Ocelot ecology and its effect on the small-felid guild in the lowland neotropics

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Ocelot *Leopardus pardalis* from eastern Amazonia. © 'Projeto Gatos do Mato—Brasil'.

Introduction

The ocelot (*Leopardus pardalis*, 6.6–18.6 kg) is the third largest of the 10 felid species found in the Neotropical region (Sunquist and Sunquist 2002; Oliveira and Cassaro 2005). Ocelots extend from south Texas through to northern Argentina, and have been the subject of several studies on feeding ecology, home range, activity patterns and density (e.g. Ludlow and Sunquist 1987; Emmons 1988; Crawshaw 1995; Jacob 2002; Di Bitetti *et al.* 2006; Moreno *et al.* 2006). The ocelot appears to be strong-ly associated with dense habitat cover and preys predominantly on small rodents (see Sunquist and Sunquist 2002). However, the extent to which environmental or biological variables constrain ocelot presence and distribution remains poorly understood. Throughout their broad geographic range ocelots live in sympatry with the smaller margays (*Leopardus wiedii*, 2.3–4.9 kg), little spotted cats (*Leopardus tigrinus*, 1.7–3.5 kg), jaguarundis (*Puma yagouaroundi*, 3.0–7.6 kg) and, to a lesser extent, with pampas cats (*Leopardus colocolo*, 2.5–3.8 kg) and

Geoffroy's cats (*Leopardus geoffroyi*, 2.8–7.4 kg) (Oliveira and Cassaro 2005; Lucherini *et al.* 2006). They also coexist with pumas and jaguars through most of their range. There is considerable overlap among these sympatric small felids, not only in geographic range but also in habitat use, feeding ecology, activity patterns, and body size, suggesting the potential for interspecific competition (Oliveira 1994; Nowell and Jackson 1996; Sunquist and Sunquist 2002). Additionally, competitive intraguild interactions are now acknowledged as important in influencing animal communities (Dayan *et al.* 1990; Creel and Creel 1996; Donadio and Buskirk 2006; St-Pierre *et al.* 2006). In this regard, the mesopredator and niche release theories are of special interest (Crooks and Soulé 1999; Moreno *et al.* 2006). The mesopredator release theory predicts that with the decline of top predators, mesocarnivore numbers would rise (Crooks and Soulé 1999), whereas the disappearance of a potential competitor would broaden the niche of its subordinate competitors (Moreno *et al.* 2006). However, it is unknown to what extent these interactions influence felid dynamics in the neotropics.

Here we tackle these issues by, first, characterizing ocelot ecology across its broad geographic range in an effort to understand the extent to which environmental variables influence ocelot demography and ecology; we then compare ocelot ecology to that of the other sympatric small cats with a view to revealing their ecological differences. We also assess the potential for competition between ocelot and other felids, combined with testing the competitive niche release hypothesis. Finally, we consider the potential role that ocelots might play as mesopredators in the dynamics of the small-felid assemblage of the lowland tropical neotropics.

Methods

To describe ocelot ecology and the environmental variables that might influence it, we compiled information from 35 sources detailing home range, habitat use, diet, and density across the species' full geographic range, including sites from the northernmost (south Texas) and southernmost (north-eastern Argentina and southern Brazil) extremities of its range (Fig. 27.1). In our analyses we consider small felids as all

those smaller than the ocelot; sympatric species to include the ocelot, jaguarundi, margay, and little spotted cat; and mesopredators as all small- to medium-sized lowland felids (i.e. ocelot, jaguarundi, Geoffroy's cat, pampas cat, margay, and little spotted cat).

Habitat was grouped into rainforest (Panama, Peru, Brazil-Pará [PA], Paraná [PR]), semi-arid habitats, which include scrub, chaparral, and dry forest (Texas and Mexico), and open flood plains/savannahs (Venezuela, Brazil-Mato Grosso do Sul-MS, and Goiás/Emas-GO) according to ecoregional similarities (Olson *et al.* 2001). Dense cover is considered here as either closed canopy or dense understorey, as described in their original studies. Body mass of adult male and female ocelots are combined for each site.

Differences in ocelot home range size and habitat use among sites and between sexes in different areas were compared using mean values. For comparing home ranges, whenever possible we used minimum convex polygons (MCP) incorporating 95% of fixes (using sources listed in Table 27.1). For habitat use and preference (but not for home range-estimates) for Emas National Park (ENP) (Brazil-GO) we only used 95% fixed kernel estimates. Preference/avoidance for each habitat type was measured using Ivlev's index of selectivity or preference (1961) (−1, complete avoidance, to +1, complete preference), on second and third order selection (Aebischer *et al.* 1993), as described in Manfredi *et al.* (2006) and Rocha (2006). Habitat categories for Emas include grassland savannah, scrub/woodland savannah, gallery forest, flooded grassland, and pasture/agriculture.

Ocelot diet was assessed by the analysis of droppings from study sites across the species range. Dietary results are presented as percent occurrence (number of times an item was found as a percentage of total number of prey items in droppings). We quantified diet using both percent occurrence and biomass contribution. For biomass calculations only mammalian prey were included. Prey were classed as very small mammals (<100 g: marsupials, rodents, others), small mammals (0.1–0.699 kg: marsupials, rodents), medium-sized mammals (0.7–1.5 kg: marsupials, rodents, rabbits, primates), large mammals (1.51–10 kg: rodents, xenarthrans, primates, carnivores, others), very large mammals (>10 kg: ungulates), birds, squamates (lizards and snakes), and other vertebrates. Maximum prey mass is defined as the mass of the

Figure 27.1 Ocelot distribution range showing the locations of study sites listed in the text. 1, S-Texas/United States (Lower Rio Grande Valley); 2, Tamaulipas/Mexico (Los Ebanos Ranch); 3, Barro Colorado Island/Panama; 4, Central Llanos-Guarico/Venezuela (Hato Masaguaral/Hato Flores Morada); 5, Carajás-Pará/Brazil; 6, Cocha Cashu Biological Station/Peru; 7, Tocantins/Brazil (Lajeado Dam); 8, ENP-GO/Brazil; 9, S-Pantanal-MS/Brazil; 10, Linhares-ES/Brazil (Vale do Rio Doce Natural Reserve); 11, Caratinga Biological Station-MG/Brazil; 12, Iguaçu National Park-PR/Brazil; 13, Serra do Tabuleiro State Park-SC/Brazil; 14, São Francisco de Paula National Forest-RS/Brazil. (Modified from Oliveira and Cassaro 2005.)

three largest species taken by each felid. Diets of sympatric species are compared using mean mammalian prey mass and niche overlap. To test for competitive niche release, we compared ocelot diet in areas with and without jaguars following Moreno *et al.*'s calculations (2006), and little spotted cat diet in the presence and absence of ocelots.

Mean prey body mass is often used as a metric in the assessment of trophic separation among carnivores (e.g. Oliveira 1994, 2002a; Ray and Sunquist 2001). The mean body mass of mammalian prey (MWMP) is determined as the arithmetic mean of the body mass of all mammalian prey consumed (geometric means tend to underestimate the mean mass of prey Walker *et al.* 2007). Body masses of prey species are from original studies, or from summaries in Fonseca *et al.* (1996) or Eisenberg and Red-

ford (1999). All prey items were assumed to be adult size, unless otherwise noted. However, to avoid over-representation, prey with a body mass larger than 1.5 times the felid's body mass were assumed to be juvenile and assigned 40% of the adult mass. Canine diameter, a metric used to evaluate carnivore segregation and character displacement (Dayan *et al.* 1990), was assessed for Brazilian specimens of sympatric species. Mean values were correlated with felid body mass, MWMP, and maximum prey mass.

Diet niche overlap is calculated using Pianka's index: $O_{jk} = \sum P_{ij}P_{ik}\sqrt{(\sum P_{ij}^2 \sum P_{ij}^2)}$, where P_{ij} and P_{ik} are the proportions of the *i*th resource used by the *j*th and the *k*th species, respectively (Pianka 1973). Values range from 0 (no similarity) to 1 (complete similarity). Calculations are made at the lowest taxonomic category of prey possible.

Table 27.1 Average home range (km^2) of adult lowland Neotropical felids in various habitats.

Species	Male	n	Female	n	Habitat	Location	Source
Ocelot	12.3	5	7.0	3	Thorn scrub/oak forest	S. Texas, United States	Tewes (1986)
	6.3	3	2.9	3	Thorn scrub/oak forest	S. Texas, Unites States	Laack (1991)
	8.1	2	9.6	2	Low tropical forest/pasture	Taumalipas, Mexico	Caso (1994)
	31.2	1	14.7	1	Central American rainforest	Cockscomb, Belize	Konecny (1989)
	30.8	2	30	3	Central American rainforest	Ciquibul, Belize	Dillon (2005)
	10.6	2	3.4	6	Gallery forest/flood plains	Llanos, Venezuela	Ludlow and Sunquist (1987)
	7.0	2	1.8	3	Amazon rainforest	Cocha Cashu, Peru	Emmons (1988)
	19.2	1			Savannah	Tocantins, Brazil	Trovati (2004)
	90.5	1	75	1	Savannah	ENP, Brazil	Silveira (unpublished data)
	5.4	1	2.6	2	Deciduous-gallery forests/flood plains	Pantanal, Brazil	Rocha (2006)
			1.3	3	Deciduous-gallery forests/flood plains	Pantanal, Brazil	Crawshaw and Quigley (1989)
Jaguarundi	11.7	4	7.2	4	Tropical forest	Morro do Diabo, Brazil	Jacob (2002)
	38.8	6	17.4	5	Subtropical forest	Iguaçu, Brazil/Argentina	Crawshaw (1995)
	9.6	8	8.9	5	Low tropical forest/pasture	Taumalipas, Mexico	Caso (1994, personal communication)
	94.1	2	20.1	1	Central American rainforest	Cockscomb, Belize	Konecny (1989)
	25.3	1	18.0	1	Savannah	Tocantins, Brazil	Trovati (2004)
			40.2	1	Savannah	Emas Nat. Park, Brazil	Silveira (unpublished data)
	8.5	1	1.4	1	Forest/savannah/eucalyptus plantation	São Paulo, Brazil	Michalski et al. (2006b)
	17.6	1	6.8	1	Subtropical forest	Iguaçu, Brazil/Argentina	Crawshaw (1995)
	23.4	3			Subtropical forest fragments/agriculture	Taquari, Brazil	Oliveira et al. (2008)
Margay	4.0	3	0.9	1	Low tropical forest/pasture	Mexico	Caso (personal communication)
	11.0	1			Central American rainforest	Cockscomb, Belize	Konecny (1989)
	15.9	1			Subtropical forest	Iguaçu, Brazil	Crawshaw (1995)
			20	1	Subtropical forest fragments/agriculture	Taquari, Brazil	Oliveira et al. (2008)

Species					Habitat	Location	Reference
Little spotted cat	4.8	2			Savannah	Tocantins, Brazil	Trovati (2004)
	17.1	1	0.9	1	Savannah	Serra da Mesa, Brazil ENP, Brazil	Rodrigues and Marinho-Filho (1999)
			25.0	1	Savannah		Silveira (unpublished data)
	8.0	2	2.0	1	Subtropical forest fragments/agriculture	Taquari, Brazil	Oliveira et al. (2008)
Pampas cat	27.7	4			Savannah	ENP, Brazil	Silveira (unpublished data)
Geoffroy's cat	3.1	2			Swamp forest/wet grassland/agriculture	Arroio Grande, Brazil	Oliveira et al. (2008)
	5.0	2	1.9	2	Wet pampas grassland	Campos del Tuyú, Argentina	Manfredi et al. (2006)
	8.9	2	5.1	1	Pampas grassland/agriculture	Tornquist Park, Argentina	Manfredi et al. (in preparation)
	2.2	4	1.1	2	Argentine Monte	Laguna de Chasicó	Manfredi et al. (in preparation)
	2.0	3	0.3	1	Scrubland	Lihue Calel National Park, Argentina	Pereira et al. (2006)
	9.2	5	3.7	2	Patagonian woodland/steppe	Torres del Paine, Chile	Johnson and Franklin (1991)

Estimates of felid abundance are based on records of tracks, photographs, or live captures. At each site felid species were ranked based on abundance indices, which varied from 1 (most abundant) to 5 (least abundant) (Oliveira *et al*. 2008, submitted).

Normality tests were conducted prior to determining the use of parametric or non-parametric statistics. Data in the form of percentages are converted into arcsin (y_t = arcsin $\sqrt{y}$) for statistical analyses (Zar 1999).

Ocelot home range and habitat use

Home range

Variation in home range size is expected to reflect differences in resource availability between areas (e.g. Sandell 1989; Gompper and Gittleman 1991). Ocelot home range size varies considerably between sites and between sexes across the continent (1.3–90.5 km^2, Table 27.1). The smallest ranges for males and females are in Brazil's Pantanal flood plains (5.4 km^2 and 1.3 km^2, respectively) and the largest in the savannahs of ENP (90.5 km^2 and 75 km^2, respectively) also in Brazil (Crawshaw and Quigley 1989; Rocha 2006; Silveira, unpublished data). Both are open areas, but the former is seasonally flooded and the latter is dry. Although sample sizes for Emas included only one male and one female, both were non-dispersing adults. At all sites, mean home range sizes of adult males (mean ± standard deviation, 22.6 km^2 ± 24.2, range 5.4–90.5 km^2, n = 30 animals from 12 sites) are significantly larger than those of adult females (14.4 km^2 ± 20.8, range 1.3–75 km^2, n = 36 individuals from 12 sites) (t = 3.386, d.f. = 10, P = 0.007) in accordance with Crawshaw (1995).

### *Relationships between home range, body size, and environmental variables*

Ocelot body mass (6.6–18.6 kg, n = 112) differs among regions (F = 5.835, P < 0.001). However, these differences do not correlate with latitude (r = −0.385, P = 0.306, Fig. 27.2), but varied with habitat types grouped as rainforests (mean = 11.1 kg ± 2.2, n = 56), open savannahs/flood plains (mean = 10.0 kg ± 2.4, n = 29), and semi-arid habitats (scrub, chaparral, and dry forest; mean = 8.7 kg ± 1.4, n = 27) (H =

21.72, d.f. = 2, P < 0.001). Pairwise comparisons show that rainforest ocelots are significantly larger than those of savannahs/flood plains (t = −2.085, d. f. = 83, P = 0.040) and scrub/chaparral/dry forest (t = 5.004, d.f. = 81, P < 0.001), but those of semi-arid habitats and savannahs/flood plains do not differ significantly (t = 664.5, P = 0.087). Ocelot body mass did not differ among evergreen forest sites (F = 1.741, P = 0.170). The pattern in ocelots contrasts with that for jaguar, which are larger in flood plains than in rainforests, due to larger size and greater abundance of large prey (>15 kg) in flood plains (Hoogesteijn and Mondolfi 1996). A possible, but untested, explanation for the greater mass of ocelots in rainforest than elsewhere is that larger ocelot prey may be more readily available in rainforests (e.g. Oliveira 1994; Nowell and Jackson 1996; Sunquist and Sunquist 2002). Agoutis (*Dasyprocta* spp.), pacas (*Agouti paca*), armadillos (Dasypodidae), large marsupials, monkeys, and sloths (*Bradypus, Choloepus*), which are important prey for ocelots, generally reach their highest densities in rainforests (see Glanz 1982; Emmons 1984).

When data from Emas are excluded due to their extremely large values, there is an intriguing, but not significant, tendency for average ocelot body mass and mean home range to be positively correlated (r = 0.767, P = 0.075, n = 6, Fig. 27.3). There are no differences in mean ocelot home range size by habitat type across all habitat categories (thorn scrub/dry forests, flood plains, savannahs, and forests) (F = 2.438, P = 0.157), suggesting that variations among areas are related to availability of prey and not to habitat structure *per se*. No correlation exists between mean annual precipitation and mean adult ocelot home range per site (r^2 = 0.079, P = 0.500); either for males (r^2 = 0.128, P = 0.384) or females (r^2 = 0.022, P = 0.729). In fact, in the Texas chaparral, where average annual rainfall is only 640 mm and habitat is considered suboptimal for the species, ocelot home range sizes are only 25% of those in wetter (1500 to 1700 mm/year) and presumably prime rainforest habitats of Belize and southern Brazil (Tewes 1986; Laack 1991; Crawshaw 1995; Dillon 2005). While precipitation in Texas is rather low, rodents and rabbits are abundant (Tewes 1986). These facts suggest, unexpectedly, that abiotic variables have little detectable direct influence on ocelots' home range size and, consequently, their density.
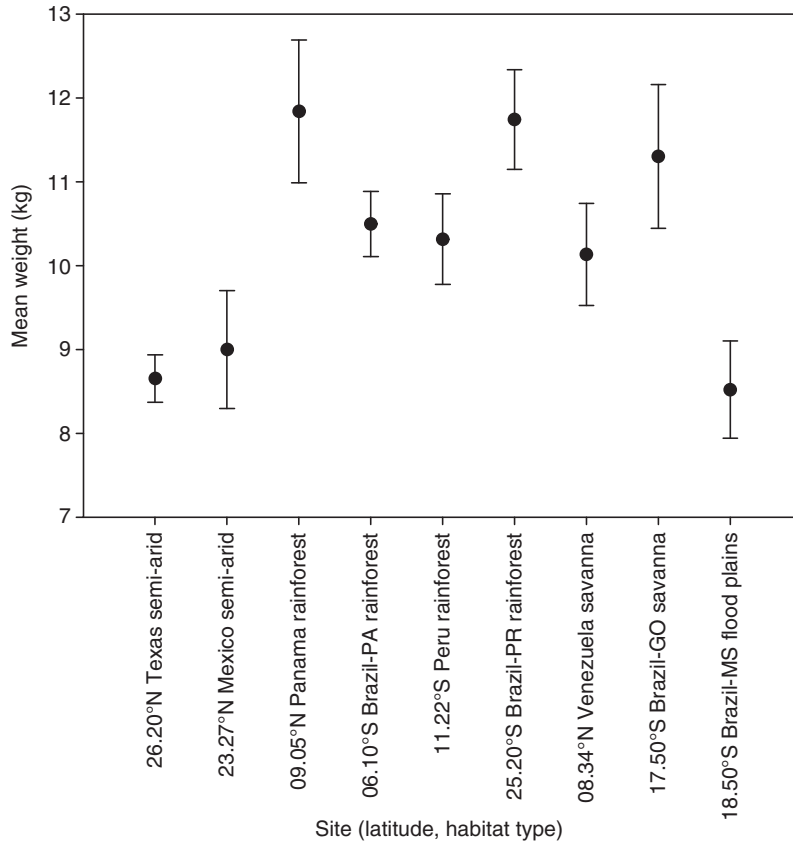
Figure 27.2 Ocelot mass (mean ± standard error) in the Americas, grouped by habitat similarity and latitude. (Data sources: Tewes 1986; Ludlow and Sunquist 1987; Emmons 1988; Laack 1991; Crawshaw 1995; Rocha 2006; Companhia Vale do Rio Doce, unpublished data; Crawshaw and Quigley, unpublished data; Moreno and Kays, unpublished data; Silveira, unpublished data.)
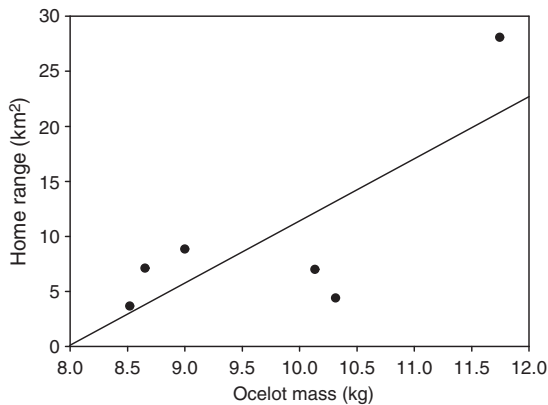
Figure 27.3 Correlation of mean ocelot body size and mean home range in the Americas.

Habitat use

Several studies highlight the importance of dense habitat cover for conservation of ocelots (e.g. Tewes 1986; Ludlow and Sunquist 1987). In South Texas, 51% of ocelot locations were in dense habitat cover, which comprised only 1% of the study area (Harveson *et al.* 2004). In northern Mexico, 97.6% were in dense brush (i.e. dense woody cover) (Caso 1994). The strong selection of ocelots for dense cover in south Texas could also be related to avoidance of the similar-sized and sympatric bobcat (*Lynx rufus*) (Tewes 1986; Fisher 1998). In the open savannahs of ENP, ocelots favoured areas of dense forest and savannah, but they also used pastoral/agricultural land, and avoided grassland savannah and flooded grasslands. Forest cover

Table 27.2 Summary of habitat use versus availability of sympatric felids at ENP (Brazil).

	Home range within each habitat type (usage within home range, %)				
	Grassland savannah	Scrub savannah	Gallery forest	Flooded grassland	Pasture/ agriculture
Availability	42.50	23.22	1.83	2.61	29.83
Ocelot M1	16.67 (0)	41.06 (55.17)	5.42 (6.90)	0.90 (0)	35.95 (37.93)
Ocelot M2	8.86 (2.70)	28.22 (29.73)	4.01 (27.03)	1.32 (5.41)	57.58 (35.14)
Ocelot F1	6.91 (4.58)	37.39 (45.04)	5.65 (4.58)	1.35 (0)	48.70 (45.80)
Jaguarundi F1	22.25 (22.37)	38.38 (42.11)	2.33 (1.32)	0.45 (0)	36.59 (34.21)
Little spotted cat F1	30.80 (29.41)	40.75 (39.71)	1.30 (0)	0.20 (2.94)	29.95 (27.94)
Pampas cat M1	100.00 (100.00)	0	0	0	0
Pampas cat M2	59.70 (36.74)	3.84 (23.53)	0 (0)	0.04 (0)	36.43 (36.74)
Pampas cat M3	54.49 (58.33)	12.58 (8.33)	2.70 (16.67)	0.16 (0)	30.07 (16.67)

comprised only 1.8% of the total area (Table 27.2). Ocelots varied individually in their habitat use in Emas but, on average, scrub/woodland savannah and pasture/agriculture were used in proportion to their availabilities (Ivlev's third order values: 0.09 and −0.08, respectively), grassland savannah and flooded grassland were avoided (−0.6, −0.5, respectively), and forest was positively selected (0.3). In the Pantanal flood plains, too, ocelot home ranges were configured to encompass forests and scrub/woodland savannahs, and under-represented open grassland savannahs (Rocha 2006).

One suggestion is that, due to their frequent association with dense cover, ocelots might occupy a narrower range of microhabitats than expected from their wide geographic distribution (Emmons 1988). However, throughout Brazil, ocelots commonly use heavily disturbed areas in the Amazon, Cerrado, Atlantic Forest, and Pantanal biomes (Oliveira, personal observation; R. Boulhosa, personal communication; E. Payan, personal communication; Silveira, unpublished data). Indeed, they have been found in habitats varying from heavily logged and fragmented, to early and late successional forests, the outskirts of major cities and towns, disturbed scrub/woodland savannah and mosaic of forest (disturbed or not), and savannah with eucalyptus plantations and agricultural areas. In short, despite being associated with dense cover, ocelots show a higher level of habitat plasticity than previously thought.

## Comparative ecology of ocelots and other sympatric cats

Comparative home range

The limited data on adult home range sizes of the smaller, sympatric lowland felids also show considerable variation (Table 27.1). Jaguarundi (mean body mass 5 kg) averages 24.2 ± 20.4 SD km^2, margay (3.3 kg) 12.3 ± 7.6 SD km^2, and little spotted cat (2.4 kg) 10.9 ± 9.6 SD km^2. The expected home range sizes based on their body mass and metabolic needs (Lindstedt *et al.* 1986) would be 8.9 km^2, 5.8 km^2, and 4.2 km^2, respectively. For ocelots (11 kg) the average and expected home range sizes are similar, at 20.0 ± 25.2 km^2 and 20.1 km^2, respectively. Thus, the average home range sizes of the smaller lowland felids are 2.5 (2.1–2.7) times larger than what would be expected based on body size. Pairwise comparisons of mean home range values of male and female of the smaller species show that male ranges are significantly larger than those of females ($W = −36.00$, $T += 0.00$, $T −= −36.00$, $P = 0.008$), as was noted for ocelots.

There is considerable inter- and intraspecific variation in home range size among the sympatric felids, resulting in extensive overlap in size and no significant differences among mean adult home ranges ($F = 0.749$, $P = 0.529$, Table 27.1).

Home range size in solitary male carnivores is, on average, 2.5 times that of females, and this value is also significantly larger than expected based on energy
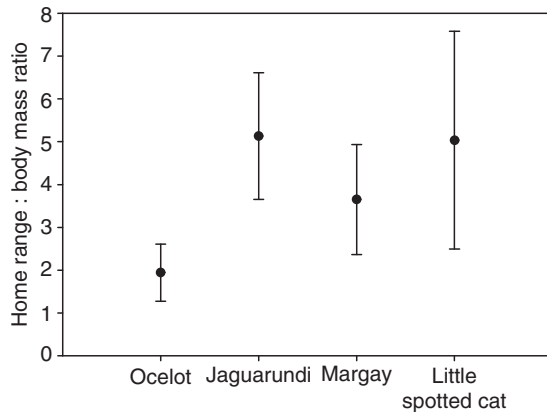
Figure 27.4 Home range size:body mass ratio (mean ± standard error) of sympatric lowland felids. (Data sources: Table 27.1.)

requirements, suggesting that access to several females plays an important role in determining male territory size (Sandell 1989). Thus, the larger home ranges of male lowland Neotropical felids should be linked to the distribution of females, rather than to the availability of food resources (Ludlow and Sunquist 1987; Manfredi *et al.* 2006), a pattern typical in the Felidae.

Average home range:felid body mass ratio among the sympatric assemblage is smallest for ocelots (1.9 km² per kg of body mass) and larger for jaguarundis, little spotted cats, and margays (5.1, 5.0, 3.7 km² per kg of body mass, respectively; Fig. 27.4). Hypotheses to explain the larger than expected home range sizes of the smaller species include avoidance of larger guild-members through the use of areas of lower prey density, living along the periphery of the dominant species range, or use of different habitats where they live in sympatry (Creel and Creel 1996; Durant 1998; Palomares *et al.* 1998). Through such mechanisms, larger, dominant species may attain higher densities and have smaller home range sizes than do some smaller, subordinate species due to avoidance of the former by the latter (Creel and Creel 1996; Woodroffe and Ginsberg 2005).

Comparative habitat use

Although most felids use open habitats, all lowland species, except pampas cats, are closely associated with forest cover. At localities with a mosaic of open and closed environments, including agricultural areas, the use of closed habitats by ocelots, jaguarundis, mar-

gays, and little spotted cats was similar, and on average 74% (40–98%) of the location records, despite the fact that dense cover sometimes comprised only 11% of the total vegetation (Ludlow and Sunquist 1987; Caso 1994; Harveson *et al.* 2004; Trovati 2004; Michalski *et al.* 2006b; Oliveira *et al.* 2008; Silveira, unpublished data). Margays seem even more strongly associated with dense cover than are ocelots (Oliveira 1998b, personal observation). Even jaguarundis, which are typically associated with open habitats (Oliveira 1998a), use forested habitats part of the time. It seems that only pampas cats are a predominantly open-habitat specialist, but they too can be found in forests (Oliveira 1994; Sunquist and Sunquist 2002).

In the savannahs of Emas, pampas cats prefer open grassland savannahs, and also use pastoral/agricultural lands, but avoid forest and scrub/woodland savannah. One female jaguarundi favoured scrub savannah and used forest and pastoral/agricultural lands slightly more than its availability, whereas one female little spotted cat used forest and pastoral/agricultural lands less than its availability; both species avoided the open grasslands. They used scrub/woodland savannah, open grassland, and pastoral/agricultural lands in proportion to availability. Unexpectedly, jaguarundis and little spotted cats both avoided forest (Ivlev's = −0.3 and −1, respectively), and differed only in that flooded grassland was strongly avoided by the former and selected by the latter. Otherwise, all species strongly avoided flooded grasslands (Table 27.2). The spatial separation among small felids in Emas could be due to avoidance of ocelots. In contrast to Emas, 92.3% and 70% of locations of two male little spotted cats in the savannah biome of Tocantins State (central Brazil) were in forests, and only 7.7% and 30% in savannah. In contrast, jaguarundis in Tocantins were located 17% of the time in forests and 83% in savannahs (Trovati 2004). Additionally, in an agriculture-forest patch mosaic, both species were strongly associated with forest cover (Oliveira *et al.* 2008).

There appear to be parallels within the Neotropical small felid guild to the differential habitat use by jackal species in areas of sympatry and allopatry. In that case, the dominant species narrows the number of habitats used by the subordinate species, which avoids the more aggressive competitor (Loveridge and Macdonald 2002; Macdonald *et al.* 2004c).

In agricultural landscapes in Brazil, radio-tracked ocelots, jaguarundis, margays, and little spotted cats only rarely used open fields, but preferred field borders near forest cover (Oliveira *et al.* 2008; Silveira, unpublished data). These edge habitats may offer both high rodent abundance and cover. While Geoffroy's cats tended to spend more time in densely vegetated habitat (Manfredi *et al.* 2006; Lucherini *et al.*, unpublished data) they may also use open agricultural fields (Oliveira *et al.* 2008). Occasional use of open areas is not restricted to jaguarundis, pampas cats, and Geoffroy's cats. Faecal analysis of little spotted cat diet in secondary Atlantic rainforest revealed prey from both forest and field/forest edges, but not from agricultural fields (Facure-Giaretta 2002). In summary, ocelots, margays, little spotted cats, and Geoffroy's cats favour dense cover, jaguarundis use both open and closed habitats, whereas pampas cats use predominantly open habitats.

Ocelot foraging ecology, niche release, and the sympatry issue

Ocelot feeding ecology

Ocelot diet varies throughout its range (Fig. 27.5). Small mammals (rodents and marsupials <600 g) are generally the numerically pre-eminent prey (61.3% $\pm$ 28), but their biomass contribution is less (10.7% $\pm$ 11.1). Conversely, large rodents (>1 kg), armadillos, ungulates, and possibly sloths and monkeys, contribute much more in terms of biomass (Table 27.3). Large rodents, especially paca and agouti, are important in terms both of biomass (27.1% $\pm$ 15.3), and the frequency with which they are eaten (11.4% $\pm$ 8.1) (e.g. Bianchi 2001; Aliaga-Rossel *et al.* 2006; Moreno *et al.* 2006), and occurred in ocelot diets at 11 of 13 study sites. This revises the earlier perception that small rodents are the major prey of ocelots (reviewed by Oliveira 1994; Nowell and Jackson 1996; Sunquist and Sunquist 2002). At some sites (e.g. Panama and Caratinga-Brazil) sloths and monkeys also make a considerable contribution (18.8–26.9%) (Moreno *et al.* 2006; Bianchi and Mendes 2007). Ungulates, especially deer (*Mazama* spp.), are infrequently taken (3.7% $\pm$ 3.4), but when they are, can contribute substantially to biomass intake (29% $\pm$ 26.7).

The MWMP taken by ocelots, while highly variable, averages 1.5 $\pm$ 1.1 kg, and is highest in Atlantic rainforest (Linhares, Espirito Santo State, in Southeast Brazil) at 3.3 kg, and lowest in the Llanos flood plains of Venezuela, at 0.3 kg (Ludlow and Sunquist 1987; Bianchi 2001) (Table 27.4). In Linhares this reflects the prevalence of armadillos and
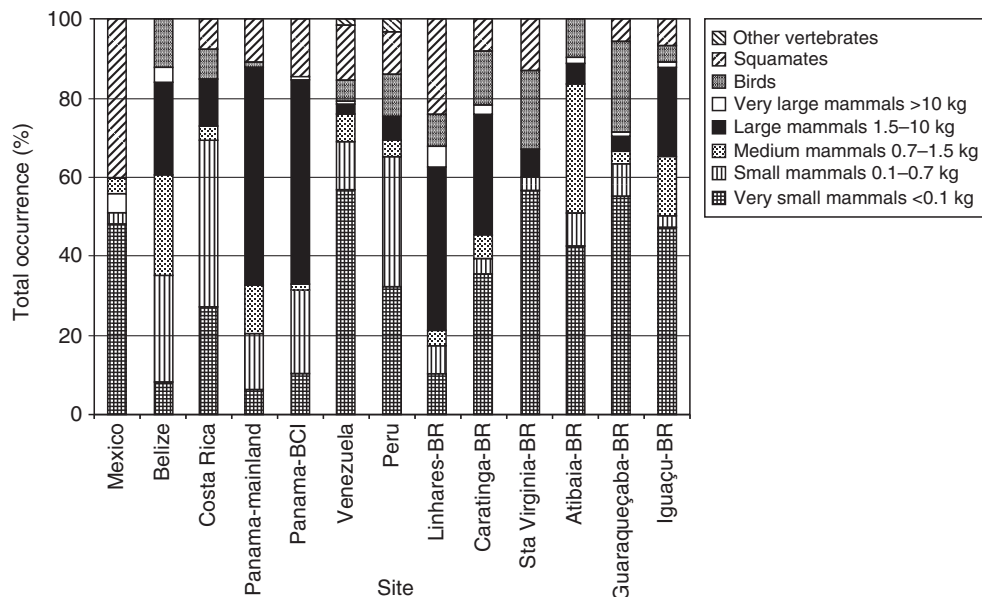
Figure 27.5 Ocelot diet (total occurrence, %) throughout the Americas. (Data sources: Table 27.3.)

Table 27.3 Contribution of main prey items by percentage of occurrence (#) and biomass to the diet of ocelots throughout the Americas (values in percentage). Percentage of occurrence is derived from the number of occurrences of each diet item as a percentage of all occurrences of all diet items.

Site	Large rodents		Armadillos		Sloths		Monkeys		Ungulates		Small mammals	
	#	Biomass	#	Biomass	#	Biomass	#	Biomass	#	Biomass	#	Biomass
Mexico[1]	9.23								9.43	90.86	90.57	9.14
Belize[2]	9.09	33.00	15.38	24.06					4.62	21.45	40.00	5.00
Costa Rica[3]		47.56									81.82	25.68
Panama-mainland[4]	17.31	18.15	11.54	14.52	26.92	41.40					15.38	1.52
Panama-BCI[4]	25.00	26.96	2.71	3.43	23.37	40.83	7.07	6.56	1.09	3.19	35.88	3.59
Venezuela[5]	1.88	12.34	0.94	8.59					0.94	33.81	87.32	23.25
Peru[6]	8.33	54.25					1.67	2.37			85.83	34.9
Linhares-BR[7]	23.81	38.53	27.38	26.59			4.76	2.78	8.33	20.74	19.05	1.11
Caratinga-BR[7]	15.29	20.68	8.24	12.52			18.82	61.94			49.41	1.09
Sta Virginia-BR[8]			5.26	43.78	5.26	46.78					84.21	9.43
Atibaia-BR[9]	1.82	9.34	3.64	13.63					1.82	22.04	56.36	3.96
Guaraquecaba-BR[10]	3.23	8.30					3.23	26.02	1.61	28.74	95.16	17.15
Iguaçu-BR[11]	10.94	28.68	10.94	29.18					1.56	11.37	56.25	2.74
Mean	11.45 ±	27.07 ±	9.56 ±	19.59 ±	18.52 ±	43.00 ±	7.11 ±	19.93 ±	3.68 ±	29.03 ±	61.33 ±	10.66 ±
Standard deviation	8.11	15.27	8.17	12.45	11.62	3.28	6.84	25.41	3.42	26.73	28.01	11.08
Paired t-test	−4.114		−2.927						−3.901		10.834	
d.f.	10		8						7		12	
P	0.002		0.019						0.006		<0.001	

Notes: [1] Villa Meza et al. 2002; [2] Konecny 1989; [3] Chinchilla 1997; [4] Moreno et al. 2006; [5] Ludlow and Sunquist 1987; [6] Emmons 1987; [7] Bianchi 2001; [8] Wang 2002; [9] Facure-Giaretta 2002; [10] Vidolin 2004; [11] Crawshaw 1995.

BR, Brazil.

Table 27.4 Primary ocelot prey by percentage of occurrence (vertebrates) and biomass contribution (mammals), and mean weight of mammalian prey (MWMP) throughout the Americas, all weights in grams (g).

Habitat/location	Main vertebrate prey (occurrence, %)			Main mammalian prey (biomass)			MWMP (g)	n
	Species	Prey mass	All items (%)	Species	Prey mass	Mammals (%)		
Tropical dry forest/ Mexico[1]	1. Ctenosaura pectinata	800	36.4	1. Odocoileus virginianus[12]	15,000	90.9	1465.74	51
	2. Liomys pictus	50	32.3	2. Liomys pictus	50	2.1		
	3. Marmosa canescens	30	9.1	3. Sigmodon mascotensis	180	0.7		
Tropical rainforest/ Belize[2]	1. Didelphis marsupialis	1000	25.7	1. Agouti paca	8000	33.0	2238.00	49
	2. Philander opossum	400	20.3	2. Dasypus novemcinctus	3500	24.1		
	3. Dasypus novemcinctus	3500	13.5	2. Mazama americana[12]	10,400	21.4		
Tropical rainforest/Costa Rica[3]	1. Proechimys semispinosus	375	34.6	1. Dasyprocta punctata	4000	47.6	764,55	23
	2. Heteromys desmarestianus	75	15.4	2. Proechimys semispinosus	375	20.1		
	3. Tylomys watsoni	240	7.7	3. Potos flavus	2500	14.9		
	3. Dasyprocta punctata	4000	7.7					
	3. Penelope purpurescens	1700	7.7					
	3. Iguana iguana	3000	7.7					
Tropical rainforest/ mainland-Panama[4]	1. Bradypus variegatus	4300	18.8	1. Bradypus variegatus	4300	37.6	2861.15	49
	2. Dasyprocta punctata	3000	13.0	2. Dasyprocta punctata	3000	18.1		
	3. Dasypus novemcinctus	3600	8.7	3. Nasua nasua	4500	15.1		
	3. Iguana iguana	3000	8.7					
Tropical rainforest/BCI- Panama[4]	1. Dasyprocta punctata	3000	16.2	1. Dasyprocta punctata	3000	24.0	2852.38	190
	2. Proechimys semispinosus	375	15.4	2. Choloepus hoffmanni	5700	22.8		
	3. Bradypus variegatus	4300	8.5	3. Bradypus variegatus	4300	18.0		
Llanos gallery forest/ floodplains/ Venezuela[5]	1. Zygodontomys brevicauda	50	37.6	1. Odocoileus virginianus[12]	16000	21.5	349.91	160
	2. Sigmomys alstoni	40	18.8	2. Sylvilagus floridanus	800	14.0		
	3. Holochilus brasiliensis	300	14.6	3. Holochilus brasiliensis	300	12.5		

Location	Prey item	Mass	%	Prey item	Mass	%	Mass	n
Amazon rainforest/Peru[6]	1. Proechimys spp.	280	31.6	1. Proechimys spp.	280	26.6	491.58	62
	2. Oryzomys spp.	70	21.5	2. Dasyprocta variegata	4000	20.3		
	3. Birds	—	10.7	3. Agouti paca	8000	13.6		
Tropical rainforest/Linhares—Brazil[7]	1. Dasypus spp.	3200	15.5	1. Agouti paca	8000	31.8	3294.94	77
	2. Tupinambis merianae	1200	8.8	2. Dasypus spp.	3200	26.6		
	3. Agouti paca	8000	7.4	3. Tayassu tajacu[12]	7600	11.0		
Tropical rainforest/Caratinga—Brazil[7]	1. Calomys sp.	25.5	12.9	1. Alouatta guariba	5650	37.9	2104.64	60
	2. Birds	—	12.1	2. Brachyteles hypoxanthus	13,500	22.6		
	3. Alouatta guariba	5650	9.7	3. Agouti paca	8000	13.4		
Tropical rainforest/Sta. Virginia—Brazil[8]	1. Akodon sp.	28.7	23.3	1. Bradypus variegatus	3900	46.8	438,76	17
	2. Monodelphis sp.	48	20.0	2. Dasypus novemcinctus	3650	43.8		
	3. Colubrid snakes	—	13.3	3. Akodon sp.	28.7	2.4		
Tropical rainforest/Atibaia—Brazil[9]	1. Sphiggurus villosus	1325	19.7	1. Sphiggurus villosus	1325	30.3	953.74	34
	2. Oligoryzomys nigripes	16.7	14.8	2. Mazama americana[12]	11,560	22.0		
	3. Didelphis spp.	1500	9.8	3. Didelphis spp.	1500	17.2		
	3. Akodon sp.	28.7	9.8					
	3. Birds	—	9.8					
Tropical rainforest/Guaraqueçaba—Brazil[10]	1. Cricetidae	50	49.5	1. Mazama spp.	9000	28.7	505.16	60
	2. Birds	—	21.5	2. Cebus/Alouatta	4075	26.0		
	3. Tupinambis merianae	1200	5.4	3. Tamandua tetradactyla	5200	16.6		
Subtropical rainforest/Iguaçu—Brazil[11]	1. Small rodents	50	37.8	1. Dasypus novemcinctus	3300	29.2	1236.86	56
	2. Didelphis aurita	1500	8.5	2. Dasyprocta azarae	3200	24.3		
	2. Dasypus novemcinctus	3300	8.5	3. Didelphis aurita	1500	13.3		
	4. Dasyprocta azarae	3200	7.3					

[1] Villa Meza et al. 2002; [2] Konecny 1989; [3] Chinchilla 1997; [4] Moreno et al. 2006; [5] Ludlow and Sunquist 1987; [6] Emmons 1987; [7] Bianchi 2001; [8] Wang 2002; [9] Facure-Giaretta 2002; [10] Vidolin 2004; [11] Crawshaw 1995; [12] 40% of body mass.

n, sample size (number of scats).

pacas (average body mass of 3.2 kg and 8 kg, respectively), which comprise 40.5% of mammalian items and 23% of total vertebrates taken (Bianchi 2001). Conversely, the mean body mass of all vertebrate prey taken in the Llanos increases to 0.6 kg when iguanas (*Iguana iguana, c.* 2.7–3.0 kg) are included (Ludlow and Sunquist 1987). The figures presented here double the previously reported (Oliveira 1994) mean size of ocelot mammalian prey, due to including a larger number of studies (e.g. Crawshaw 1995; Bianchi 2001; Moreno *et al.* 2006).

Emmons (1987) predicted that the average adult ocelot would eat 0.56–0.84 kg of meat per day, and the figures reported in this review either fall within this range or above it. Given that the average carnivore biomass is typically 1–3% of the biomass of their prey (Vézina 1985), the prey biomass predicted to sustain one ocelot for a year would range from 366 to 1100 kg, or 33–100 kg of prey per kilogram of ocelot, which is below the ratio reported for the larger jaguars and pumas (Emmons 1987). At all sites where MWMP was >1 kg, prey mass of at least one of the main vertebrate species was ≥0.8 kg. At 10 of 13 sites (76.9%), at least one main prey of ocelots weighed ≥0.8 kg (Table 27.4). However, there was no statistically significant relationship between MWMP with the body mass of the three main (in terms of biomass consumed) mammalian prey ($r^2 = 0.344$, $P = 0.262$), but a significant positive correlation existed between MWMP and the body mass of the three most numerically prominent vertebrate prey ($r^2 = 0.904$, $P = 0.006$).

Carnivore density is known to be constrained by metabolic needs and prey abundance (Carbone and Gittleman 2002). Sunquist (1992) argued that it would be virtually impossible for a lactating female to raise cubs on a diet of small mice (*c.* 50 g, e.g. *Oryzomys, Zygodontomys* spp.). Emmons (1988) reported that a lactating female ocelot increased her activity from 12–14 h/day to almost 23 h/day, and still was unsuccessful in rearing her kittens. This prompts the hypothesis that the limiting factor for ocelot persistence may be the availability of larger sized prey (≥0.8 kg), such as agouti and armadillos, to complement the intake of small mammals.

## Dietary comparisons within the Neotropical felid assemblage

The ocelot's fundamental niche is much broader than those of the smaller species, with prey ranging from small mice to collared-peccary (*Tayassu tajacu*), brocket (*Mazama* spp.), and white-tailed deer (*Odocoileus virginianus*) (Konecny 1989; Bianchi 2001; Villa Meza *et al.* 2002). Jaguarundis, margays, and little spotted cats prey predominantly on small mammals (<1 kg) (Fig. 27.6), but, like ocelots, they also prey on birds, squamates, and occasionally larger mammals. This raises the possibility that exploitative competition occurs between ocelots and smaller cats as well as among the smaller felids, as has been noted for larger carnivores (Woodroffe and Ginsberg 2005). However, among the array of prey, predators tend to specialize on those that they can capture most easily, effectively, and profitably (Sinclair *et al.* 2003).

The ocelot is the only felid within its guild that consistently takes prey weighing ≥1 kg. The smallest prey size for all sympatric felid species is in the range of 10–20 g (bats, small mice, and marsupials). However, maximum prey masses diverge considerably, but are positively correlated with mean felid mass ($r = 0.884$, $P = 0.0001$, see also Oliveira 1994, 2002a; Oliveira and Paula, unpublished data). Competition within carnivore guilds is probably asymmetrical. Larger species, whilst supported by larger prey not available to their smaller competitors, may deplete the latter's food supply by opportunistic predation on small prey (Woodroffe and Ginsberg 2005). The diets of sympatric felids (Fig. 27.5 and Fig. 27.6) suggest competitive pressure from the larger ocelots upon the smaller jaguarundis, margays, and little spotted cats.

Canine diameter, a useful measure of ecological segregation among carnivores (Dayan *et al.* 1990), differs significantly between sympatric Neotropical small felids, excepting margays and jaguarundis (Oliveira, unpublished data). Mean upper canine diameters correlate with felid mean body mass ($r = 0.980$, $P = 0.0199$, Fig. 27.7) and average MWMP ($r = 0.987$, $P = 0.0125$). Conversely, there is no correlation between canine diameter and maximum prey mass. Thus, canine diameter seems to reflect the modal, rather than the maximal, size of prey.
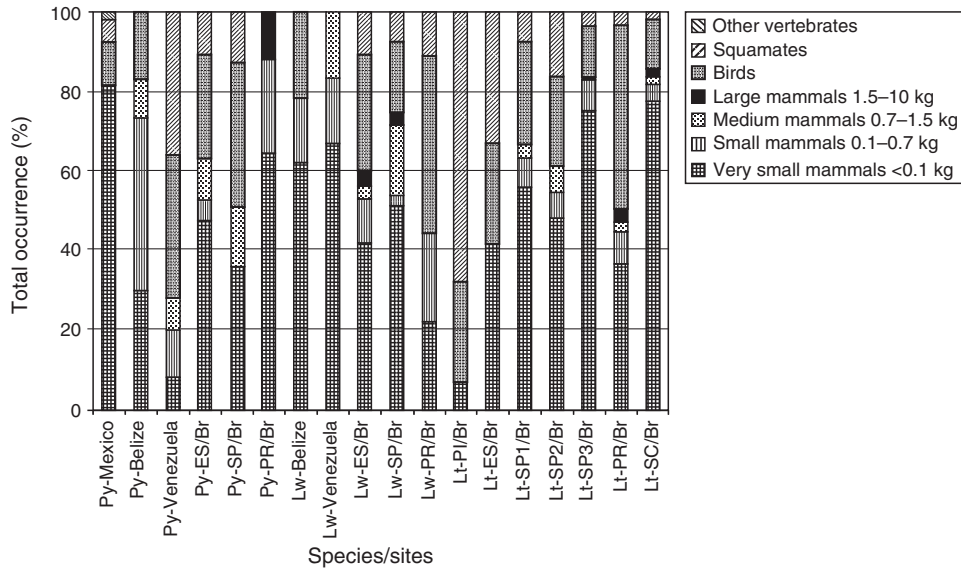
Figure 27.6 Jaguarundi (Py), margay (Lw), and little spotted cat (Lt) main prey items (total occurrence, %) in the Americas. (Data sources: Py: Bisbal 1986; Mondolfi 1986; Konecny 1989; Facure and Giaretta 1996; Felipe 2003; Guerrero *et al*. 2002; Oliveira 2002a; Rocha-Mendes 2005; Lw: Mondolfi 1986; Konecny 1989; Wang 2002; Felipe 2003; Rocha-Mendes 2005; Lt: Olmos 1993; Facure and Giaretta 1996; Facure-Giaretta 2002; Nakano-Oliveira 2002; Wang 2002; Rocha-Mendes 2005; M. Tortato, unpublished data.)
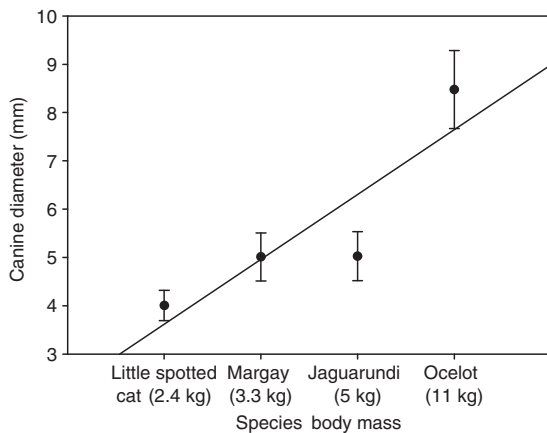
Figure 27.7 Correlation of mean upper canine diameter (±SD) and mean body mass for little spotted cats (*n* = 28), margays (*n* = 34), jaguarundis (*n* = 24), and ocelots (*n* = 47) in Brazil (*r* = 0.980, *P* = 0.0199). (Data source: Oliveira, unpublished data.)

Food niche overlap values between ocelots and margays average 0.41 (0.68–0.19, *n* = 3), between ocelots and little spotted cats it is 0.66 (0.81–0.45, *n* = 3), and between ocelots and jaguarundis it is 0.49.

Given the differences in body size and canine dimensions, these values are high. The highest overlap for ocelots is with the smallest species, the little spotted cat, but small sample sizes (and scarcity of studies of sympatric felids) may distort these comparisons.

A pairwise comparison of the food niches of the smaller species shows an average overlap of 0.62 (±0.253, range 0.18–0.91) (Konecny 1989; Olmos 1993; Facure and Giaretta 1996; Facure-Giaretta 2002; Nakano-Oliveira 2002; Wang 2002; Felipe 2003; Rocha-Mendes 2005). Therefore, the available datasets provide no evidence of any significant difference in overlap in food niche between ocelots and other sympatric felids (*t* = −0.757, d.f. = 14, *P* = 0.461) or among the smaller species (*F* = 0.841, *P* = 0.484).

The obvious potential for competition amongst these felids may be offset by the considerable difference in MWMP between ocelots and the smaller species, and despite their overlap on more abundant prey, each may be selecting specific prey (Pimm 1991). Dietary overlaps varying from very high to very low have been reported for Neotropical felids (Oliveira 2002a; Moreno *et al.* 2006). In the high

Andes dietary overlap of pampas cats and Andean cats (*Leopardus jacobita*) was very high (82%), but they nonetheless emphasized different principal prey (Walker *et al.* 2007; see Marino *et al.*, chapter 28, this volume). Furthermore, high overlap in one niche dimension might be compensated by low overlap in other axes, such as space use and time of activity, or even seasonal temporal variation in hunting of prey (Fig. 27.8), thus facilitating the sympatry (Konecny 1989, Oliveira *et al.* 2008; Silveira, unpublished data).

MWMP differs significantly between sympatric Neotropical felids ($H = 20.362$, d.f. $= 3$, $P < 0.001$; Table 27.4, Fig. 27.9). Pairwise comparisons are also significantly different ($P < 0.05$) for every combination except for margay–little spotted cat and margay–jaguarundi. Margays are intermediate between the other two species, in so far as they are closer in size and appearance to little spotted cats, but closer to jaguarundis in feeding morphology (e.g. canine diameter, jaw length; Kiltie 1984; Oliveira and Cassaro 2005; Oliveira, unpublished data). Not surprisingly, the largest difference between the smallest and largest MWMP is for the ocelot (9.4-fold), whereas the range of prey sizes taken by jaguarundi, margay, and little spotted cats is 2.3-, 3.9-, 4.9-fold, respectively. Mean MWMP represents 13.7% of ocelot mass (3.8–30%), 6.2% of jaguarundi mass (4–9.1%), 7.3% of margay mass (3.1–12.2%), and 6.3% of little spotted cat mass (2.4–11.9%).

Assessing the potential for competitive release

While ungulates, armadillos, and large rodents are taken by pumas and jaguars (see Oliveira 2002a), and are favoured by humans as well (Jorgenson and Redford 1993; Oliveira 1994), these prey are also taken by ocelots (Table 27.3). Thus, there is potential for niche overlap between ocelots and big cats. Alternatively, ocelots could be taking larger prey only in areas where jaguars are absent (Moreno *et al.* 2006). To test for a jaguar dietary release on mesopredators, as suggested by Moreno *et al.* (2006), we compared ocelot MWMP from areas with robust jaguar populations ($n = 8$) to those areas with marginal occurrence or absence ($n = 5$) of jaguars, and found no dietary

differences ($t = -0.951$, d.f. $= 11$, $P = 0.362$). In fact, the highest MWMP was from an area with a substantial jaguar population (Bianchi 2001; Garla *et al.* 2001). MWMP for ocelots was $11.8 \pm 11.0\%$ of the jaguar's and $19.6 \pm 13.4\%$ of the puma's mean prey body mass where all three were sympatric (Fig. 27.10; Emmons 1987; Crawshaw 1995; Chinchilla 1997; Brito 2000; Bianchi 2001; Garla *et al.* 2001). Therefore, it seems unlikely, on the basis of their MWMP, that ocelot compete substantially with the big cats.

To test for dietary release in the absence of ocelots, we compared the MWMP of little spotted cats from areas with moderate to robust ocelot populations ($n = 2$) to those where ocelots were rare or absent ($n = 3$), and found no dietary differences ($t = -1.627$, d.f. $= 3$, $P = 0.202$). Although sample sizes were small, this suggests that, just as jaguars do not constrain ocelot diets, ocelots do not appear to be constraining the diets of little spotted cats. Furthermore, the average MWMP of little spotted cats is 9.7% of the ocelot's (references in Table 27.3 and Fig. 27.6), suggesting considerable scope for resource partitioning between them.

Factors affecting ocelot density and dynamics

A species' abundance is influenced by proximate factors such as prey density, habitat, presence of potential competitors and predators, and ultimately by environmental variables, especially those that influence prey productivity.

Abundance rank

The larger ocelot seems to be the most versatile felid within the lowland, small-medium Neotropical assemblage. In Brazil, regardless of habitat type ($n = 24$), ocelots were the most abundant cat in 84.2% of all areas examined (Fig. 27.11). Of the smaller sympatric species, margays usually ranked second in abundance in rainforests and last in savannahs, where jaguarundis were most abundant. Little spotted cats usually ranked second or first only in areas where ocelots were absent or rare (Oliveira *et al.*

(a)

(b)
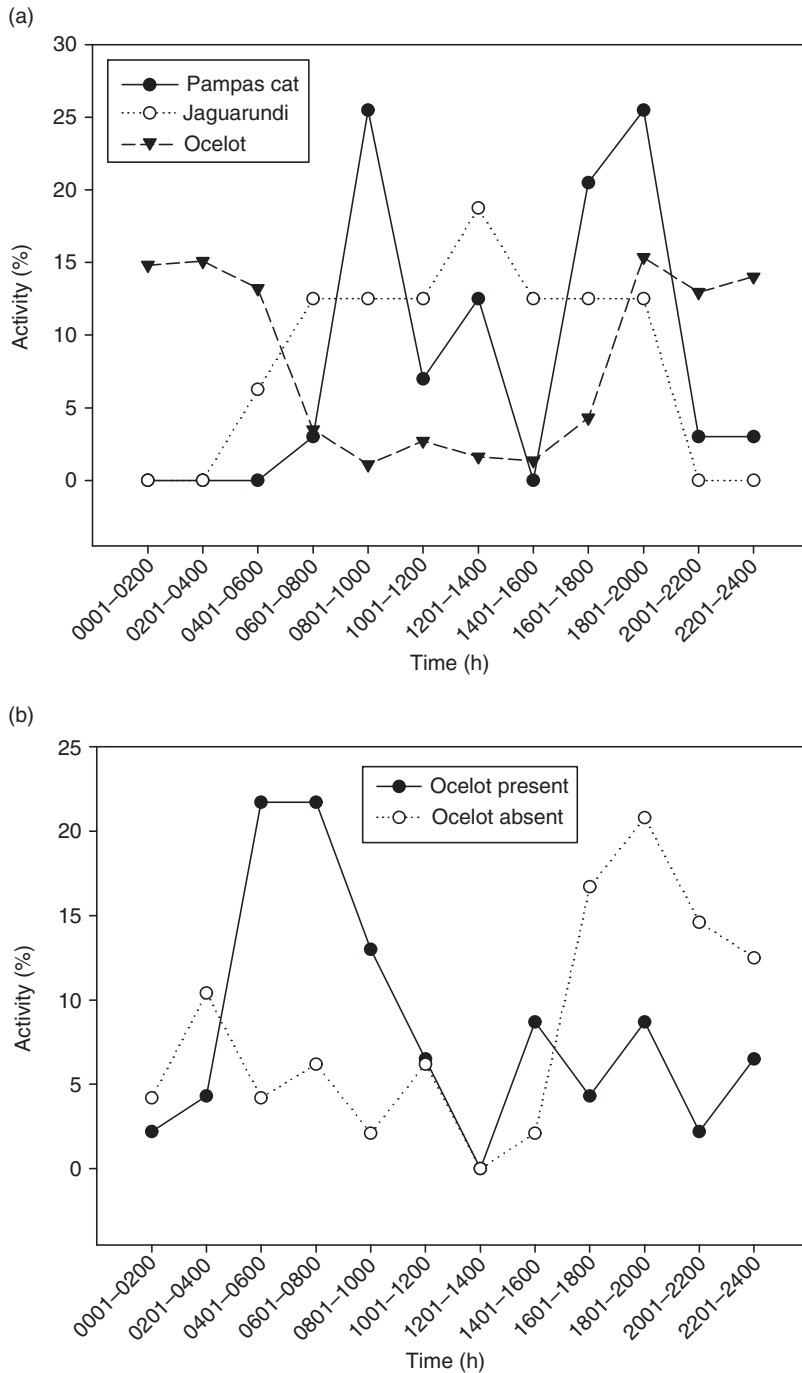
Figure 27.8 Activity patterns of (a) ocelots, jaguarundis, and pampas cats in the savannahs of ENP, central Brazil; and (b) little spotted cats in mixed broadleaf–pine forests in the presence (São Francisco de Paula National Forest) and absence (Serra do Tabuleiro State Park) of ocelots in southern Brazil, determined by photographic records. In Emas ocelots are nocturnal, whereas jaguarundis and pampas cats are predominantly diurnal. Differences in little spotted cat activity between areas in Fig. 27.8b could be related to avoidance of predominantly nocturnal ocelots (Data sources: Oliveira *et al.* 2008; Silveira, unpublished data.)
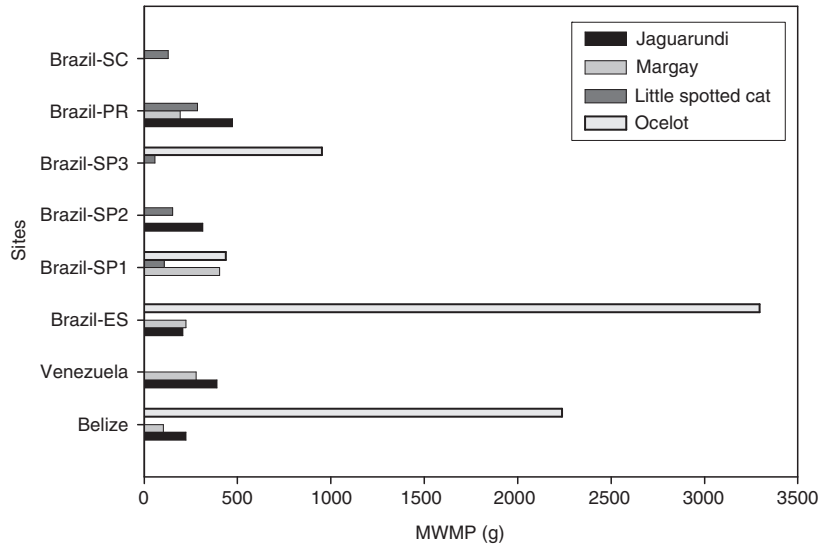
Figure 27.9 Mean weight of mammalian prey (MWMP, g) of jaguarundis, margays, little spotted cats, and of ocelots in areas of sympatric occurrence with the smaller species. (Data sources: same as Figs. 27.5 and 27.6.)
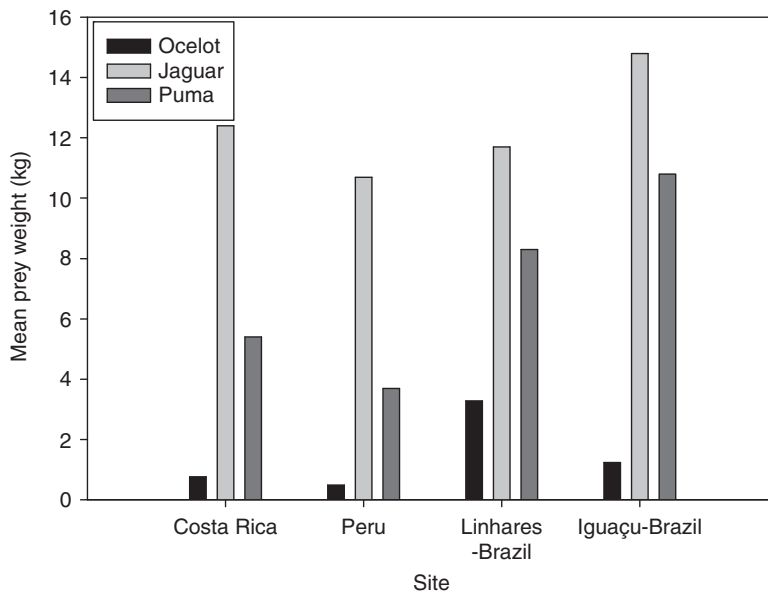
Figure 27.10 Mean weight of ocelet mammalian prey, and mean weight of jaguar and puma vertebrate prey in areas of sympatry. (Data source: Emmons 1987; Crawshaw 1995; Chinchilla 1987; Brito 2000; Bianchi 2001; Garla *et al.* 2001.)

2008, submitted). In the temperate Southern Cone, where the ocelot is absent, Geoffroy's cats might take its ecological role. Geoffroy's cat abundance-ranked first in four locations where this species was sympat-ric with other small cats and ocelots were absent (Lucherini and Luengos Vidal 2003; Cuellar *et al.* 2006; Lucherini *et al.*, unpublished data; Pereira *et al.*, unpublished data).

The effect of environmental variables

Maffei *et al.* (2005) reported a positive but insignificant correlation ($r^2 = 0.332$) between ocelot density and precipitation. Expanding their dataset and grouping estimates from the same vegetation type of the same region led to a significant and stronger relationship between these two variables ($r^2 = 0.415$, $P = 0.032$, $n = 11$). However, if the data were not grouped in this way, the correlation disappeared ($r^2 = 0.114$, $P = 0.145$, $n = 20$), as did the correlation between precipitation and home range size. Ocelot density and home range size did not correlate with habitat types (grouped in forest, transitional, and open formations) ($F = 0.309$, $P = 0.738$).

The influence of prey

Prey biomass is known to influence carnivore space use and density (Litvaitis *et al.* 1986). Carbone and Gittleman (2002) highlighted the remarkable consistency in average population density of carnivores in general (despite their ecological variations) to that of prey biomass.

Analysis of food habits clearly indicates that larger prey (≥ 0.8 kg) is especially important for ocelots. The only study on predator–prey relations for a small Neotropical felid that combines data on predator density and prey density or biomass is of Geoffroy's cats in Argentina. The cat's density declined from 0.29 km^{-2} to 0.03 km^{-2} following the numerical decline of its main prey from 0.56 km^{-2} to 0.06 km^{-2} (Pereira *et al.* 2006).

A test of MWMP against ocelot density at five sites (using Konecny [1989] MWMP for Dillon [2005] density estimation; Emmons 1987, 1988; Ludlow and Sunquist 1987; Crawshaw 1995; Moreno *et al.* 2006), revealed no correlation ($r = 0.247$, $P = 0.688$). Although the dataset is very limited, it does suggest that mean prey mass is not a predictor of ocelot density, although the density of main prey by percentage of occurrence might be.

Ocelot density and comparisons with the smaller species

Ocelot density varies considerably between areas, from 0.08 to 1.0 individuals per km^2, and averaged 0.31 ± 0.22 ($n = 22$) (Ludlow and Sunquist 1987; Emmons 1988; Jacob 2002; Trolle and Kéry 2003, 2005; Dillon 2005; Maffei *et al.* 2005; Cuellar *et al.* 2006; Di Bitetti *et al.* 2006; Rocha 2006; Oliveira *et al.* 2008, submitted; Moreno and Kays, unpublished data). Ocelot densities were higher than those of the smaller jaguarundi, Geoffroy's cat, margay, and
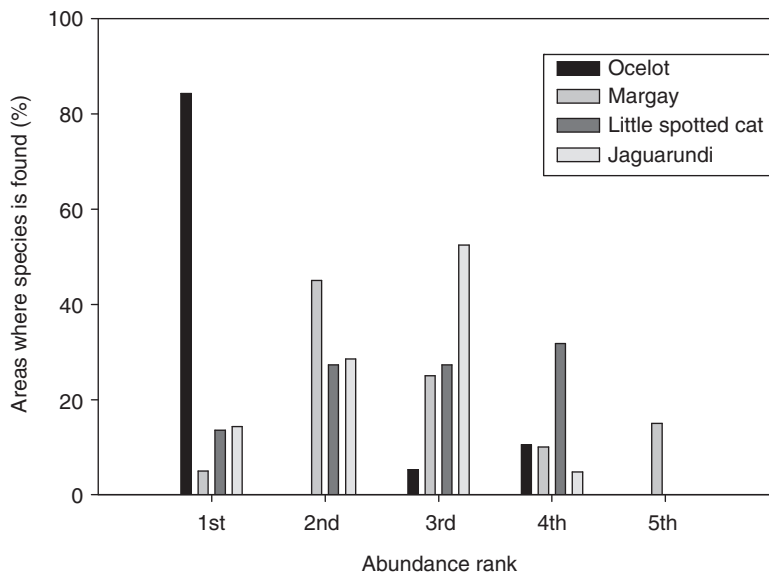
Figure 27.11 Lowland sympatric felid species ranked according to their order of abundance (1, most abundant; 5, least abundant) at each site where they occur in forests ($n = 12$ areas), savannahs ($n = 5$), transitional areas/mosaic ($n = 5$), semi-arid scrub ($n = 1$), and Pantanal flood plains ($n = 1$) in Brazil. (Adapted from Oliveira *et al.* 2008.)

little spotted cat combined (mean, 0.187 km^{-2} ± 0.159 km^{-2}, $n = 22$; Cuellar et al. 2006; Oliveira et al. 2008, submitted; Caso, unpublished data). Thus, density estimates of ocelots and those of the smaller species are significantly different ($t = 2.161$, d.f. = 42, $P = 0.036$). Density estimates of the smaller Neotropical felids (Oliveira et al. 2008, submitted) would suggest that they should, according to Yu and Dobson (2000), be categorized as 'widespread, but everywhere small population size'.
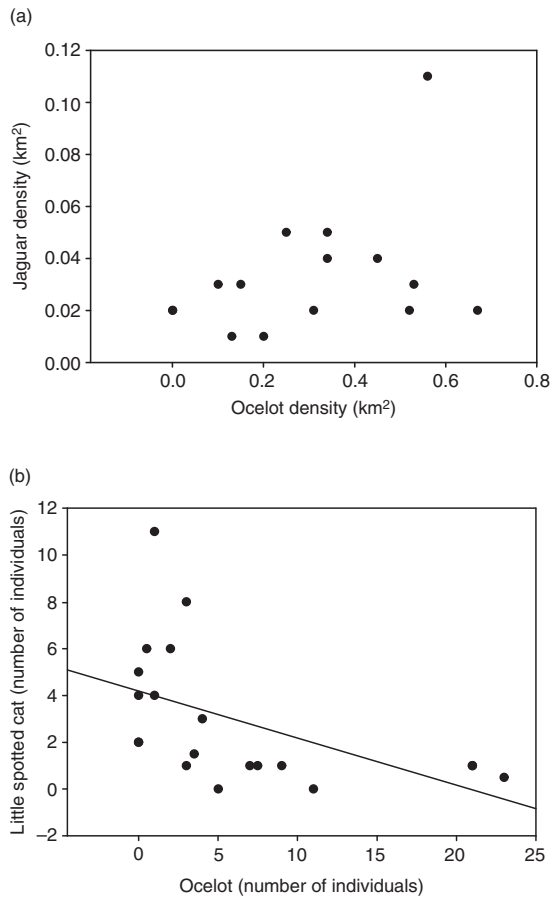
Carbone and Gittleman (2002) report strong negative correlation in average population density of carnivores in relation to carnivore mass and strong positive correlation with prey biomass, despite variation in species' ecology. However, in Brazil, felid density estimates are not correlated with body mass (Oliveira et al., submitted). Based on their body size, the small cats should have smaller home ranges and higher population densities than ocelots. In fact, the smaller felids have larger than expected home ranges and lower than expected population densities. Their expected population densities, based on Carbone and Gittleman (2002), would be 0.91 km^{-2} for little spotted cats, 0.69 km^{-2} for margays, 0.48 km^{-2} for jaguarundis, and 0.54 km^{-2} for Geoffroy's cats, which are, on average, 3.5 times larger than their observed mean density. Conversely, the expected density of ocelots (0.24 km^{-2}) is 1.3 times less than its observed mean. This suggests that the smaller sympatric felids may deviate from expected densities due to the effect of the larger ocelots.

Interestingly, the smaller felids reach higher densities only in areas where ocelots are either absent or in low numbers. Ocelot densities, on the other hand, are all from areas where both larger and smaller felid species are found. Additionally, even the highest densities of jaguarundis, margays, little spotted cats, and Geoffroy's cats (0.2–0.4 individuals per km^2) are lower than that of the ocelot (0.5–1.0 individuals per km^2) (Emmons 1988; Cuellar et al. 2006; Oliveira et al. 2008, submitted; Caso, unpublished data; Moreno and Kays, unpublished data). The density of smaller cats in areas where ocelot density was <0.1 km^{-2} or absent was significantly higher than where ocelot density was >0.1 km^{-2} ($t = -5.564$, d.f. = 19, $P < 0.001$). Interspecific predation and competition, major factors influencing carnivore population density (Fuller and Sievert 2001; Donadio and Buskirk 2006), seem to strongly influence the pop-

ulation dynamics of lowland Neotropical felids. The larger and dominant species, contrary to expectation, attain higher densities than smaller subordinate species, which range far more widely than the larger guild members, presumably to avoid intraguild predation (Palomares and Caro 1999; Woodroffe and Ginsberg 2005). Dominance rank is highly correlated with body mass and has been detected in other assemblages (Brown and Maurer 1986; Buskirk 1999; French and Smith 2005). Body-size differences associated with interference competition normally vary by a factor of 1.5–4, but could be as high as 7 (Buskirk 1999). The frequency and intensity of carnivore interspecific killing reaches its maximum when the larger species is 2–5.4 times larger than the other guild members, as at this size range there is a higher potential for high diet overlap and, in this way, a higher benefit for the larger species to eliminate the smaller potential competitors (Donadio and Buskirk 2006). The ocelot is 2.2–4.6 times larger than the jaguarundi, margay, and little spotted cat. Dietary overlap of ocelots with these smaller sympatric species is also high (as shown above) and, as dietary overlap seems to be a factor likely to motivate interspecific killing (Donadio and Buskirk 2006), we speculate that intraguild killing, or its potential (Woodroffe and Ginsberg 2005), might be the mechanism by which ocelots affect small cat dynamics in the neotropics.

Ocelot density does not appear to be impacted by the presence of the larger puma and jaguar (Oliveira et al., unpublished data), as predicted by the mesopredator release theory of Crooks and Soulé (1999). Conversely, ocelot density appears to impact negatively the numbers of smaller little spotted cat, margay, jaguarundi, and Geoffroy's cat (Fig. 27.12) in what has been called the 'ocelot effect' (or the 'pardalis effect'; Oliveira et al. 2008, unpublished data). If true, then this dominant mid-sized carnivore might determine the dynamics of the mesopredator community in the neotropics, rather than the top predators, as predicted by the mesopredator release theory. In this case, the prediction is that as ocelot numbers decrease small felid numbers should rise due to reduced intraguild predation by ocelots (Fig. 27.13). This is what has been observed over the past 8 years (2000–07) at a site in southern Brazil (Oliveira et al. 2008).

The emerging pattern within the lowland felid guild is that the density of ocelots is not influenced by that

(a)

(b)

Figure 27.12 Demographic interactions of ocelots with (a) potential predators, jaguars; and (b) potential competitors, little spotted cats. (Modified from Oliveira *et al.* 2008, unpublished data.)
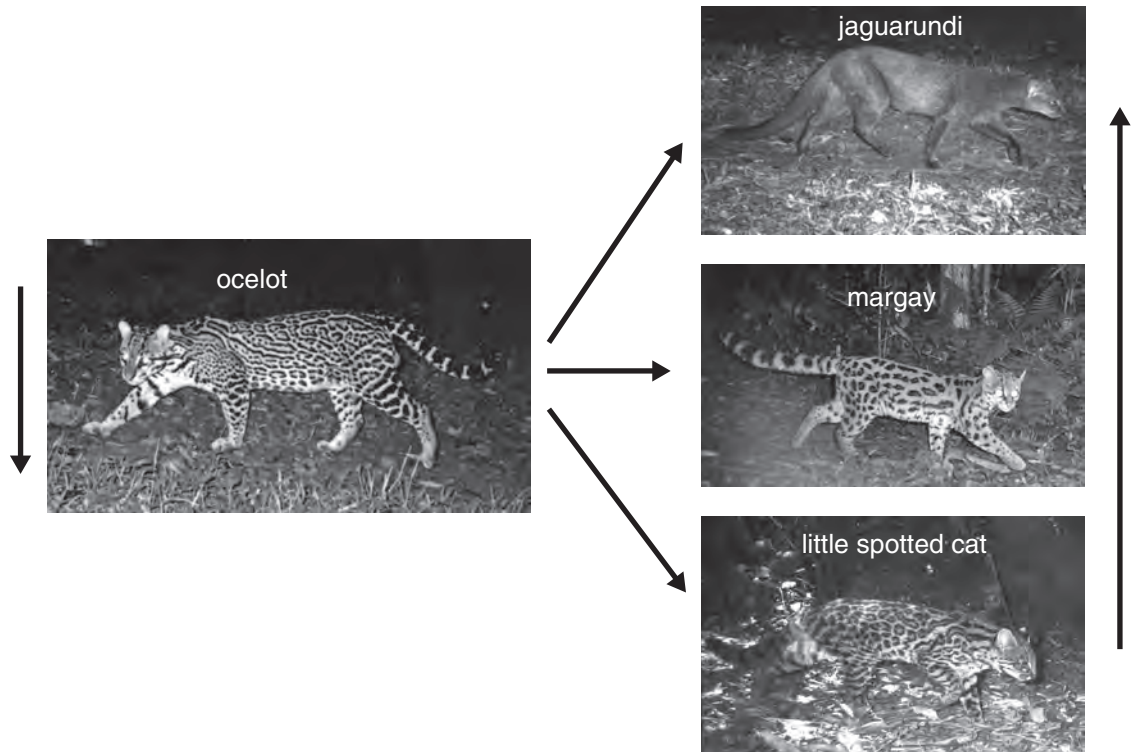
et al. 1995; Creel and Creel 1996; Mills and Gorman 1997; Palomares and Caro 1999). A similar relationship between the density of ocelots and the smaller felid species is expected and would have conservation implications for the latter species. Even the largest protected areas, that typically harbour ocelot population densities >0.1 km^2, may not hold viable populations of the smaller species, whose conservation would be dependent upon their protection outside reserves, in ever dwindling natural habitats (Oliveira *et al.* 2008).

Concluding remarks

Ocelots are generalists, highly adaptable, and the dominant felid in the lowland mesopredator assemblage of the neotropics. According to first principles, we had expected environmental variables to play a key role in determining ocelot numbers through primary productivity, and thus the influence of prey abundance on their home range and population density. However, although rainfall was correlated with ocelot density, it was not correlated with home range size, so these relationships cannot be assumed and merit further exploration.

Among the sympatric small cats, small rodents were the prey whose undigested remains were most commonly found in droppings; however, ocelots were the only species that consistently took larger prey (>1 kg), such as agoutis, pacas, armadillos, sloths, and monkeys. Small rodents contributed relatively little to the ocelot's intake of biomass, and the abundance of larger prey emerges as the likely limiting factor on their persistence. Furthermore, we detected no evidence of competitive dietary niche release within the lowland Neotropical felid assemblage, at least in so far as the absence of larger species had no observable effect on the diet of the smaller species. Body mass of main vertebrate prey (as defined by occurrence in diet) emerged as a useful predictor of the average mass of prey taken by ocelots. The patterns of ocelot habitat use revealed by our review indicate a greater degree of plasticity than often thought. Ocelots have been associated not only with dense cover (from pristine to highly disturbed), but also use adjacent open areas, including boundary areas of agricultural fields. This versatility

of other felids, but rather by availability of prey and adequate habitat. In turn, the density of the smaller sympatric jaguarundis, Geoffroy's cats, margays, and little spotted cats seem to be influenced first by ocelot numbers and then by other environmental factors typically associated with habitat and prey base (Oliveira *et al.* 2008, unpublished data). Carnivore assemblages elsewhere show similar trends (see Macdonald *et al.*, Chapter 1, this volume). Cheetahs (*Acynonyx jubatus*) and African wild dogs (*Lycaon pictus*) avoid areas with high prey densities because these are areas where their intraguild competitors and predators such as lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) reach high population densities (Laurenson

Figure 27.13 The 'ocelot effect' (or the '*pardalis* effect') occurs when the dominant mid-sized carnivore (ocelots) impact the dynamics of the mesopredator community in tropical America. As ocelot numbers decline, smaller felids numbers increase due to reduced intraguild predation (pictures not to scale). © 'Projeto Gatos do Mato—Brasil'.

may explain why ocelots are generally the most abundant species in most of the habitats in which they occur.

Our synthesis of available data also suggests that ocelot numbers have not been detectably influenced by either the larger jaguar and puma (potential predators) or by the smaller species (potential competitors). Density estimates of ocelots are significantly higher than those of the smaller jaguarundis, Geoffroy's cats, margays, and little spotted cats. The pattern that emerges is apparently one of coexistence between ocelots and the smaller species, but the lower densities of the smaller felids may reflect intraguild predation by ocelots, or the threat of it. If these premises hold true, then the 'ocelot effect' may be a key factor shaping the dynamics of the small-felid community of the lowland neotropics.

Acknowledgements