NUMERICAL AND SPATIAL RESPONSES OF GEOFFROY'S CAT (*ONCIFELIS GEOFFROYI*) TO PREY DECLINE IN ARGENTINA

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We examined the numerical and spatial responses of Geoffroy's cats (*Oncifelis geoffroyi*) to a prey decline in central Argentina between April 2002 and November 2003. The 2nd year of the study coincided with a severe drought. Relative abundance of brown hares (*Lepus europaeus*) declined from 5.6 individuals/10 km during the predrought period to about 0.6 individuals/10 km during the drought. Small-rodent biomass also showed the lowest level for the study area during the drought of 2002–2003 (134.5 g/ha). During the predrought and drought periods, 3 male and 1 female, and 1 male and 9 female Geoffroy's cats, respectively, were radiotagged and monitored. Home ranges for males of the predrought period averaged 202.8 ha $\pm$ 156.8 *SD* and that of the single female was 27.3 ha. During the drought period, 4 females occupied an average home range of 254.9 $\pm$ 254.1 ha, and the home-range size of the single predrought female increased by a factor of 2. No obvious change in mean daily distance traveled between the 2 periods was observed. Geoffroy's cats predominantly used habitats of dense cover during the predrought period, but they became more habitat generalists during the drought. Recruitment of juveniles was only recorded during the predrought period, and all monitored Geoffroy's cats dispersed or died of starvation after the prey decline. Consequently, density of Geoffroy's cats dropped from 2.9 individuals/10 km^2 before the drought to 0.3 individuals/10 km^2, probably because of food scarcity. This is the 1st study to examine the spatial ecology of a small wild cat species under nutritional (energetic) stress in South America.

Key words: Argentina, drought, Geoffroy's cat, home range, Monte, *Oncifelis geoffroyi*, prey decline, radiotelemetry, space use

In general, predator populations respond to changes in prey availability either numerically or functionally. Numerical response refers to absolute changes in the number of individuals by changes in reproductive rates, survival, immigration, or emigration, whereas functional response refers to behavioral changes, such as switching to alternative prey (Angerbjorn et al. 1999; Murdoch and Oaten 1975; Ward and Krebs 1985). Strong variation in food abundance might elicit one or both responses.

Models of optimal feeding relative to territory size predict that an animal's energetic needs and the density of available food are important factors influencing home-range size (Mace and Harvey 1983; McNab 1963; Schoener 1983). An increase in home-range size of felids responding to low prey density has been observed

on temporal (Norbury et al. 1998; Poole 1994; Ward and Krebs 1985) and geographical (Edwards et al. 2001; Grigione et al. 2002) scales. When a prey base declines rapidly, home ranges may shift or be abandoned altogether (Edwards et al. 2001; Norbury et al. 1998). In these situations, increases in mortality and rates of emigration also are apparent (Harper 2004; Poole 1994).

In arid and semiarid regions where water is a limiting resource, drought periods can have a strong effect on the abundance of small rodents (Lima et al. 2003; Meserve et al. 2003) and lagomorphs (Myers and Parker 1974; Palomares et al. 2001). Despite the frequency of these events and their importance in conservation planning, observational studies spanning drought are relatively uncommon in South America, especially regarding predator responses over time (but see Jaksic et al. 1997; Jaksic and Simonetti 1987).

Geoffroy's cat (*Oncifelis geoffroyi*) is a solitary, primarily nocturnal small felid, distributed from southern Brazil and Bolivia throughout southern Patagonia in Argentina and Chile (Nowell and Jackson 1996; Ximénez 1975). Little is known

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about the ecology of this species (Lucherini et al. 2004), which is classified as "near threatened" (Nowell 2002). It has been described as an opportunistic predator (Canepuccia 1999) feeding mainly upon introduced brown hares (*Lepus europaeus*) and small rodents (Johnson and Franklin 1991; Novaro et al. 2000; Vuillermoz and Sapoznikow 1998). In southern Chile, Johnson and Franklin (1991), in the only representative radiotelemetry study of the species, reported that Geoffroy's cats tend to use habitats with dense vegetation and probably high prey density.

Most of the range of Geoffroy's cat encompasses arid and semiarid environments (Ximénez 1975). In central Argentina, where the species inhabits mainly shrublands and xeric forests, a severe drought occurred in the summer of 2002–2003. This natural disturbance provided us with the opportunity to study the effects of extreme conditions on the abundance of small- and medium-sized herbivores and its consequences for Geoffroy's cat density and spatial behavior. Specifically, we focused on variations in home-range size, daily movements, habitat preference, and density of Geoffroy's cats relative to changes in prey availability.

MATERIALS AND METHODS

Study area.—The study was conducted in Lihue Calel National Park, Argentina (37°57′S, 65°33′W; 9,900 ha) and surrounding lands in La Pampa Province, Argentina. This area is composed of flat terrain except for a large, isolated set of bare rock hills. The vegetation is characterized by a mosaic of creosote bush flats (*Larrea*, hereafter "jarilla" scrubland), grasslands dominated by bunch grasses (*Stipa*), and mixed shrub patches (e.g., *Condalia microphylla* and *Prosopis flexuosa*). There are some ephemeral ponds, but no permanent surface water exists in the study area.

We observed that 5 sigmodontine rodents (*Akodon azarae*, *A. molinae*, *Calomys musculinus*, *Eligmodontia typus*, and *Graomys griseoflavus*), 1 hystricognath rodent (the common yellow-toothed cavy [*Galea musteloides*]), and the brown hare form a majority of the diet of Geoffroy's cats at the study site. The plains vizcacha (*Lagostomus maximus*), a large herbivorous rodent preyed upon by Geoffroy's cat (Branch 1995), disappeared from the region in 1998. The pampas fox (*Pseudalopex gymnocercus*), pampas cat (*Oncifelis colocolo*), jaguarundi (*Herpailurus yaguarondi*), and puma (*Puma concolor*) are potential competitors of Geoffroy's cats in the area.

Mean daily temperatures are <8°C in winter and >25°C in summer. Annual rainfall is 498 mm (± 141 *SD*, 1986–2002), 72% of which (range 63–82%) is concentrated within spring and summer (October–March). However, the amount of rain from October 2002 through March 2003 was markedly lower (148.7 mm) than the seasonal average, resulting in a prolonged drought until November 2003 (data from Lihue Calel weather station).

Prey availability.—Brown hares were counted seasonally between autumn (April–May) of 2002 and spring (October–November) of 2003, along a fixed 22.1-km transect traversing the main vegetation communities in the study area. Spotlighting counts were conducted by vehicle after sunset 2–5 times per season. Relative abundance of hares was estimated as number of individuals/10 km of road traveled.

A rodent survey was initiated in the winter of 2003 (drought period). The density and biomass of sigmodontine rodents were determined in the jarilla scrubland by livetrapping two 7 × 8 grids with 10 m between traps (7.6 × 8.9 × 22.8 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida). The grids were operated for 5 consecutive nights using rolled oats and peanuts as bait. Captured individuals were identified to species, weighed, individually identified (by natural marks, color markers, or, as the last option, toe-clip), and released at the capture site. Rodent density was estimated using minimum number of individuals known alive per 0.42-ha grid. Biomass was estimated as a product of the density and mean body mass of individuals captured. Biomass values were then compared with those obtained by S. Heinonen (National Parks Administration, in litt.) during winter of 1993, the only previous study conducted in the area during a nondrought period. A new rodent survey was done in winter 2004 (after the drought), on the same sites and following the same protocol as in 1993 and 2003.

Geoffroy's cat captures.—Trapping was conducted in April 2002 (predrought, 224 trap-nights) and May 2003 (drought, 440 trap-nights) with Tomahawk live traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin) baited with live domestic pigeons. Captured individuals were immobilized with ketamine and medetomidine administered intramuscularly (average dosage: 6 mg/kg and 0.1 mg/kg, respectively). Geoffroy's cats were sexed, weighed, measured, and aged (based on a physical examination and tooth eruption patterns). Individuals >2.0 kg were fitted with radiocollars (Advanced Telemetry Systems, Isanti, Minnesota). During the predrought and drought periods, 42-g M1940 radiocollars with internal antenna and 60-g M1950 radiocollars with external antenna, respectively, were used. These radiocollars represented on average 1.1% (range 0.9–1.5%) and 2.2% (range 1.6–3.0%) of the cat's body weight. Each animal was released at the capture site after it had recovered from anesthesia. Manipulation and care of animals involved during this study followed guidelines approved by the American Society of Mammalogists (Animal Care and Use Committee 1998) and by the Argentine Society for the Study of Mammals.

Home range and movements.—The locations of Geoffroy's cats were obtained by triangulation from the ground (White and Garrott 1990), using a hand-held 5-element Yagi antenna (Wildlife Materials, Carbondale, Illinois) or an H-antenna (Telonics, Mesa, Arizona) and a portable receiver (TR-4; Telonics). Radiolocation was conducted from a vehicle by a single observer, and locations were plotted on a 1:30,000 satellite image of the study area using universal transverse mercator coordinates. Visual sightings of radiocollared animals (*n* = 23) were georeferenced using a Garmin E-Trex Legend global positioning system (Garmin International Inc., Olathe, Kansas) and included in the analysis of home-range sizes. Individuals were located 1–5 times per week, usually 1–3 times during the day and 1 or 2 times at night on different days. In most (79%) instances, the distance between the observer and the monitored animals was <260 m (range 58–831 m). Location errors were minimized by using only azimuths that differed by 60–120° (White and Garrott 1990). The accuracy of telemetry fixes was checked by using test transmitters, and on 76% of occasions error was <100 m.

Home-range size was estimated using the minimum convex polygon (MCP—Mohr 1947) and the adaptive kernel (AK—Worton 1989) methods in the CALHOME software package (Kie et al. 1996). The MCP is relatively robust with low sample sizes (Harris et al. 1990) and is the most commonly used technique for estimating the home-range size of cats. We report the 100% MCP to allow comparison with the study of Johnson and Franklin (1991). We calculated the 50% AK (as an area of core use) and the 95% AK (as a commonly referenced contour) with a level of smoothing selected by least-squares cross-validation and a grid cell size of 30 × 30 m. Because of the low number of evaluated individuals and the high variability in home-range sizes, no statistical analysis was performed on home-range data.

Independence of locations was assumed by taking only 1 location within a 24-h period interval (Swihart and Slade 1985). The minimum number of locations needed to adequately describe home-range size was estimated by plotting home-range sizes against the number of locational fixes (Harris et al. 1990). Home-range overlaps were calculated by averaging percentage overlap between pairs of 100% MCP ranges.

Daily movements were calculated by measuring the linear distance between consecutive 24-h diurnal and nocturnal radiolocations (Poole 1994; Rabinowitz 1990). This parameter was considered as an indicator of the time and effort spent searching for prey (Brand et al. 1976; Poole 1994; Ward and Krebs 1985). Mean daily movements were compared between years using *t*-tests, except for female 4. For this cat, differences between years were evaluated using a paired *t*-test.

Habitat use.—We defined our study area by obtaining the 100% MCP of all independent locations for all Geoffroy's cats. We developed a geographic information system of this area (9,572 ha) based on vegetation information obtained from 5 random transects crossing the area and from a Landsat 7 TM satellite image (CONAE, Buenos Aires, Argentina; bands 3, 4, and 5) from January 2002. We performed a supervised classification using the maximum-likelihood decision rule (Lillesand and Kiefer 1994) using ERDAS IMAGINE 8.4 software (ERDAS Inc., Atlanta, Georgia). We assessed the accuracy of the land-cover classification map that we obtained by evaluating randomly selected pixels, approximately 0.1% of all images. The number of correct points was divided by total number of pixels in the contingency matrix to calculate overall image accuracies (Congalton et al. 1983). The overall accuracy obtained was 83%.

Locations of each Geoffroy's cat were digitized and converted to a spatial data layer using ArcView 3.2/Thematic mapper (Environmental Systems Research Institute Inc., Redlands, California). Habitat use was investigated at 1 scale of selection, defined as the selection of a home range within a study area (2nd-order selection—Johnson 1980). We considered distinct vegetation types as different habitat types (jarilla scrubland, mixed scrubland, dense grassland, xeric forest, and others). Each Geoffroy's cat location was assigned 1 habitat type. A chi-square goodness-of-fit test was used to determine if the observed frequencies of habitat use differed significantly from expected frequencies based on habitat availability (McClean et al. 1998; Neu et al. 1974). The null hypothesis tested was that usage occurs in proportion to availability, considering all habitats simultaneously (Neu et al. 1974). After a chi-square test, we used a Bonferroni correction of the Z-statistic ($\alpha = 0.10$) to maintain an experimentwise error rate (Miller 1981) and to create a normal approximation of the confidence intervals to determine which habitat types were either selected, avoided, or neither. Although we know that we violate the assumption of independence of observations within and among individuals (cf. Alldredge and Ratti 1986), the small sample of monitored cats precluded their use as experimental units (Aebischer et al. 1993).

Because few locations were obtained on many animals, data were pooled for all males during the predrought period and for all females (except female 4) during the drought period in order to compare habitat preference between both periods. Habitat preference of female 4 was analyzed separately because we obtained a large number of locations for her.

Geoffroy's cat density.—Minimum Geoffroy's cat density was calculated seasonally between autumn 2002 and spring 2003 based upon radiocollared cats in addition to the number of unmarked individuals using the 9,572-ha study area, as estimated by visual sightings (Franklin et al. 1999; Palomares et al. 2001; Poole 1994). The number of observers ($n = 2$) and the search effort (6 h/week; 5 weeks per season) were constant in all seasons. Of the unmarked individuals, the only ones considered were those that could be pos-
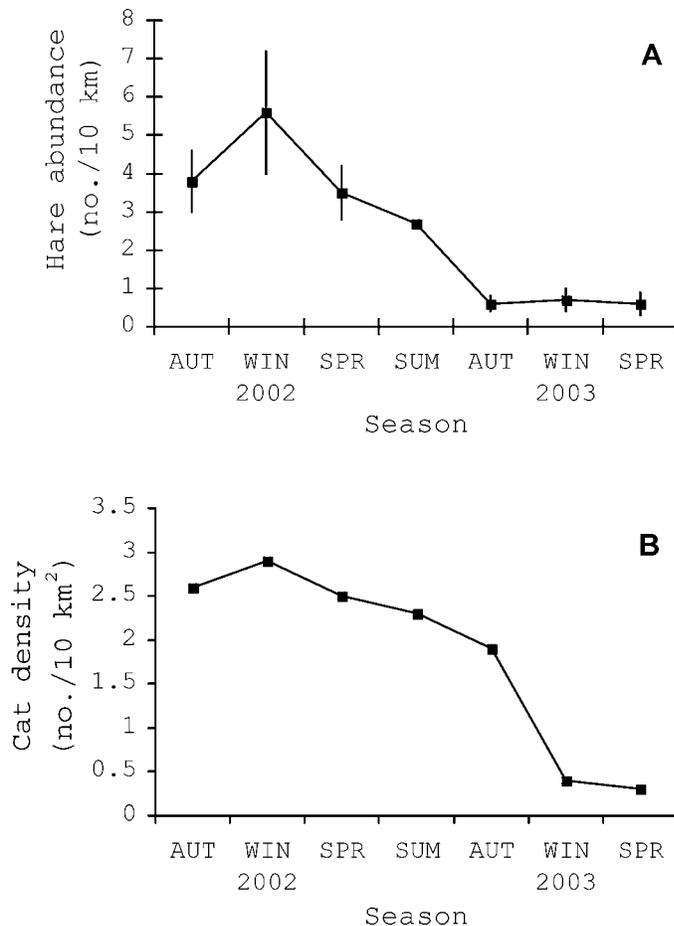

Fig. 1.—Estimates of A) relative abundance (mean ± SD) of brown hares and B) density of Geoffroy's cats, by season (AUT = autumn, WIN = winter, SPR = spring, SUM = summer) in Lihue Calel National Park, Argentina, from autumn 2002 to spring 2003.

itively identified as different individuals, based on sighting location, body size, color patterns, or other characteristics. As a result, density estimates were conservative and should be considered minimum values (Poole 1994).

RESULTS

Prey abundance.—Hare relative abundance was high between autumn and spring 2002 (predrought), peaking at 5.6 individuals/10 km in winter. Abundance began to decline progressively until autumn 2003, when it dropped to 0.6 individuals/10 km and remained low (<0.8 individuals/10 km) through spring 2003 (Fig. 1A). This represented a decline in hare relative abundance of >88% in 9 months.

Rodent biomass estimated during the 2003 drought period (134.5 g/ha ± 89.2 *SD*) was 66% lower than that estimated for a nondrought period in 1993 (393.1 ± 89.4 g/ha—S. Heinonen, National Parks Administration, in litt.). Six rodent species were captured during the 1993 nondrought period (*A. azarae*, *A. molinae*, *C. musculinus*, *E. typus*, *G. griseo-flavus*, and *Reithrodon auritus*), whereas only 2 (*E. typus* and *R. auritus*) were captured during the 2003 drought. However, because of the long time period between the 2 rodent surveys, causes other than the drought (e.g., succession) may have been

TABLE 1.—Home range (ha) of Geoffroy's cats radiocollared during the predrought (2002) and drought (2003) periods in Lihue Calel National Park, Argentina. Total home ranges were estimated as the 100% minimum convex polygon (MCP) and the 95% adaptive kernel (AK) and core areas were estimated as the 50% AK. Mostly males before the drought and only females during the drought were captured and monitored. M = male; F = female.

				Home-range size		
Cat no.	Period tracked	No. fixes	Asymptote reached	100% MCP	95% AK	50% AK
Predrought						
M 1	2 April–18 June	24	Yes	371.1	834.8	178.5
M 2	6 April–9 July	18	Yes	60.8	96.4	23.3
M 3	7 April–19 August	25	Yes	176.5	268.1	73.1
F 4	7 April–12 January	70	Yes	27.3	26.8	5.1
Drought						
F 7	11 May–20 June	26	Yes	130.1	217.1	12.5
F 4	13 May–13 June	18	Yes	52.5	87.5	6.1
F 8	15 May–28 June	8	No	270.7	474.7	124.5
F 9	16 May–28 June	23	Yes	214.0	427.1	100.4
F 12	23 May–17 July	28	Yes	622.9	617.7	181.5
F 13	25 May–10 June	10	No	34.1	118.4	17.0
F 14	25 May–11 June	11	No	101.9	245.4	5.6

responsible for the observed species loss. On the other hand, recovery of the rodent community after a normal rainy season was notable; the average biomass increased to 306.1 ± 35.5 g/ha in winter 2004, with 4 species captured (*A. azarae*, *A. molinae*, *C. musculinus*, and *G. griseoflavus*). Although the density of common yellow-toothed cavies was not evaluated during the study, visual sightings recorded while traveling the study area suggested that their abundance also decreased considerably during the drought.

Cat captures and radiotracking.—During the predrought period (2002) 4 (3 males and 1 female, all adults) Geoffroy's cats were captured and radiocollared, and during the drought period (2003) 10 (1 adult male, 8 adult females, and 1 subadult female) Geoffroy's cats were captured and radiocollared. One additional male (in 2002) and 2 additional females (in 2003) also were captured, examined, and released without collaring because of their poor physical condition or equipment restrictions. Although in 2002 only 1 individual was recaptured (an old, dehydrated male), 5 females were recaptured in 2003. Female 4 was captured and monitored during both the predrought and drought periods. Adult males outweighed adult females (3.96 kg ± 0.53 *SD* compared to 2.69 ± 0.38 kg, *t* = 5.35, *d.f.* = 13, *P* < 0.01) and were larger (body length; 925.2 mm ± 39.3 *SD* compared to 838.5 ± 26.6 mm, *t* = 5.10, *d.f.* = 13, *P* < 0.01).

The 4 predrought individuals were monitored an average 146.3 days (range 77–280 days). The tracking period ended for the 3 males because of their long-distance (>10-km) dispersal, and for female 4 because of transmitter failure.

During the drought period, 2 Geoffroy's cats abandoned the area shortly after capture and the subadult female with a nonoptimal body condition when initially captured was found dead; she had lost >15% of body weight during this time. Three females moved out of the home range that they had maintained

for 39, 42, and 43 days and were found dead 1–2 days later at 11.3, 5.8, and 9.6 km, respectively, from capture points. Another 3 females died within their home ranges after 16, 17, and 54 days of being collared. Necropsies were conducted on 5 of these cats, and, because of their condition, deaths were attributed to starvation. The remaining female was killed by another felid (probably a jaguarundi or another Geoffroy's cat, based on feces found at the death site and teeth marks found on the neck); also, she showed signs of starvation. The radiosignal of female 4 ceased after 1 month of radiocollaring for the second time and we were unable to find her thereafter.

Home range and movements.—An asymptotic home range was not obtained for 3 females that had <12 locations, all of them during the drought period, and they were not considered reliable estimates. Thus, these animals were not included in home-range analysis.

During the predrought period, the average home range (100% MCP, mean ± *SD*) of males was 202.8 ± 156.8 ha whereas the home-range size of female 4 was 27.3 ha (Table 1). The areas used by males 1 and 2 were contiguous and nonoverlapping. After the prey decline, the mean home-range size of females was 254.9 ± 254.1 ha (Table 1). The home-range size of female 4 was 2 times larger than that during the predrought period. Three cases of home-range overlap were found during the drought period between females 7 and 9 (17.3%), 13 and 14 (15.7%), and 4 and 7 (1.4%). Although 95% AK home-range estimates averaged 1.5 times larger than 100% MCP estimates (Table 1), the trends between the 2 years were similar with both methods.

The average core area (50% AK, mean ± *SD*) of males of the predrought period was 70.0 ± 77.8 ha (range 5.1–178.5 ha), whereas those of the females during the drought period were 75.1 ± 82.9 ha (range 6.1–181.5 ha; Table 1). These values indicate how little of the home range (22.9 ± 3.6% and 16.4 ± 11.8% of the 95% AK during the predrought and the drought periods) was used intensively. No cases of core-area overlap between individuals were found.

Geoffroy's cats were located on consecutive days 38 times during the predrought period and 52 times during the drought period. Differences in mean daily distance traveled between males of the predrought period (750.1 ± 460.3 m; range 17.0–1,473.6 m) and females of the drought period (850.1 ± 832.2 m; range 12.7–3,757.8 m) were not significant (*t* = −0.44, *d.f.* = 65, *P* = 0.66). All females with a body weight > 3 kg showed average daily movements > 1 km. If only these 3 females with body weight similar to those of the predrought males are considered, daily distance traveled showed again nonsignificant differences (*t* = 1.79, *d.f.* = 40, *P* = 0.08). Female 4 exhibited greater daily movements during the drought (370.5 ± 318.2 m versus 240.0 ± 153.8 m), but differences between years were not significant (*t* = −0.84, *d.f.* = 11, *P* = 0.42).

Habitat use.—The most abundant habitat type in the study area was jarilla scrubland (59.2%), followed by dense grassland (23.8%), mixed scrubland (8.8%), xeric forest (0.7%), and others (7.7%, including rocky terrain, open grassland, and bare soil). During both predrought and drought periods, Geoffroy's cats (except female 4) mainly used jarilla scrubland, dense grasslands, and mixed scrubland (Table 2). However, the

TABLE 2.—Chi-square test and Bonferroni Z-test with 95% confidence intervals (*CI*s) of habitat preference by Geoffroy's cats (except female 4) during the predrought and drought periods in Lihue Calel, Argentina.

Habitat type	Availability (proportion of area)	Use (proportion of fixes)	95% *CI*	Selection
Predrought period				
Jarilla scrubland	0.592	0.423	$0.264 \leq P \geq 0.582$	Avoid
Mixed scrubland	0.088	0.173	$0.051 \leq P \geq 0.295$	
Grassland	0.238	0.366	$0.209 \leq P \geq 0.521$	
Xeric forest	0.007	0.019	$-0.025 \leq P \geq 0.064$	
Other	0.075	0.019	$-0.025 \leq P \geq 0.064$	Avoid
χ^2 statistic		13.199		
d.f.		4		
P		0.010		
Drought period				
Jarilla scrubland	0.592	0.462	$0.349 \leq P \geq 0.575$	Avoid
Mixed scrubland	0.088	0.132	$0.056 \leq P \geq 0.209$	
Grassland	0.238	0.340	$0.233 \leq P \geq 0.447$	
Xeric forest	0.007	0.028	$-0.009 \leq P \geq 0.066$	
Other	0.075	0.038	$-0.005 \leq P \geq 0.081$	
χ^2 statistic		18.787		
d.f.		4		
P		<0.001		

TABLE 3.—Chi-square test and Bonferroni Z-test with 95% confidence intervals (*CI*s) of habitat preference by female Geoffroy's cat 4 during the predrought and drought periods in Lihue Calel, Argentina.

Habitat type	Availability (proportion of area)	Use (proportion of fixes)	95% *CI*	Selection
Predrought period				
Jarilla scrubland	0.592	0.100	$0.017 \leq P \geq 0.183$	Avoid
Mixed scrubland	0.088	0.014	$-0.019 \leq P \geq 0.047$	Avoid
Grassland	0.238	0.257	$0.136 \leq P \geq 0.379$	
Xeric forest	0.007	0.586	$0.449 \leq P \geq 0.723$	Prefer
Other	0.075	0.043	$-0.013 \leq P \geq 0.099$	
χ^2 statistic		3,383.119		
d.f.		4		
P		<0.001		
Drought period				
Jarilla scrubland	0.592	0.262	$0.028 \leq P \geq 0.498$	Avoid
Mixed scrubland	0.088	0.053	$-0.067 \leq P \geq 0.172$	
Grassland	0.238	0.158	$-0.037 \leq P \geq 0.353$	
Xeric forest	0.007	0.474	$0.207 \leq P \geq 0.740$	Prefer
Other	0.075	0.053	$-0.067 \leq P \geq 0.172$	
χ^2 statistic		595.535		
d.f.		4		
P		<0.001		

former habitat type was used less than expected by chance in both periods. Open habitats (grouped under "others") were used less than expected by chance during the predrought period (Table 2). Female 4 used predominantly xeric forest during the entire study period. This habitat type was used more than expected and the jarilla scrubland was used less than expected in both predrought and drought periods (Table 3). The frequency of mixed scrubland use changed between predrought and drought periods, being avoided during the former and used as expected by chance during the later (Table 3).

Geoffroy's cat density.—At the beginning of the study density of Geoffroy's cat was estimated to be 2.6 individuals/ 10 km^2. Numbers remained high (>2.3 individuals/10 km^2) until summer 2003 and declined progressively to about 0.3 individuals/10 km^2 during periods of food scarcity (Fig. 1B). Despite extensive searching, no young of Geoffroy's cat were found during the drought period, whereas during the predrought period at least 4 young were recorded. Similarly, we did not detect follicles in ovaries or pregnancies in necropsied females during the drought.

DISCUSSION

Our results indicate that before the drought, male Geoffroy's cats were sedentary, occupying home ranges for up to 4 months before abandoning them. In a colder and wetter area in southern Chile, male Geoffroy's cats maintained a home range for 3–5 months (Johnson and Franklin 1991). The home-range sizes of all collared cats in the present study (except female 12) were markedly smaller than those reported by Johnson and Franklin (1991) for both sexes. Body weights of males and females in the present study were on average 18% and 33% lighter than those of

males and females in the study of Johnson and Franklin (1991). This could explain the differences in home-range sizes between sites; this parameter scales allometrically with body size (Harestad and Bunnell 1979; Mace and Harvey 1983; McNab 1963; but see also Grigione et al. 2002). The estimated prey density reported by Johnson and Franklin (1994) suggests that the prey availability hypothesis does not explain home-range size differences between sites, given that prey densities at the Chilean site (mean hare density = 86.6 individuals/km^2 and mean rodent density = 62.2 individuals/ha) were greater than that at our study area.

In Lihue Calel, Bonaventura et al. (1998) found a positive correlation between small-rodent biomass and vegetation complexity, suggesting that vegetation plays an important role in structuring rodent communities in this area. Although quantitative data are lacking, we observed that severe drought in our study area resulted in the vegetation becoming markedly more sparse and insects and seeds less abundant, and these changes may have been the driving force behind the decline in rodent biomass. The reduction in the herbaceous layer probably also triggered the decline of brown hare density, because they are herbivorous (Campos et al. 2001). It is also possible that some hares were actually more vulnerable to predators because of the lack of foliage cover (Brown 1988).

Bailey (1981) and Ward and Krebs (1985) reported that bobcats (*Lynx rufus*) and Canadian lynx (*Lynx canadensis*) that defended territories during periods of prey abundance became nomadic when prey declined. These authors suggest that if prey density is unpredictable or very low, it would be adaptive for these cats to become transient and search out widely separated concentrations of prey. In the present study, during the period of prey scarcity, 2 Geoffroy's cats abandoned the area a few days after being radiocollared, but it is unclear if this was a behavioral

response to declining prey abundance or if they were transient animals without stable territories. In 1 month, 4 female cats monitored during the drought occupied an average home range greater than those occupied by males during 2–4 months in the predrought period. Previous studies on small felids showed that home ranges of males are substantially larger than those of females (Grassman 2000; Konecny 1990). For Geoffroy's cats, Johnson and Franklin (1991) reported a similar pattern, with adult males occupying home ranges more than twice as large as those of adult females. Based on these 2 trends, female Geoffroy's cats may have responded to declining prey abundance by expanding their home ranges, because they exceeded the home-range size of males estimated for the predrought period. In support of this idea, female 4 doubled the size of her home range between the predrought and drought periods.

The movement patterns of predators have been observed to increase if prey abundance declines or prey becomes less detectable (Knowles 1985; Sunquist and Sunquist 1989; Ward and Krebs 1985). In agreement with these observations, the daily distance traveled by female 4 increased once prey declined, and daily distances traveled by females monitored during the drought period were greater than those of males monitored during the predrought period. These results suggest that Geoffroy's cats increased the time and effort spent in search for prey to fulfill their energetic needs.

Despite drought-related environmental changes, little variation in habitat use was found between predrought and drought periods. However, comparisons between both periods should be considered carefully because they involve different individuals. Previous studies conducted on small felids (Dunstone et al. 2002; Harper 2004) have reported interindividual differences in habitat use. Johnson and Franklin (1991) reported that Geoffroy's cats predominantly used areas of dense vegetative cover because they provide higher prey availability and protection. Our results support these findings; during the predrought period, Geoffroy's cats used habitats of dense cover (such as xeric forest and dense grassland) and avoided open habitats. When prey became scarce, Geoffroy's cats responded by expanding their home range to increase opportunities for encountering prey. As a result, habitats avoided during the predrought period, such as mixed scrubland, rocky terrain, and open grassland, changed in frequency of use, being used in proportion to availability during the drought period.

Six radiocollared Geoffroy's cats died due to starvation during the drought period, when hare relative abundance was <0.8 individuals/10 km. A critical level for rodent abundance could not be determined because of a lack of rodent surveys during the decline period. After the prey decline, density of Geoffroy's cat declined from 2.3 individuals/10 km^2 to 0.4 individuals/10 km^2 between summer and winter 2003, with a mortality peak between June and July. A similarly elevated mortality rate within a 1- to 2-month period was reported by Edwards et al. (2001) for feral cats (*Felis catus*) during a period of prey scarcity in a semiarid area of Australia.

The absence of young recruitment for Geoffroy's cats during the prey decline is consistent with that observed for other felid species (Brand et al. 1976; Knick 1990; Mowat 1993; Nellis et al. 1972; Poole 1994). Lack of body fat and emaciation were common findings for all dead animals, which may have contributed to reduce reproductive activity (Gill and Rissmann 1997; Schillo 1992; Wade et al. 1996). Body condition also can affect an animal's immunity, rendering them more susceptible to pathogens (Hulsewe et al. 1999; Lloyd 1995; Ullrey 1993). However, no evidence of infectious disease was found in the necropsied cats, although parasite loads were very high in most individuals (Beldoménico et al. 2005). We did not find additional evidence of disease-related mortality, such as observation of sick animals or epidemic-type simultaneous deaths.

Based on the decrease in abundance of preferred prey species, the exploitation of an alternative food source (prey-switching) by Geoffroy's cats might have been expected. This kind of behavioral response during prey scarcity has been reported in other felids such as the puma (Pessino et al. 2002) and the Iberian lynx (*Lynx pardinus*—Beltrán and Delibes 1991). Johnson and Franklin (1991) and Canepuccia (1999) also reported prey-switching by Geoffroy's cat following seasonal changes in prey abundance. In Lihue Calel, potential alternative prey for Geoffroy's cat, such as armadillos (*Zaedyus pichyi* and *Chaetophractus villosus*), the Patagonian mara (*Dolichotis patagonum*), or the elegant crested-tinamou (*Eudromia elegans*), were relatively uncommon (Lihue Calel National Park—Conservation Value Species Register, Period 1995–2004) and, although they were not monitored during the study period, we observed that their abundance was likely lower during the drought. Other vertebrate taxa, such as amphibians and reptiles, constitute a seasonal food resource virtually unavailable during the colder winter months. As a result, potential alternative prey may have been insufficient at a local scale to allow Geoffroy's cats to fulfill their energetic requirements, and that may have contributed to the increased mortality and emigration.

Before its extinction from Lihue Calel, the vizcacha may have been important prey for Geoffroy's cats (Branch 1995). During events of decline in small rodents and hares, vizcachas could have constituted a key resource for Geoffroy's cat survival, because they are large rodents that live in fixed communal burrow systems, thus providing a spatially predictable resource for predators (Branch 1995). On the other hand, replacement of native by introduced prey in predator diets appears to be widespread in southern South America and the brown hare has become an important component of the Geoffroy's cat diet (Novaro et al. 2000). More research is required to understand the dynamics of interactions between this predator and its native and introduced prey species and how climate affects this chain of trophic interactions.

RESUMEN

Examinamos la respuesta espacial y numérica del gato montés (*Oncifelis geoffroyi*) a una declinación en la abundancia de sus presas en Argentina central, entre Abril de 2002 y Noviembre de 2003. El segundo año del estudio coincidió con una sequía severa. La abundancia relativa de liebres europeas (*Lepus europaeus*) declinó desde 5.6 individuos/10 km en el período previo a la sequía hasta 0.6 individuos/10 km durante la sequía. La biomasa de roedores mostró también el valor más bajo registrado para el área de estudio durante la sequía de 2002–2003

(134.5 g/ha). Previo a la sequía y durante la sequía, 3 machos y 1 hembra y 1 macho y 9 hembras de gato montés, respectivamente, fueron capturados y monitoreados por radiotelemetría. El área de acción de los machos en el período previo a la sequía promedió las 202.8 ha ± 156.8 *DE,* mientras que el de la ùnica hembra fue de 27.3 ha. Durante la sequía, cuatro hembras ocuparon un área de acción promedio de 254.9 ha ± 254.1 *DE* y el área de acción de la hembra del período de previo a la sequía se duplicó. No se observaron cambios en la distancia media diaria recorrida entre años. Los gatos utilizaron predominantemente hábitats con cobertura densa antes de la sequía, pero se volvieron más hábitat generalistas durante la sequía. El reclutamiento de juveniles fue registrado sólo en el período previo a la sequía, y todos los gatos monteses monitoreados dispersaron o murieron por inanición luego de la declinación de las presas. En consecuencia, la densidad de gatos monteses cayó desde 2.9 individuos/10 km^2 antes de la sequía hasta 0.3 individuos/10 km^2, probablemente por la escasez de alimento. Este es el primer estudio que examina la ecología espacial de una especie de pequeño felino sometida a estrés nutricional (energético) en América del Sur.

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