       | 15.94            |
| Arboreal           | 19.83    | 26.25       | 30.43            |

DISCUSSION

*The presence of large predators.*—By deliberately searching for large felid prints and scats on BCI over 4 years we have confirmed the regular presence of puma on the island, but found no evidence for jaguars (Fig. 1; see also Smithsonian Tropical Research Institute 2003). Although examination of this type of data cannot address questions of puma density, residency, or historical status (before 1999), it does confirm that puma were roaming BCI on a regular basis during this study. Some might argue that puma could be so rare as to not be ecologically important to the area. Given the consistent and abundant puma

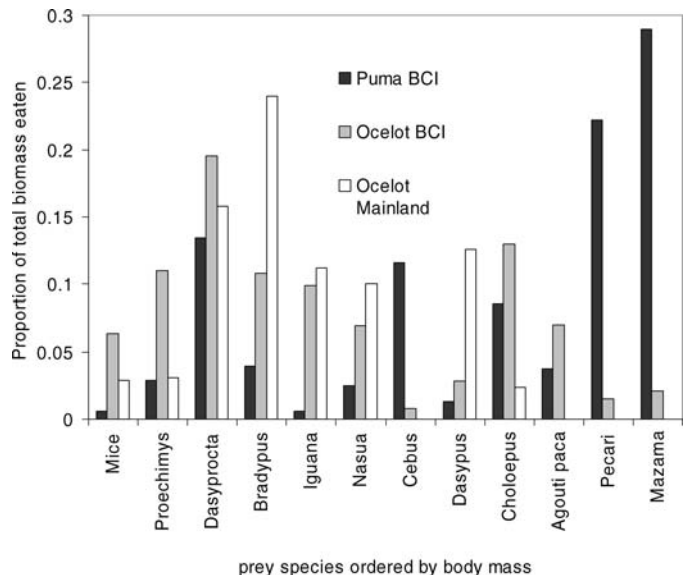


FIG. 3.—Estimated proportion of total biomass made up of major (top 12) prey types for 3 populations of felids.

sign we found in a relatively small area (BCI is  $\sim 16 \text{ km}^2$ ), we suspect that their effective density may be typical of the region (Smallwood 1997), and similar to anecdotal estimates for BCI in the 1920s and 1930s (Chapman 1929; Enders 1935). No puma sign was observed in 1 year of fieldwork on the mainland at Plantation Loop Road, although puma are known from other areas in the park (park guards, pers. comm.).

We found no direct evidence (i.e., footprints, scats, or visual observation) of the presence of jaguars in this study. Jaguar sightings are occasionally reported from BCI, although none are recorded in the sightings book since 1970 (BCI visitors log book). Jaguars are more often, but still rarely, reported from the mainland forests surrounding the Panama Canal, although our weekly surveys did not detect their presence along the Plantation Road trail (Wright and Duber 2001; Wright et al. 1994). During this study, it appears as though jaguars were, at most, rare visitors to our 2 study sites, and we consider them ecologically extinct there.

*Regional comparisons.*—Like most other studies of puma and ocelot diets (reviewed by Sunquist and Sunquist 2002), we found that both felids eat mostly mammalian prey and feed on a diversity of mammalian species (Table 1). Overall, there was considerable dietary overlap between sympatric ocelot and puma populations on BCI (especially in the wet season), and between ocelots on BCI and the mainland, with fewer similarities between the diets of BCI puma and the mainland ocelots. This general comparison suggests that the food choice of these populations is governed by a combination of opportunistic predation of locally abundant prey species (i.e. similarities between puma and ocelots on BCI, and differences between mainland and BCI ocelots) and species-specific prey specialization (i.e., difference between puma and ocelots).

Although they share a number of prey species, a closer look shows that the diet of BCI puma is significantly different from both ocelot populations in terms of size of prey taken and forest layers used by prey (Table 2). Not surprisingly, the larger puma preyed upon more large mammals (i.e., peccaries and deer) than did ocelots, hunting less small prey (i.e., mice), and favoring terrestrial species over those in the trees (Sunquist and Sunquist 2002). This difference is consistent with the energetic model of Carbone et al. (1999) of carnivore diet, which suggests that predators  $>21.5 \text{ kg}$  (i.e., puma) focus on prey  $>45\%$  their body mass (i.e., deer and peccaries).

*Continental comparisons and competitive release.*—The diets of tropical felids have been studied together at a variety of sites across their range, allowing us to draw broadscale comparisons with our results from central Panama. The emerging story shows relatively consistent niche partitioning according to body mass. Jaguar and puma both typically eat medium and large mammals, with jaguars eating relatively more peccaries and puma relatively more deer (Aranda 1994, 2002; Oliveira 2002; Sunquist and Sunquist 2002). Across their range, ocelots have consistently been reported feeding primarily on small ( $<1\text{-kg}$ ) mammal species (reviewed by Sunquist and Sunquist 2002).

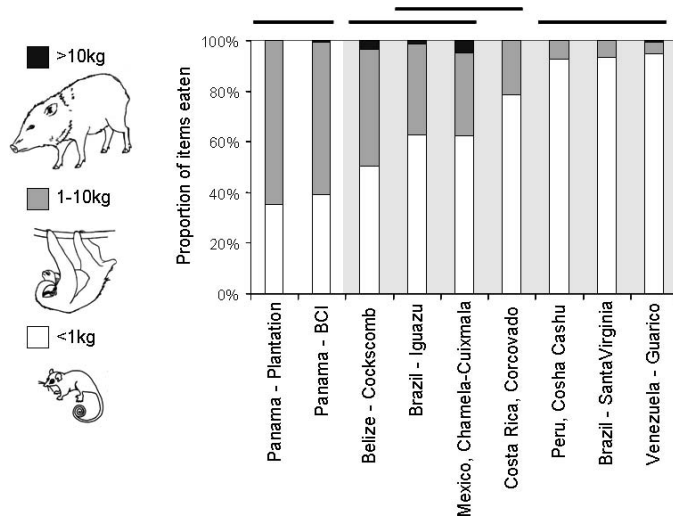
Although all 3 species originally occurred sympatrically across the Neotropics, human encroachment has affected them

differently, with jaguars being driven out of much of their former range (Sanderson et al. 2002), and puma and ocelots appearing to endure human-caused landscape changes better (Núñez et al. 2000). However, the effect of the loss of one of these predators on the ecology of the others is unknown because their diets have only been described from fully intact carnivore communities. Although jaguars are known to occur in central Panama, they were never detected in our study areas, and we consider them ecologically extinct. Our dietary results suggest that this ecological extinction of jaguars has resulted in a dietary shift by both ocelots and puma.

Although both puma and jaguar eat species of peccaries and deer, peccaries are typically more important to jaguars, whereas deer are more important for puma (Aranda 1994, 2002). We found peccaries in the diet of puma on BCI slightly more than deer. Although this difference was not significant, only 1 other study (in a review of 14, all with sympatric jaguars) reported a similar trend of peccaries being so important to a population of puma (Oliveira 2002). We suspect that the absence of a regular competitive presence of jaguars on BCI has allowed puma to hunt more peccaries, either because peccaries are more abundant or because puma face less direct interaction with the larger jaguar.

The dietary shift found by our study for ocelots in the absence of jaguars was substantial. Panama ocelots ate more medium-sized prey than any of the other 7 ocelot populations studied in sites with robust jaguar populations (Fig. 4). Ocelot populations that co-occur with both jaguars and puma always focus on small prey, typically  $<1 \text{ kg}$ , rarely eating medium-sized mammals (reviewed by Sunquist and Sunquist 2002). The importance of these larger prey to both populations was even more pronounced after taking into account the mass of food provided by each prey species (Fig. 3), emphasizing the importance of sloths and agoutis for ocelots of the region. Together, these 3 species represent  $\sim 33\%$  of the diet of ocelots in our study, corresponding to  $\sim 43\%$  of total biomass intake of ocelots. Across their range, most ocelot populations also overlap with 2 species of sloths and 1 species of agouti; however, nowhere are these medium-sized mammals as important in their diet as in our study (Fig. 4). For example, sloths and agoutis together make up 0% of ocelot diet in the Atlantic forests of Brazil (Wang 2002), 1.4% in Venezuela (Ludlow and Sunquist 1987), 1.7% in Peru (Emmons 1987), 8.7% in Costa Rica (Chinchilla 1997), and 10.7% in Iguazu, Brazil (Crawshaw 1995). This trend goes further than just sloths and agoutis, however, because the ocelots in our study also ate more pacas, green iguanas, white-nosed coatis (*Nasua narica*), and other medium-sized animals than other populations studied.

Given the lack of puma and jaguar sign at our mainland site, the ocelot population there likely faces less competition from large felids than the BCI population, where puma still occur, and might be expected to experience even more competitive release. Indeed, mainland ocelots fed slightly more on medium-sized prey compared to the BCI population, although this difference was not significant (Table 2). Competitive release at this mainland site may be limited by competition with human hunters (Wright et al. 2000).



**FIG. 4.**—Weight of prey eaten by ocelots across 9 sites. Hatching indicates presence of robust sympatric jaguar populations. Horizontal lines above graph connect sites that are not significantly different from one another; distributions of prey size for all pairs of unconnected sites were significantly different (chi-square or Fisher's exact test on number of items detected in each size class,  $P < 0.05$ ). Sources: Plantation and Barro Colorado Island (BCI), Panama (this study); Cockscomb, Belize (Konecny 1989); Iguazu, Brazil (Crawshaw 1995); Chamela-Cuixmala, Mexico (Meza 2002); Corcovado, Costa Rica (Chinchilla 1997); Cosha Cashu, Peru (Emmons 1987); Santa Virginia, Brazil (Wang 2002); and Guanico, Venezuela (Ludlow and Sunquist 1987).

Examination of our dietary data from ocelots and puma in central Panama suggests that they are experiencing an ecological release in the absence of competition from jaguars. The most obvious alternative explanation for these differences, that prey densities on BCI are higher than elsewhere in the tropics, is not supported by a review of 48 mammal density estimates across the Neotropics (Wright et al. 1994). That the effect is less obvious in the puma is not surprising given their high dietary overlap with jaguars at sites where they do occur together (up to 82%—Oliveira 2002). The main difference in their diets at most sites is in the relative importance of peccaries and deer, and this is where we see some evidence for release in the BCI population. The response of ocelots to this competitive release is more striking, suggesting that their realized niche from sites with extant jaguars is significantly different from their fundamental niche. In the absence of jaguars, ocelots in our study expanded their niche by increasing their consumption of medium-sized animals (1–10 kg). Ocelots did not extend their use of large prey (>10 kg), suggesting that they are not capable of regularly killing such large animals or are still constrained by the presence of puma. Although different from all other reported ocelot diets, this shifted diet is still consistent with the energetic model of Carbone et al. (1999) in explaining why smaller predators (<21.5 kg) typically exploit prey <45% their body mass.

Although the precise mechanism to explain ecological release remains unknown, it probably involves interference, resource competition, or both. Interference competition should

be greatest between pairs of species with larger differences in body size; jaguars are more likely to interfere with ocelots than with puma (Palomares and Caro 1999). Thus, the stronger ecological response of ocelots in our study supports the prediction that aggressive interactions with larger predators may function to limit the niche of smaller predators. If the expanded niches of ocelots and puma were the result of abundant larger prey left unexploited by jaguars, prey populations should be higher at our study site than at other sites with extant jaguar populations—a result not found by Wright et al. (1994). However, if the dietary shifts we observed in ocelots and puma compensate for the missing jaguar, differences in prey abundance may not be detectable with modern surveys.

The magnitude of the response of ocelots is also surprising given the regular presence of puma on the island during our study. Why competition from puma has not been sufficient to replace that of the missing jaguar remains unknown. One possibility is that puma also were absent from BCI for much of the time between the studies of Chapman (1929) and Enders (1935) and the beginning of our study (1999). This has been suggested by Terborgh (1990) and Wright et al. (1994), although there was no systematic attempt to document status of the puma during this period. If this is the case, ocelots may return to their traditional diets of smaller prey if puma continue to persist on BCI in the upcoming decades. A 2nd possibility is that competitive interactions between ocelots and puma are fundamentally different than those between ocelots and jaguar. Interspecific interactions are notoriously difficult to study, especially for solitary carnivores, and we know of no available data to test this hypothesis.

Although ocelot predation on larger prey is not unheard of (Sunquist and Sunquist 2002), it has primarily been attributed to large adult males (Mondolfi 1982). Because camera-traps found females and smaller males, as well as large males, using the latrines sampled in our study (Moreno and Giacalone, in press), we are confident that our sampling is representative of the entire population and not biased toward large individuals.

The amount of sloths and other arboreal prey in the diet of both populations of ocelots also was surprising, given their record of being a predominantly terrestrial hunter (Emmons 1987; Handley 1976; Mondolfi 1982; Sunquist et al. 1989; but see Leopold 1959). Sloths have been documented at high densities in Panama in the past (Montgomery and Sunquist 1978), although these may not be representative for our study (Wright et al. 1994). If ocelots were simply taking advantage of a resource that was hyperabundant, we would expect that puma also would do so and we would find high amounts of sloths in their diets. However, the amount of sloths and arboreal prey eaten by BCI puma were similar to what has been found in other tropical studies (Núñez et al. 2000; Oliveira 2002), suggesting that the local ocelot population has indeed specialized on sloths. Whether ocelots climb to catch these prey, wait for them to venture into the understory, or opportunistically pounce when they fall to the ground remains unknown.

**Conclusions.**—Predator ecology is important because of the potential for top-down effects on the ecosystem. Many top

predators are facing local or global extinction, highlighting the importance of understanding their competitive interactions with smaller predators and the response of these smaller predators to the absence of top predators (Macdonald and Kays 2005; Schaller 1996). Previous research has focused on size or dietary character displacement as evidence for such competition, assuming a link between these characters and the ecology of a population. However, direct tests for competitive release in the diet of medium-sized or large carnivores have either not been done, or, when done, have found no change. Here we show that, after the disappearance of jaguar populations in our study areas in central Panama, the diets of ocelots and puma are different from other studies where the 3 predators occur together. This highlights the potential for ocelots to hunt medium-sized prey, although the precise mechanisms limiting this behavior in the presence of jaguars remain unknown. Future studies of predator diets should consider recent changes in the competitor community and consider competitive release as a possible explanation for dietary shifts. Studies of direct interactions between predator species also are needed to understand the mechanisms of these shifts. Given the dire status of many top predators, such research opportunities should be abundant. Hopefully, understanding what happens when we lose a predator will help justify their conservation.

## RESUMEN

Nosotros usamos el análisis de heces para documentar la dieta de los ocelotes (*Leopardus pardalis*) y del puma (*Puma concolor*) en dos sitios en el centro de Panamá. Nosotros detectamos el puma en la Isla de Barro Colorado (IBC) casi todos los meses durante el estudio pero nunca encontramos evidencia de los jaguares (*Panthera onca*) en cualquiera de los sitios. Tanto el ocelote como el puma se alimentan predominantemente de presas de mamíferos, pero consumen una diversidad de especies. El saíno de collar blanco (*Pecari tajacu*) y el venado corzo (*Mazama americana*) fueron los más importantes alimentos para el puma, mientras que el ñeque centroamericano (*Dasyprocta punctata*) y los perezosos (*Choloepus hoffmanni* y *Bradypus variegatus*) fueron los más importantes para los ocelotes. Hubo un considerable traslape en la dieta entre las poblaciones y las especies, pero la dieta del puma de la IBC fue significativamente diferente de las 2 poblaciones de ocelotes en que contenía más presas grandes, lo que sugiere que las diferencias en dietas entre estas especies de depredadores está mayormente relacionada al tamaño corporal relativo. Comparando a través de grandes escalas, ambas poblaciones de ocelotes en nuestro estudio comían más presas grandes que en otras partes de su rango, lo que sugiere que su nicho fundamental incluye más presas grandes que su nicho realizado en otros sitios. El puma en IBC come proporcionalmente más saíno y venado que en la mayoría de las otras poblaciones. Estas dietas inusuales en el inicio de una reciente disminución o extinción local de los jaguares son consistentes con un cambio de presas en respuesta a una liberación de la competencia.

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## LITERATURE CITED

- ACKERMAN, B. B., F. G. LINDSEY, AND T. P. HEMKER. 1994. Cougar food habits in southern Utah. *Journal of Wildlife Management* 48:147–155.
- ARANDA, M. 1994. Importancia de los pecaríes (*Tayassu* spp.) en la alimentación del jaguar (*Panthera onca*). *Acta Zoológica Mexicana* 62:11–22.
- ARANDA, M. 2002. Importancia de los pecaríes para la conservación del jaguar en México. Pp. 101–105 in *El jaguar en el nuevo milenio* (R. A. Medellín, et al., eds.). Universidad Nacional Autónoma de México/Wildlife Conservation Society, New York.
- ASOCIACION NACIONAL POR LA CONSERVACION DE LA NATURALEZA. 1995. Evaluación ecológica de la cuenca del Canal de Panamá. Editora Silvestre S.A., Panama City, Panama.
- BERGER, J., J. E. SWENSON, AND I. L. PERSSON. 2001. Recolonizing carnivores and naïve prey: conservation lessons from Pleistocene extinctions. *Science* 291:1036–1039.
- BROWN, W. L., JR., AND E. O. WILSON. 1956. Character displacement. *Systematic Zoology* 5:49–64.
- CARBONE, C., G. M. MACE, S. C. ROBERTS, AND D. W. MACDONALD. 1999. Energetic constraints on the diet of terrestrial carnivores. *Nature* 402:286–288.
- CHAPMAN, F. M. 1929. *My tropical air castle*. Appleton & Co., New York.
- CHINCHILLA, F. A. 1997. La dieta del jaguar (*Panthera onca*), el puma (*Felis concolor*), y el manigordo (*Felis pardalis*) (Carnivora, Felidae) en el Parque Nacional Corcovado. *Revista de Biología Tropical* 45:1223–1229.
- COURCHAMP, F., M. LANGLAIS, AND G. SUGIHARA. 1999. Cats protecting birds: modeling the mesopredator release effect. *Journal of Animal Ecology* 68:282–292.
- CRAWSHAW, P. G. 1995. Comparative ecology of ocelot (*Felis pardalis*) and jaguar (*Panthera onca*) in a protected subtropical forest in Brazil and Argentina. Ph.D. dissertation, University of Florida, Gainesville.
- CROOKS, D. R., AND M. E. SOULÉ. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400:563–566.
- DAYAN, T., AND D. SIMBERLOFF. 1994. Character displacement, sexual dimorphism, and morphological variation among British and Irish mustelids. *Ecology* 75:1063–1073.
- DICKMAN, C. R. 1988. Body size, prey size, and community structure in insectivorous mammals. *Ecology* 69:569–580.
- EISENBERG, J. F. 1980. The density and biomass of tropical mammals. Pp. 35–55 in *Conservation biology: an evolutionary–ecological perspective* (M. E. Soulé and B. A. Wilcox, eds.). Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.

- EMMONS, L. H. 1987. Comparative feeding ecology of felids in a neotropical rainforest. *Behavioral Ecology and Sociobiology* 20: 217–283.
- ENDERS, R. K. 1935. Mammalian life histories from Barro Colorado Island, Panama. *Bulletin of the Museum of Comparative Zoology* 78:383–502.
- FARRELL, L. E., J. ROMAN, AND M. E. SUNQUIST. 2000. Dietary separation of sympatric carnivores identified by molecular analysis of scats. *Molecular Ecology* 9:1583–1590.
- GEHRT, S. D., AND W. R. CLARK. 2003. Raccoons, coyotes, and reflections on the mesopredator release hypothesis. *Wildlife Society Bulletin* 31:836–842.
- GITTLEMAN, J. L. 1985. Carnivore body size: ecological and taxonomic correlates. *Oecologia* 67:540–554.
- HANDLEY, C. O., JR. 1976. Mammals of the Smithsonian Venezuelan project. *Brigham Young University Science Bulletin* 20:1–90.
- HENKE, S. E., AND F. C. BRYANT. 1999. Effects of coyote removal on the faunal community in western Texas. *Journal of Wildlife Management* 63:1066–1081.
- IRIARTE, A. J., W. L. FRANKLIN, W. E. JOHNSON, AND K. H. REDFORD. 1990. Biogeographic variation of food habits and body size of the American puma. *Oecologia* 85:185–190.
- KASPARIAN, M. A., E. C. HELLGREN, AND S. M. GINGER. 2002. Food habits of the Virginia opossum during raccoon removal in the Cross Timbers ecoregion, Oklahoma. *Proceedings of the Oklahoma Academy of Sciences* 82:73–78.
- KITCHENER, A. 1991. *The natural history of the wild cats*. Comstock Publishing Associates, Ithaca, New York.
- KONECNY, M. J. 1989. Movement patterns and food habits of four sympatric carnivore species in Belize, Central America. Pp. 243–264 in *Advances in neotropical mammalogy* (K. H. Redford and J. F. Eisenberg, eds.). Sandhill Crane Press, Inc., Gainesville, Florida.
- LEIGH, E. G., JR. 1999. *Tropical forest ecology: a view from Barro Colorado Island*. Oxford University Press, Oxford, United Kingdom.
- LEOPOLD, A. 1959. *Wildlife of Mexico*. University of California Press, Berkeley.
- LUDLOW, M. E., AND M. E. SUNQUIST. 1987. Ecology and behavior of ocelots in Venezuela. *National Geographic Research* 3:447–461.
- MACDONALD, D. W., AND R. W. KAYS. 2005. The Carnivora: the evolution, adaptive significance and conservation of their diversity. Pp. 1–67 in *Walker's carnivores of the world* (R. Nowak, ed.). Johns Hopkins University Press, Baltimore, Maryland.
- MCDONALD, R. A. 2002. Resource partitioning among British and Irish mustelids. *Animal Ecology* 71:185–200.
- MEZA, A. D. V., E. M. MEYER, AND C. A. L. GONZÁLEZ. 2002. Ocelot (*Leopardus pardalis*) food habits in a tropical deciduous forest of Jalisco, Mexico. *American Midland Naturalist* 148:146–154.
- MILLER, B., AND A. RABINOWITZ. 2002. ¿Por qué conservar al jaguar? Pp. 303–315 in *El jaguar en el nuevo milenio* (R. A. Medellín, et al., eds.). Universidad Nacional Autónoma de México/Wildlife Conservation Society, New York.
- MONDOLFI, E. 1982. Biology and status of the small wild cats of Venezuela. *International Cat Symposium*, Texas A&I University, Kingsville, Texas (abstracts).
- MONTGOMERY, G. G., AND M. SUNQUIST. 1978. Habitat selection and use by two-toed and three-toed sloths. Pp. 329–359 in *The ecology of arboreal folivores* (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.
- MORENO, R., AND J. GIACALONE. In press. Ecological data obtained from latrine use by ocelots (*Leopardus pardalis*) on Barro Colorado Island, Panama. *Tecnociencia*.
- NÚÑEZ, R., B. MILLER, AND F. LINDZAY. 2000. Food habits of jaguars and pumas in Jalisco, Mexico. *Journal of Zoology (London)* 252: 373–379.
- OLIVEIRA, T. G. 2002. Ecología comparativa de la alimentación del jaguar y del puma en el Neotrópico. Pp. 265–288 in *El jaguar en el nuevo milenio* (R. A. Medellín, et al., eds.). Universidad Nacional Autónoma de México/Wildlife Conservation Society, New York.
- PALOMARES, F., AND T. M. CARO. 1999. Interspecific killing among mammalian carnivores. *American Naturalist* 153:492–508.
- PIANKA, E. R. 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics* 4:53–74.
- SANDERSON, E. W., ET AL. 2002. Planning to save a species: the jaguar as a model. *Conservation Biology* 16:58–72.
- SCHALLER, G. 1996. Carnivores and conservation biology. Pp. 1–10 in *Carnivore behavior, ecology and evolution* (J. L. Gittleman, ed.). Cornell University Press, Ithaca, New York.
- SMALLWOOD, K. S. 1997. Interpreting puma (*Puma concolor*) population estimates for theory and management. *Environmental Conservation* 24:283–289.
- SMITHSONIAN TROPICAL RESEARCH INSTITUTE. 2003. Biennial report of the Smithsonian Tropical Research Institute, October 1, 2001 through September 30, 2003. Smithsonian Institution, Washington, D.C.
- STATSOFT, INC. 1997. *STATISTICA for Windows*. StatSoft, Inc., Tulsa, Oklahoma.
- SOKAL, R. R., AND F. J. ROHLF. 1995. *Biometry: the principles and practice of statistics in biological research*. W. H. Freeman and Company, New York.
- SUNQUIST, M., AND F. SUNQUIST. 2002. *Wild cats of the world*. University of Chicago Press, Chicago, Illinois.
- SUNQUIST, M. E., F. C. SUNQUIST, AND D. E. DANEKE. 1989. Ecological separation in a Venezuelan llanos carnivore community. Pp. 197–232 in *Advances in neotropical mammalogy* (K. H. Redford and J. F. Eisenberg, eds.). Sandhill Crane Press, Inc., Gainesville, Florida.
- TERBORGH, J. 1990. The role of the felid predators in neotropical forests. *Vida Silvestre Neotropical* 2:3–5.
- TERBORGH, J. 1992. Maintenance of diversity in tropical forests. *Biotropica* 24:283–292.
- TERBORGH, J., ET AL. 2001. Ecological meltdown in predator-free forest fragments. *Science* 294:1923–1926.
- TOSI, J. 1971. Zonas de vida. Una base ecológica para la investigación silvícola e inventario forestal en la República de Panamá. Programa de las Naciones Unidas para la Agricultura y la Alimentación (FAO), Rome, Italy.
- VAN VALKENBURGH, B., AND R. K. WAYNE. 1994. Shape divergence associated with size convergence in sympatric East African jackals. *Ecology* 75:1567–1581.
- WANG, E. 2002. Diets of ocelots (*Leopardus pardalis*), margays (*L. wiedii*) and oncilla (*L. tigrinus*) in the Atlantic rainforest in southeast Brazil. *Studies on Neotropical Fauna and Environment* 37:207–212.
- WINDSOR, D. M. 1990. Climate and moisture variability in a tropical forest: long-term records from Barro Colorado Island, Panama. Smithsonian Institution Press, Washington, D.C.
- WOODROFFE, R., AND J. G. GINSBERG. 2005. King of the beasts? Evidence for guild redundancy among large mammalian carnivores. Pp. 154–176 in *Large carnivores and biodiversity: does saving one conserve the other?* (J. Ray, J. Berger, K. H. Redford, and R. Steneck, eds.). Island Press, New York.



- WRIGHT, S. J., C. CARRASCO, O. CALDERON, AND S. PATON. 1999. The El Niño Southern Oscillation, variable fruit production, and famine in a tropical forest. *Ecology* 80:1632–1647.
- WRIGHT, S. J., AND H. DUBER. 2001. Poachers and forest fragmentation alter seed dispersal, seed survival, and seedling recruitment in the palm *Attalea butyraceae*, with implications for tropical tree diversity. *Biotropica* 33:583–595.
- WRIGHT, S. J., M. E. GOMPPER, AND B. DE LEÓN. 1994. Are large predators keystone species in neotropical forests? The evidence from Barro Colorado Island. *Oikos* 71:279–294.
- WRIGHT, S. J., H. ZEBALLOS, I. DOMINGUEZ, M. M. GALLARDO, M. C. MORENO, AND R. IBANEZ. 2000. Poachers alter mammal abundance, seed dispersal, and seed predation in a neotropical forest. *Conservation Biology* 14:227–239.

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