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Author(s): Javier A. Pereira and Andrés J. Novaro
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Javier A. Pereira* and Andrés J. Novaro

Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET)—Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Avenida Ángel Gallardo 470 (C1405DJR), Ciudad de Buenos Aires, Argentina (JAP)
CONICET—Instituto de Investigación en Biodiversidad y Medioambiente (INIBIOMA)—Centro de Ecología Aplicada del Neuquén, Casilla de Correos 7, Junín de los Andes (8371), Neuquén, Argentina (AJN)
Wildlife Conservation Society—Patagonian and Andean Steppe Program, Calle Curruhue y Río Chimehuín, Junín de los Andes (8371) Neuquén, Argentina (AJN)

* *Correspondent: jpereira@conicet.gov.ar*

The understanding of the spatial structure and dynamics of populations can guide conservation decisions, but studies of this type focused on small (< 7-kg) carnivores are rare. We compared survival, reproduction, and dispersal of radiocollared Geoffroy's cats (*Leopardus geoffroyi*) in a protected area and adjacent cattle ranches in Argentina to assess the effects of livestock management and its associated disturbances (i.e., hunting by humans) on the demography of this felid. Thirteen cats in the park and 13 in the ranches were radiotracked for up to 556 days in 2007–2008. We evaluated the Geoffroy's cat population trajectory at the landscape level using a stage-structured, stochastic matrix model based on our estimated vital rates. The study occurred during a prolonged drought, likely affecting estimated vital rates. Survival in the ranches was 52% lower than in the park; mortalities were due to intraguild predation in the park and were human-related in the ranches. Dispersal from the ranches was 32% lower than from the park and dispersal distances were up to 128 km. The number of cubs per litter was similar between areas. Assuming persistence of drought conditions and estimated vital rates, the simulated metapopulation rapidly collapsed and cat survival on ranches was the vital rate to which the model was most sensitive. Because projected climatic scenarios predict increased drought frequency for the region, we explored management options that would enhance chances of persistence, simulating 2 "adaptation" strategies: hunting restrictions on ranches and expanding protected areas. More than doubling of cat survival on ranches or a 9-fold increase in protected area extension would be required, involving major investments, to avoid the extinction of this cat metapopulation if droughts become prevalent. Our analysis may be helpful to improve our predictive capacity to identify new threats and facilitate adaptation strategies for Geoffroy's cat or other similar carnivores.

Key words: adaptation strategies, demography, drought, *Leopardus geoffroyi*, livestock management, Monte, population dynamics, simulations

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An understanding of how demographic parameters and dynamics of a population vary in relation to environmental and management factors is fundamental for the conservation of animal populations (Williams et al. 2002). For example, mortality induced by humans largely affects survivorship of carnivores outside protected areas (Jedrzejewski et al. 1996; Lambert et al. 2006; but see also Woodroffe and Ginsberg 1998), whereas habitat disturbance can generate areas with different reproductive success (Kerley et al. 2002; Blaum et al. 2007). This spatial heterogeneity can produce a mosaic of patches with different habitat quality and population demographics, with dramatic effects on landscape-scale population responses (Doak 1995; Novaro et al. 2005). In this context, a low adult survival in low-quality patches does not necessarily imply a population decline (or even a local extinction) if an increase in immigration of individuals from high-quality patches compensates the loss (source–sink dynamics—Pulliam 1988).

Insight into the spatial structure and dynamics of carnivore populations has guided conservation and management decisions, but most of these efforts have been primarily focused on large (> 15-kg) species, that is, puma (*Puma concolor*—Ruth et al. 2011), grizzly bear (*Ursus arctos*—Doak 1995), and wolf (*Canis lupus*—Carroll et al. 2003), likely because large carnivores are more vulnerable or are strategically considered umbrella or flagship species (Simberloff 1998). In contrast, research on habitat-specific demography and dynamics of small (< 7-kg) carnivores has received much less attention, although some of the lesser-known small species also are of conservation concern (e.g., Brodie 2009). Recent studies showed that some small carnivores are declining in human-dominated landscapes (e.g., Blaum et al. 2009), whereas other species have benefited from human presence (e.g., Otali and Gilchrist 2004). Further, land use and climate are likely to interact strongly with each other (Dale 1997), and the consequences of these influences on most small carnivores are difficult to project due to lack of knowledge. This is particularly important considering that global climate is rapidly changing, triggering responses in species ranges and ecological dynamics that imply new challenges for biodiversity conservation (Brooke 2008; Mawdsley et al. 2009). In that way, the understanding of the spatial structure and dynamics of small carnivore populations could help in the identification of practical strategies to reduce anticipated effects of climate change, that is, "adaptation measures" (Intergovernmental Panel on Climate Change 2001), improving our predictive capacity to conserve them.

Geoffroy's cat (*Leopardus geoffroyi*) is a small felid (approximately 4–5 kg body mass) categorized as "Near Threatened," occurring from Bolivia and Brazil to southern Argentina and Chile (Lucherini et al. 2008). Although it is considered a relatively common carnivore, there are no demographic data for the species, and knowledge of litter size is based on sporadic observations (Ximénez 1975; Johnson and Franklin 1991; Yanosky and Mercolli 1994); only 2 studies estimated population density (Cuéllar et al. 2006; Pereira et al. 2011).

The core area of Geoffroy's cat distribution encompasses arid and semiarid scrublands in the Monte ecoregion of central Argentina. Livestock production is the prevailing human activity in the Monte, with more than 1.3 million head of cattle (4% of the national production—Guevara et al. 2009). As is the case with other carnivores that inhabit rangelands (e.g., Pia et al. 2003; Blaum et al. 2009), livestock strongly impact Geoffroy's cat habitat (i.e., vegetation structure and prey abundance—Pereira et al. 2012). However, the effects of this activity and its associated disturbances (i.e., hunting by humans) on population dynamics of Geoffroy's cat are largely unknown. On the other hand, current climate projections for the Monte suggest an increase in annual mean temperature and more abundant precipitation in summer (Labraga and Villalba 2009). However, the distribution of precipitation is substantially influenced by El Niño Southern Oscillation phenomena, which induce precipitation anomalies (i.e., droughts) both locally and temporally (Jaksic 2001). These anomalies have increased in intensity and duration over the past century, and projections predict that this trend is likely to increase rapidly in the next 50 years (Walther et al. 2002). The combination of rising temperatures and interannual variability of precipitation can generate occasional droughts of different frequency and severity, potentially affecting Geoffroy's cat population dynamics.

The effects of livestock management and its associated disturbances on the demography of Geoffroy's cats were studied in an agricultural landscape dominated by cattle ranches that surround a 320-km^2 protected area in the semiarid scrublands of Argentina. This landscape is typical of the Monte ecoregion where wildlife refugia (protected areas or ranches without livestock and hunting) are small and isolated. Specifically, our objectives were to estimate the annual survival rate, cause-specific mortality, litter size, and dispersal rates and distances. Further, these demographic data were used to simulate the population dynamics of this Geoffroy's cat population at the landscape level. Because the years of data collection in this study coincided with a prolonged drought (see below), the estimated vital rates likely represent drought conditions that may differ from those occurring in "normal" years. Thus, simulations were performed with the observed estimates instead of changing them arbitrarily, to explore management scenarios that allow the chance of metapopulation persistence under pessimistic circumstances (assuming droughts may be more frequent in the coming decades). Through these simulations, 2 adaptation strategies (i.e., strengthening hunting restrictions and expanding the area where cats are protected) for reducing extinction risk of this Geoffroy's cat population were tested.

Materials and Methods

Study area.—Geoffroy's cats were studied at 2 sites: Lihué Calel National Park (hereafter, "the park"; 37°57′S, 65°33′W, 320 km^2) and in 2 adjacent cattle ranches ("Aguas Blancas" and "Los Ranqueles," both > 50 km^2) in La Pampa Province, central Argentina (Fig. 1). Animals that dispersed from these areas were radiotracked over a matrix of cattle ranches with similar land use and hunting patterns to the 2 ranches adjacent to the park. Thus, these ranches were also included in our study area.

The region has mainly flat terrain covered by a mosaic of creosote bush (*Larrea* sp.) flats, grasslands dominated by bunch grasses (e.g., *Stipa* spp.), and mixed shrub patches (with *Condalia microphylla* and *Prosopis flexuosa*). Cattle ranches (hereafter "ranches") consisted of private lands devoted almost exclusively to livestock management. Landscape physiognomy and management practices in most of these ranches were relatively homogeneous in the region (i.e., current livestock densities ranging between 9 and 21 head of cattle/km^2, paddock rotation, vegetation management with fire, sanitary protocols for livestock, and so on [J. A. Pereira, pers. obs.]). Abundance of the main prey of Geoffroy's cats (small rodents and birds) was significantly lower in the ranches than in the park during the study, probably due to livestock-induced changes in vegetation and soil (Pereira et al. 2012). Hunting of

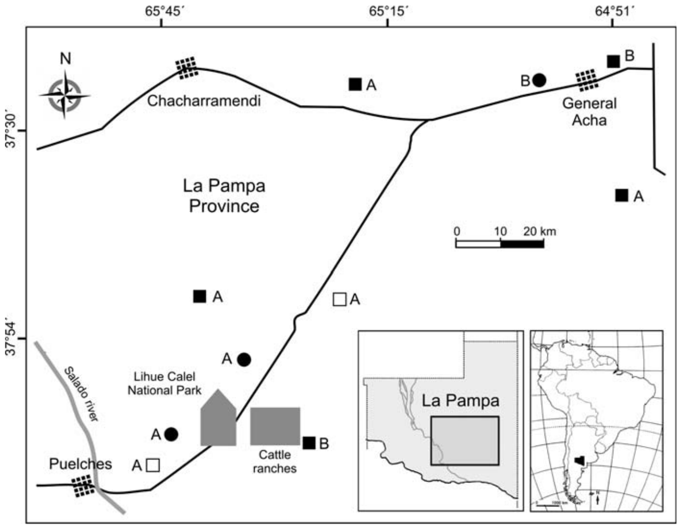

Fig. 1.—Dispersal of Geoffroy's cats (*Leopardus geoffroyi*) radiocollared in Lihué Calel National Park and cattle ranches, La Pampa, Argentina, in 2002–2003 and 2007–2008. Solid boxes and solid circles denote site of death of radiocollared males and females, respectively. Open boxes denote site of settlement of radiocollared males. An "A" beside the symbol denotes radiocollared cats marked at the national park, whereas a "B" denotes cats marked at ranches.

wildlife by ranchers and their workers for traditional or commercial use is common. On the other hand, livestock was absent in the park, the habitat was relatively undisturbed, and hunting was not permitted there.

Mean daily temperatures were 7.8°C in winter and 25.4°C in summer. Annual rainfall in the period 1983–2002 averaged 498 mm (± 141 mm *SD*), mostly concentrated in October–March (data from the park weather station). However, a severe drought occurred in 2003 (annual rainfall was 148 mm), which was followed by a prolonged drought that occurred in the area during the 2005–2008 period (mean annual rainfall was 337.1 ± 19.0 mm).

Survival and cause-specific mortality.—Survival of Geoffroy's cats was studied based on 22 individuals radiocollared and monitored in 2007 and 2008. Cats were captured using Tomahawk live traps (Tomahawk Live Trap Co., Hazelhurst, Wisconsin) baited with live domestic pigeons. Animals captured were immobilized with ketamine and medetomidine administered intramuscularly. The age of individuals was determined based on physical examinations and tooth eruption patterns and only adults were fitted with radiocollars with mortality switches (Advanced Telemetry Systems, Isanti, Minnesota), which weighed < 1.7% of the cats' body masses. Manipulation and care of animals followed guidelines of the American Society of Mammalogists (Sikes et al. 2011). Radiocollared cats were monitored by triangulation from the ground, usually 2–3 times a week, using a handheld 5-element yagi antenna and a portable receiver (Telonics, Mesa, Arizona). When a mortality signal was detected, the individual was located to determine cause of death through inspection of the carcass and field evidence or by performing necropsies. Annual survival rates and 95% confidence intervals (95% *CI*s) were estimated for cats monitored at each site using the staggered entry design, a modification of the nonparametric Kaplan–Meier product-limit estimator (Pollock et al. 1989). Then, the log-rank test ($\alpha = 0.05$) was used to compare survival rates between sites based on monthly intervals (Pollock et al. 1989). Those cats whose signals were lost ($n = 10$), possibly due to a transmitter failure or another unknown cause, were censored from the analysis (White and Garrott 1990). In the case of the park, those animals that dispersed to the ranches ($n = 4$) also were censored and included in the survival analysis for the ranches.

Annual cause-specific mortality rates were estimated using the Mayfield estimator (Heisey and Fuller 1985), considering 3 mortality categories (Pereira et al. 2010): natural (including starvation and predation by puma), human-related (including poaching, vehicle collision, and predation by domestic dogs), and unknown causes. The year was divided into 2 intervals (austral fall–winter [April–September] and spring–summer [October–March]) based on differences in climate and prey availability. Interval and annual rates were calculated for each area by pooling data across years (Fuller et al. 1985; Haines et al. 2005).

Litter size.—Average litter size was derived based on information gathered from 2001 to 2009 and obtained from multiple sources, as done in other studies (e.g., Olson and Lindzey 2002; Novaro et al. 2005). First, cubs at dens (hollow trees or cavities in rocks) of radiotracked females were counted when we detected denning behavior (Poole 1994; Palomares et al. 2005). Second, periodic surveys (at least 2 times a month) of potential denning sites (Palomares et al. 2005) such as hollow logs and rocky coves were conducted. Third, the number of fetuses or placental scars in the uterus of females subjected to necropsy was recorded (Quinn and Thompson 1987). Although different authors noted that this last method may overestimate (Lindstrom 1981) or underestimate (Elder 1952) litter size in carnivores, this information is particularly useful when cubs are difficult to find. Finally, records provided by rural people also were considered when the reliability of the information could be corroborated with other data (e.g., pictures, behavior of the mother and offspring, and so on).

The methods used provided data on litter size at the time of observation and likely led to an underestimation of litter size at birth (Kelly et al. 1998), particularly if cub mortality was high during the 1st weeks of life. However, ours represents the 1st systematic data set obtained for this species in the wild. Given the various sources of information used to calculate litter size and the small sample sizes, no statistical comparison of the data was made between sites.

Dispersal rates and distances.—Dispersing cats were radiotracked from a vehicle equipped with an omnidirectional antenna or from a Cessna 182 aircraft. Dispersal rates were calculated similarly to mortality rates (Pollock et al. 1989) but considering the date of dispersal of individuals rather than their deaths (Poole 1997). Differences in dispersal rates between sites were examined with a log-rank test (Pollock et al. 1989).

The dispersal distance was calculated as the straight-line distance from the home-range center (for residents prior to dispersal) or from the site of capture (for transients) to the last known dispersal location associated with mortality or post-dispersal location associated with settlement (new home-range center). To estimate this variable, data from cats radiotracked in 2007–2008 were combined with data from 13 Geoffroy's cats radiotracked in the park and the same ranches in 2002–2003 (see Pereira et al. [2006] for details on these animals). Because both 2002–2003 and 2007–2008 periods showed drought conditions, this combination was considered valid. Because several cats were killed by ranchers during their dispersal (Pereira et al. 2010) these distances should be considered a minimum estimate. When the exact start date of dispersal could not be established, it was estimated as the midpoint between the date of the last location in the area where the cat was marked and the date of its discovery either via radiotelemetry or from kill data provided by ranchers. Because dispersal distances are not normally distributed (Murray 1967), medians were presented and compared using the Mann–Whitney test.

Simulation of population dynamics.—RAMAS Metapop 5.0 (Akçakaya and Root 2007) was used to simulate the population dynamics of Geoffroy's cat at the landscape level. Because radiocollared cats dispersed up to 128 km from the study area (see "Results"), dynamics were simulated considering a landscape of 110 $\times$ 110 km, centered in our telemetry study areas. The prevailing activity in the ranches of the region was cattle management, thus the demographic characteristics of cat subpopulations studied on ranches were assigned to all ranches included in our simulated landscape. As a result, a continuous landscape of approximately 7,100 km^2 composed of Lihué Calel National Park and 56 cattle ranches (varying from 20 to 400 km^2) was generated (see Supporting Information S1, DOI: 10.1644/14-MAMM-A-012.S1). Each ranch was defined as a subpopulation because we could determine the type of management (i.e., livestock husbandry and hunting of cats) and the resulting vital rate to each of them, totaling 57 subpopulations.

Leslie matrices were constructed using vital rates estimated in the field study (drought conditions), assuming age structures from a postbreeding census. The model had a spatial structure defined by the geographical location of subpopulations, dispersal among subpopulations, and correlation among their vital rates. The age of 1st reproduction was set at 1.5 years for male and female cats, based on captive breeding data (Foreman 1997; Sunquist and Sunquist 2002). Similarly to Canada lynx (*Lynx canadensis*—Quinn and Thompson 1987) and European lynx (*L. lynx*—Breitenmoser-Würsten et al. 2007), young adult Geoffroy's cats have lower productivity than prime adults (Foreman 1997). Because of this difference, 2 separate adult stages were considered and the model was built considering 3 age classes: juveniles ($<$ 1.5 year), young adults (1.5–3 years), and prime adults ($>$ 3 years).

Eight prime adult females with signs of pregnancy (i.e., fetuses in a necropsy or "denning behavior" in radiotracked cats) were found out of 10 prime adult females examined or monitored in this study during the breeding period (early January–early March). Thus, it was assumed that 80% of prime adult female Geoffroy's cats produce a litter every year. This value is similar to that estimated for ocelots (*Leopardus pardalis*—Laack et al. 2005) and European lynxes (Andrén et al. 2002). As observed in Canada lynxes (Quinn and Thompson 1987), it was assumed that only 30% of young adult female Geoffroy's cats produced litters. Because it was not possible to estimate age-specific survival rates, annual survival of young adults was assumed to be the same as that of prime adults and survival of juveniles was assumed to be 80% that of adults, as estimated for pumas (Cooley et al. 2009).

Because of the higher cat density in the park compared to the ranches, the large dispersal rate from the park, and the unidirectional dispersal of cats from the park to ranches (see "Results"), the park appeared to be at carrying capacity for Geoffroy's cats during the data collection period. However, density independence was considered in the simulations because when populations are subject to "systemic" pressures such as regular droughts, inclusion of density dependence in simulations can lead to an underestimation of extinction risks (Ginzburg et al. 1990). Environmental stochasticity was incorporated into the model by randomly sampling vital rates from lognormal distributions based on the mean and variance of each rate (Akçakaya 2000). However, coefficients of variation (*CV*s) of 40% and 20% were assumed for fecundities of young and prime adults, respectively, because insufficient data were available to estimate interannual environmental variation. These *CV*s correspond to *SD*s of 0.11 and 0.17 for fecundity rates of young and prime adults in the park, respectively, and 0.05 and 0.09 for fecundity of young and prime adults in the ranches, respectively. These values are similar to those estimated for other carnivore species (e.g., Novaro et al. 2005; Haines et al. 2006). On the other hand, standard deviations of survival obtained in our study were large (i.e., 0.25), likely due to small sample sizes. However, instead of lowering the variance artificially, the estimated standard deviations of survival were used as a more accurate mean value based on our data. Demographic stochasticity was incorporated in model simulations by sampling the number of survivors from a binomial distribution, the number of offspring from a Poisson distribution, and the number of individuals dispersing among subpopulations from a binomial distribution (Akçakaya 1991).

Dispersal among subpopulations was modeled using the RAMAS dispersal-distance function, with $a = 1$, $b = 5$, $c = 0.5$, and a maximum dispersal distance of 128 km, as recorded with radiotelemetry (see "Results"). All intersubpopulation migration rates were calculated with RAMAS based on center-to-center distances. The initial population size of each subpopulation was based on ranch size and Geoffroy's cat densities estimated during our 2007–2008 survey (Pereira et al. 2011) performed in the park (2.3 cats/km^2 $\pm$ 1.0 *SE*) and ranches (1.4 $\pm$ 0.7 cats/km^2). The density estimate for ranches was extrapolated to nonsurveyed ranches because habitat characteristics within the overall landscape were relatively uniform.

Table 1.—Cause-specific mortality rates of Geoffroy's cats (*Leopardus geoffroyi*) radiotracked in Lihué Calel National Park ($n = 13$) and cattle ranches ($n = 13$) in central Argentina in 2007–2008.

		National park[a]			Cattle ranches[b]		
Interval	Days in interval	Transmitter days[c]	Cause of death	Rate (deaths)	Transmitter days[c]	Cause of death	Rate (deaths)
Fall–winter[d]	361	1154	Natural	0.269 (1)	1460	Natural	0.390 (2)
			Human-related	0.000 (0)		Human-related	0.524 (3)
			Unknown	0.000 (0)		Unknown	0.390 (2)
Spring–summer[e]	210	401	Natural	0.408 (1)	1145	Natural	0.000 (0)
			Human-related	0.000 (0)		Human-related	0.424 (3)
			Unknown	0.000 (0)		Unknown	0.000 (0)
Annual	571	1555	Natural	0.520 (2)	2605	Natural	0.355 (2)
			Human-related	0.000 (0)		Human-related	0.732 (6)
			Unknown	0.000 (0)		Unknown	0.355 (2)

[a] Based on 2 individuals that died after 36 and 125 days of monitoring, 10 that were censored after 1–459 days, and 1 that survived until the end of the study.
[b] Based on 10 individuals that died after 5–496 days and 3 that were censored after 3–366 days.
[c] Total number of days different Geoffroy's cats were radiotracked during interval.
[d] 1 April–30 September.
[e] 1 October–31 March.

Annual rainfall is a determinant of primary productivity and hence food availability for Geoffroy's cat in the area (Pereira et al. 2006). Years with conditions that lead to high survival are also likely to be years in which reproduction is high. Thus, a perfect correlation between survivorships and fecundities within the population was assumed.

Different scenarios for our Geoffroy's cat metapopulation were simulated, each of them based on 5,000 iterations and a time step $t = 1.5$ years for 30 years. The baseline scenario, built with the estimated vital rates and landscape structure (1 protected area and 56 cattle ranches), produced a rapid metapopulation collapse (see "Results"). This collapse may be the result of an overestimation of the proportion of the landscape under ranchlike conditions and also of having estimated demographic rates during adverse environmental conditions (see "Discussion"). To assess the potential effect of these sources of error in the field study, and also to model conditions that could change with improved management, changes in demographic rates and landscape structure were simulated.

A sensitivity analysis was performed to examine the effects of each parameter on baseline model results (Caswell 2001). Mean estimates for fecundity, survival in the park, and survival on ranches were increased by 10%, 20%, 30%, and 40%. Because survival on ranches was the demographic rate that had the largest potential for modifying the population trend (see "Results"), and also because survival on ranches was the variable most likely to be affected by changes in land use, increases of 50%, 100%, and 120% in survival rates on ranches were modeled as an adaptation strategy. Because cats were subjected in our study mostly to human-related mortality (see "Results" and Pereira et al. [2010]), these scenarios represented either a strengthening in hunting restrictions or a reduction in cat vulnerability to hunters.

Changes in landscape structure were simulated by gradually increasing the number of ranches with demographic characteristics as in the protected area (i.e., this could occur if ranches were converted into private protected areas, abandoned, or subutilized for livestock). Cattle ranches were switched to protected areas one at a time and the model was run with remaining parameters unchanged. To analyze a range of changes in landscape structure, the effects of ranch switching were investigated in 2 sequences by starting from the smallest and ascending in ranch size; and by starting from the largest and descending in ranch size. The risk of decline was computed as the probability of a 5%, 25%, 50%, 75%, and 100% decline from the initial population size. Finally, a combination of changes in landscape proportions and cat survival on ranches was evaluated.

Results

Survival and cause-specific mortality.—Thirteen Geoffroy's cats in the park and 13 in the ranches (4 of them emigrants from the park) were monitored for 1–556 days. Average annual survival rate of Geoffroy's cats was 0.70 (95% $CI = 0.17–1.00$; $n = 13$) in the park and 0.33 (95% $CI = 0.12–0.55$; $n = 13$) in the ranches, but the difference was not statistically significant ($\chi^2 = 3.23$, $P = 0.07$). The cause-specific mortality rates were different between areas (Table 1); mortalities of Geoffroy's cats in the park ($n = 2$) were the result of predation by pumas, whereas mortalities in the ranches were attributed to poaching (4 of 10 deaths), starvation (2 deaths), predation by domestic dogs (1 death), vehicle collision (1 death), and unknown causes (2 deaths).

Litter size.—Data on 14 litters were obtained (4 by direct observation, 1 from necropsy, and 9 from reports by ranchers) between early January and late February in 2000 ($n = 1$ litter), 2001 (2), 2002 (2), 2005 (1), 2006 (5), 2008 (2), and 2009 (1). The number of cubs per litter was 1.67 ± *SD* 0.58 (range = 1–2, $n = 3$) in the park and 1.73 ± 0.47 (range = 1–2, $n = 11$) in the ranches.

Dispersal rates and distances.—During 2007–2008, 10 (77%) of 13 and 5 (56%) of 9 Geoffroy's cats monitored in the park and in the ranches, respectively, abandoned their home ranges or moved away from the areas where they were

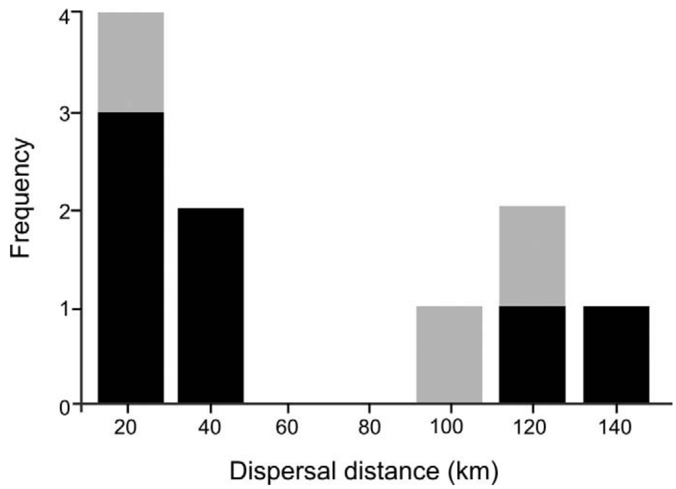

FIG. 2.—Dispersal distances of Geoffroy's cats (*Leopardus geoffroyi*) radiotracked in Lihué Calel National Park and adjacent cattle ranches in central Argentina. Values on the x-axis represent the upper limit of the distance interval. Black bars denote radiocollared cats marked at the national park, whereas gray bars denote cats marked at ranches.

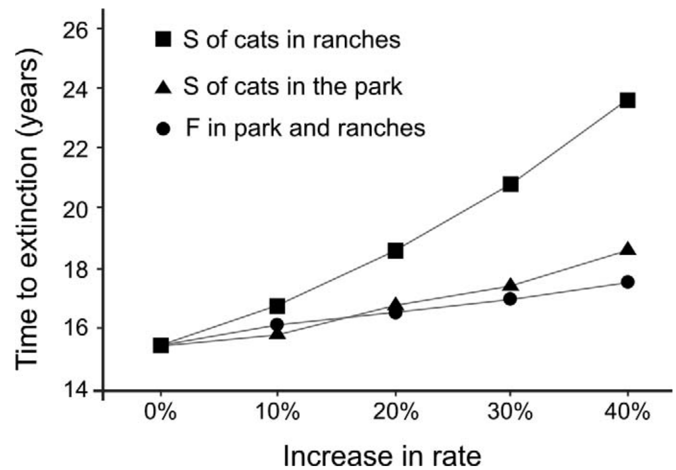

FIG. 4.—Sensitivity analysis of time to extinction of a Geoffroy's cat (*Leopardus geoffroyi*) metapopulation in the Monte ecoregion to increases of 10–40% in the survival rate of cats on ranches, survival rate of cats in the park, and fecundity in park and ranches.

captured. Probability of dispersal of Geoffroy's cats was 0.72 (95% $CI = 0.39–1.00$) in the park and 0.46 (95% $CI = 0.17–0.75$) in the ranches, but the difference was not statistically significant ($\chi^2 = 3.15$, $P = 0.08$).

Considering also the Geoffroy's cats monitored in 2002–2003, at least 63% (22 of 35) of the individuals dispersed from the areas where they were captured. Between 2002 and 2008, 23 cats were marked in the park and 12 were marked in the ranches. All dispersal events occurred from the park to a ranch (70% of individuals; $n = 16$) or from ranch to ranch (50% of individuals; $n = 6$) and no event from a ranch to the park was recorded. The final destination of dispersers could only be recorded for 8 cats that died during these movements (representing at least 36% of dispersers' mortality, 4 due to poaching) and 2 other individuals that established new home ranges on ranches 35 and 16 km from their capture points in the park (9% successful dispersal [Fig. 1]). Transmitter signal of the remaining 12 cats was lost during their dispersal through cattle ranches. Dispersal distances of the 10 cats with known final dispersal destination ranged between 8.7 and 128 km (median = 29.5 km; Fig. 2). Median dispersal distance of Geoffroy's cats was 24 km (range = 9.6–109 km) for individuals marked in the park ($n = 7$) and 106 km (range = 8.7–128 km) for those marked in the ranches ($n = 3$). All dispersal events started between early fall (April) and late winter (August).

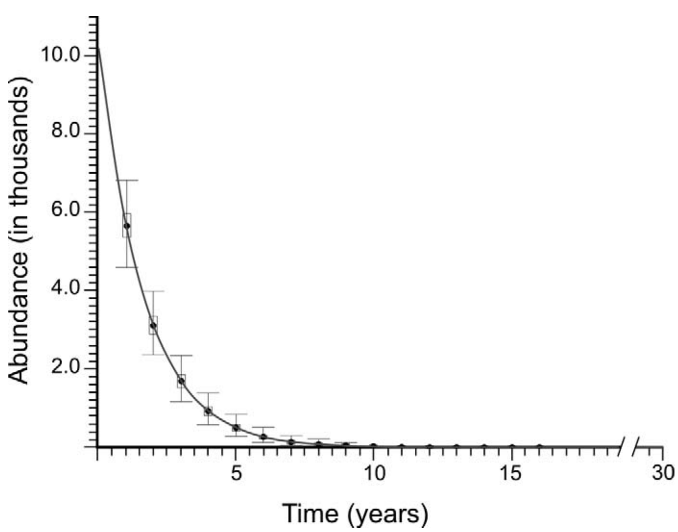

FIG. 3.—Simulated 30-year trajectory for the Geoffroy's cat (*Leopardus geoffroyi*) metapopulation in the Monte ecoregion, Argentina, under the baseline scenario (calculated vital rates; 1 national park and 56 cattle ranches). The average, ± *SD*, minimum, and maximum abundances are shown.

Simulation of population dynamics.—Under the baseline scenario (estimated vital rates; 1 national park and 56 cattle ranches) the metapopulation rapidly collapsed, declining at an annual rate of nearly 8% (Fig. 3). Survival of cats on ranches was the rate to which the model was most sensitive; a 40% increase in this rate delayed time to metapopulation extinction by 8.3 years (Fig. 4). Conversely, a 40% increase in fecundity and survival in the park delayed time to extinction by 1.9 and 3.2 years, respectively.

The metapopulation trajectories after 30 years were largely unreactive to increases of 50% and 100% in survival of Geoffroy's cats on ranches; most ($P > 0.78$) projections still resulted in a decline of > 95% of the metapopulation (Table 2). In contrast, an increase of 120% in survival (to $S = 0.792$, above estimated survival in the park) resulted in a null chance of even a 10% metapopulation decline after 30 years (Table 2).

Using estimated vital rates, Geoffroy's cats were likely to persist (i.e., probability of extinction < 5%) over the 30-year simulation if at least 20 small ranches or 18 large ranches were switched to protected areas (Supporting Information S2, DOI: 10.1644/14-MAMM-A-012.S2). These switches represented

Table 2.—Change in metapopulation abundance, extinction risk, and probabilities of a 10% and 95% terminal decline in total metapopulation size relative to changes in survival rates of adult and juvenile Geoffroy's cats (*Leopardus geoffroyi*) on ranches in the Monte ecoregion, Argentina.

Survival rates of adults and juveniles (%)	Change (%) in mean metapopulation abundance	Extinction risk (falling by 100%)	Probability of decline from initial metapopulation size	
			10%	95%
Estimated	−100.0	1.000	1.000	1.000
+50	−99.9	0.861	1.000	1.000
+100	−95.9	0	1.000	0.786
+120	+213	0	0.000	0.000

13.4% and 68.9% of the landscape under protection, respectively. However, to avoid (with high confidence: $P > 0.95$) a large decline in abundance (i.e., 50%), at least 44 small ranches (51% of the landscape) or 45 large ranches (96.2%) needed to be protected (Supporting Information S2).

A combination of changes in landscape proportions and survival increases in cattle ranches reduced moderately the number of ranches that needed to be switched to avoid ($P > 0.95$) a 50% decline in abundance after 30 years (Supporting Information S2). A 50% increase in survival on ranches (to $S = 0.495$) reduced the number of ranches that needed to be switched to 40 small ranches (40.1% of the landscape under protection) or 42 large ranches (95.1%). A 100% increase in survival (to $S = 0.66$) reduced this number to 28 small and 29 large ranches, representing 20.1% and 85.5% of the landscape under protection, respectively (Supporting Information S2).

Discussion

Geoffroy's cat demography in the park and ranches.—This study provides the 1st estimates of survival, cause-specific mortality, and dispersal rates and distances of Geoffroy's cats in the wild. Survival rate of adult Geoffroy's cats in the park (0.70) was within the range of survival estimates for other populations of small- and medium-sized felids inhabiting protected areas (e.g., 0.92 for leopard cats [*Prionailurus bengalensis*—Haines et al. 2004], 0.87 and 0.57 for resident and transient ocelots [Haines et al. 2005], and 0.88 for resident bobcats [*Lynx rufus*—Blankenship et al. 2006]). In our study, Geoffroy's cat survival in the ranches was 52% lower than in the park. Although differences between areas were not significantly different, probably as a result of small sample sizes, these values could be considered as biologically different. Other studies have found differences in survival rates of felids inhabiting areas with different land use or human activities. For example, Fuller et al. (1985) and Knick (1990) estimated bobcat survival rates that were 70% and 27% lower, respectively, in areas with than without hunting by humans.

The small sample size concerning sources of mortality limited our ability to test for differences between the park and ranches, thus caution is warranted when interpreting natural versus human-related mortality. Geoffroy's cats studied in the park died only as a result of predation by pumas. Drought conditions during this study may have increased interspecific competition among carnivores, a process that often leads to intraguild mortality (Donadio and Buskirk 2006). Accordingly, pumas were recorded killing and consuming small wild cats in Lihué Calel Park during a previous period of low prey abundance in 1995–2000 (Pessino et al. 2001). In the ranches, human-related mortality accounted for most Geoffroy's cat mortalities recorded during our study. Abundance of the main prey of Geoffroy's cats was remarkably lower in the ranches than in the park (Pereira et al. 2012), and low abundance of preferred prey usually increases predator movements (Hayward et al. 2009). Accordingly, some Geoffroy's cats tracked in the ranches showed longer daily movements than in the park (Pereira et al. 2012), likely because they had a more difficult time finding prey. These longer movements may have increased their probability of encounter with, and thus their vulnerability to, humans and their dogs or traps, as has been reported for other carnivores (Kamler and Gipson 2000).

The average litter size and range of cubs per litter were similar in the park and ranches. Some studies have reported declines in reproductive parameters (e.g., ovulation or pregnancy rates) of felid populations facing reductions in prey abundance (Knick 1990; Poole 1994), usually related to dietary deficiencies (Gill and Rissmann 1997). Body condition of adult cats studied was similar between the park (mean body mass = 3.5 ± *SD* 0.4 kg; $n = 14$) and the ranches (3.4 ± 0.8 kg; $n = 10$), which indicates that low prey abundance in the ranches apparently did not affect body condition. Thus, dietary deficiency in the ranches may not be strong enough to affect reproduction, although lack of data on pregnancy rates and litter sizes at birth prevented us from thoroughly analyzing differences in reproductive parameters between areas. In addition, similarity in observed litter sizes between sites also may indicate that this parameter is phylogenetically fixed, limiting further our ability to draw conclusions on the effect of prey abundance on reproduction.

An inverse relationship between prey abundance and dispersal rate has been well documented in Canada lynxes (Slough and Mowat 1996; Poole 1997) and bobcats (Hornocker and Bailey 1986; Knick 1990). Dispersal rate in lynxes shows a high-amplitude cycle in response to the cycle of the snowshoe hare (*Lepus americanus*), the lynx's major food source (Slough and Mowat 1996; Poole 1997). In our study, high dispersal rates of Geoffroy's cats may have been influenced by the decline in prey abundance (Pereira et al. 2012) due to the drought. In the park, the high dispersal level also could be a density-dependent response to the low prey level, because Geoffroy's cat density in the park was 32% higher than in the ranches during the study period (Pereira et al.

2011). In arid and semiarid areas, annual rainfall is often the main determinant of primary productivity and hence food availability for wildlife (Kemp 1989). Because we radiotracked Geoffroy's cats solely during periods of drought (2002–2003 and 2007–2008), data during nondrought years are needed to further test if high dispersal rates in this population are associated with periods of droughts and low food levels.

To our knowledge, dispersal distances of Geoffroy's cats in this study are the largest reported for a small-sized (< 7-kg) felid (Konecny 1989; Edwards et al. 2001). Long-range movements may be an important mechanism for maintaining populations in heterogeneous landscapes, where resource availability may be highly dispersed or change over time (Roff 1975) or in human-disturbed landscapes where marked population declines, and even local extinctions, may occur as a result of hunting. Long-distance dispersal appears to play a role in rebuilding depleted populations of lynxes during recovery from cyclic low snowshoe hare numbers or after localized overharvest (Slough and Mowat 1996; Poole 1997). Long-distance dispersal of Geoffroy's cats in the Monte ecosystem may be an adaptive mechanism to respond to recurrent periods of pronounced drought and may help their populations respond to heavy localized hunting. These movements could help cats find patches with better food or habitat conditions, but risk of death increases during long-distance dispersal because cats must travel through unfamiliar areas, usually facing altered landscapes and human presence (Kamler and Gipson 2000; Haines et al. 2005). In agreement, human-related mortality was responsible for all recorded Geoffroy's cat deaths that occurred during dispersal.

Simulation of population dynamics.—Vital rates estimated during this study likely represent drought conditions that have continued to be representative and may become more frequent with projected climatic scenarios. However, our model was inherently pessimistic because the positive potential effects of eventually more favorable (i.e., rainy) years on vital rates and thus, population dynamics, were not incorporated. In this context, our simulation represents a worst-case scenario for this Geoffroy's cat metapopulation whose conservation would be strongly management-dependent. Although the strengthening of hunting restrictions and the expansion of the area where cats are protected are 2 realistic measures that could help face this challenge (Heller and Zavaleta 2009; Mawdsley et al. 2009), major investments would be required to avoid the extinction of this metapopulation if droughts become prevalent.

As showed by the sensitivity analysis, Geoffroy's cat survival on ranches had the greatest potential to influence population changes, emphasizing the importance of focusing management on decreasing cat mortality, as it has been shown with other felids (Litvaitis et al. 1996). Poaching was the main cause of Geoffroy's cat deaths in this study, whereas incidental mortality in traps set for pampas foxes (*Lycalopex gymnocercus*) and predation by domestic dogs also are frequent in this region (Pereira et al. 2010). Thus, strengthening hunting restrictions (i.e., law enforcement), finding alternate harvest methods for foxes, and enhancing dog management may contribute to increase cat survival. For an Iberian lynx (*Lynx pardinus*) metapopulation, Gaona et al. (1998) found that an improvement of 20% in survival of lynxes that inhabit the largest sink would reduce the metapopulation extinction risk from 34% to 8%. An increase of > 100% in survival of cats on ranches was necessary in our model to avoid metapopulation extinction, suggesting that management options to decrease cat mortality need to be strong and intensive.

If hunting restrictions are not applied or are ineffective, our model indicated that at least 44 cattle ranches need to be protected to avoid a 50% decline in cat abundance after 30 years. Thus, the lowest-cost strategy to expand the area where cats are protected would be based on converting small ranches. However, the amount of area needed under parklike conditions (51% of the landscape) to avoid a large population decline represents a 9-fold increase compared with the current landscape configuration, a goal difficult to achieve considering the livestock-production matrix of the region. Frequent drought conditions and the consequent low yield of the livestock industry as well as low beef prices have often forced local ranchers to sell their cattle and even temporarily abandon their properties during recent years. If drought conditions are likely to persist under future climates, changes in the agricultural utility of land may constitute an opportunity for conservation (Estes et al. 2014). These abandoned ranches, where livestock is absent and there is no hunting, may act as areas with demographic characteristics of the national park. Thus, a close monitoring of this drought-induced dynamic in livestock production could facilitate identifying the additional number of ranches that need to be implemented as temporal refugia, complementing the contribution of new protected areas to the population dynamics of Geoffroy's cats.

The area under protection required for cat population persistence increased as the landscape matrix became more hostile, implying that small protected areas may fall below the threshold for species persistence if parks become habitat islands (Mace and Waller 1998; Carroll et al. 2004). Although Lihué Calel National Park may act as a source of dispersers (deterministic growth rate $\lambda_{\text{Park}} = 1.08$), contributing to maintain population levels on ranches, its role was not sufficient for the long-term persistence of the metapopulation under drought conditions. This probably was due to low survival of cats on ranches, high dispersal of cats from the park, and also the small area (4.5%) of the park. Populations with source–sink dynamics that inhabit heterogeneous landscapes often are stable when sources occupy at least 10% of the landscape (Pulliam 1996), but this source-area threshold can greatly increase (i.e., to 30%) if mortality in sinks and dispersal from sources to sinks are high (Novaro et al. 2005). In our study, the parklike area required to avoid a large decline in metapopulation abundance increased to 51% of the landscape, indicating that survival rates of cats on ranches (where most of the population occurs) are strongly depressed. Similarly, Lambert et al. (2006) showed that heavy hunting of pumas by humans (leading to an annual mortality rate of 0.38) in a large proportion of the landscape can cause population declines due to the lack of surviving emigrants from sources. This suggests that severe climate and anthropogenic activities can greatly affect source–sink dynamics. Thus, although Lihué Calel National Park may have a crucial role in the current persistence of this cat population, the area under protection should be increased if the studied pessimistic scenario indeed occurs.

In conclusion, livestock management and the associated hunting by humans strongly affect the dynamics of Geoffroy's cats at the landscape level. If projected climate change does indeed result in frequent and prolonged regional droughts, adaptation measures (such as strengthening hunting restrictions and expanding the area where cats are protected) will be required to conserve this metapopulation. Although Geoffroy's cats are currently common felids, our analysis may be helpful to improve our predictive capacity to identify new threats and to facilitate adaptation strategies for this carnivore or other species living in human-dominated landscapes.

Resumen

La comprensión de la estructura espacial y la dinámica de las poblaciones pueden guiar decisiones de conservación, pero los estudios de este tipo centrados en pequeños carnívoros ($<$ 7 kg) son raros. Se comparó la supervivencia, reproducción y dispersión de gatos monteses (*Leopardus geoffroyi*) equipados con radiocollar en una zona protegida y campos ganaderos adyacentes en Argentina, para evaluar los efectos del manejo ganadero y sus disturbios asociados (p.e., la cacería) sobre la demografía de este felino. Trece gatos en el parque y 13 en los campos fueron monitoreados por hasta 556 días durante 2007–2008. Se simuló la trayectoria de la población monitoreada a nivel del paisaje utilizando un modelo matricial estocástico estructurado por edades, basado en las tasas vitales estimadas. El estudio tuvo lugar durante una sequía prolongada, lo que probablemente afectó las tasas vitales estimadas. La supervivencia de los gatos en los campos fue 52% menor que en el parque; la mortalidad se debió a depredación intragremio en el parque y estuvo mayormente relacionada al hombre en los campos. La dispersión desde los campos fue 32% menor que desde el parque y las distancias de dispersión fueron de hasta 128 km. El número de crías por camada fue similar entre áreas. Asumiendo la persistencia de la sequía prolongada y las tasas vitales estimadas, la metapoblación simulada declinó rápidamente, siendo la supervivencia de los gatos en los campos la tasa vital más sensible para el modelo. Dado que los escenarios climáticos proyectados predicen una mayor frecuencia de sequías para la región, se exploraron opciones de manejo para mejorar las posibilidades de persistencia de esta población, simulando dos "estrategias de adaptación": restricciones de cacería en los campos y ampliación del área protegida en el paisaje estudiado. Para evitar la extinción de esta metapoblación si las sequías se hacen frecuentes, sería necesario incrementar a más del doble la supervivencia de los gatos en los campos o aumentar 9 veces la extensión de superficie protegida en el paisaje, lo que implica importantes inversiones de manejo. Nuestro análisis puede ser útil para mejorar la capacidad de predicción en la identificación de nuevas amenazas y para facilitar estrategias de adaptación para el gato montés u otros carnívoros similares.

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Supporting Information

Supporting Information S1.—Study area in the Monte ecoregion, La Pampa Province, Argentina.
Found at DOI: 10.1644/14-MAMM-A-012.S1

Supporting Information S2.—Simulated effects of different strategies on the Geoffroy's cat's probability of decline from the initial population size over 30 years.
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Literature Cited

Akçakaya, H. R. 1991. A method for simulating demographic stochasticity. Ecological Modeling 54:133–136.

Akçakaya, H. R. 2000. Population viability analyses with demographically and spatially structured models. Ecological Bulletins 48:23–38.

Akçakaya, H. R., and W. Root. 2007. RAMAS Metapop: viability analysis for stage-structured metapopulations (version 5.0). Applied Biomathematics, Setauket, New York.

Andrén, H., et al. 2002. Estimating total lynx *Lynx lynx* population size from censuses of family groups. Wildlife Biology 8:299–306.

Blankenship, T., A. Haines, M. Tewes, and N. Silvy. 2006. Comparing survival and cause-specific mortality between resident and transient bobcats *Lynx rufus*. Wildlife Biology 12:297–303.

Blaum, N., E. Rossmanith, G. Fleissner, and F. Jeltsch. 2007. The conflicting importance of shrubby landscape structures for the reproductive success of the yellow mongoose (*Cynictis penicillata*). Journal of Mammalogy 88:194–200.

Blaum, N., B. Tietjen, and E. Rossmanith. 2009. Impact of livestock husbandry on small- and medium-sized carnivores in Kalahari savannah rangelands. Journal of Wildlife Management 73:60–67.

Breitenmoser-Würsten, Ch., J. M. Vandel, F. Zimmermann, and U. Breitenmoser. 2007. Demography of lynx *Lynx lynx* in the Jura Mountains. Wildlife Biology 13:381–392.

Brodie, J. F. 2009. Is research effort allocated efficiently for conservation? Felidae as a global case study. Biodiversity and Conservation 18:2927–2939.

Brooke, C. 2008. Conservation and adaptation to climate change. Conservation Biology 22:1471–1476.

Carroll, C., R. E. Noss, P. C. Paquet, and N. H. Schumaker. 2004. Extinction debt of protected areas in developing landscapes. Conservation Biology 18:1110–1120.

Carroll, C., M. K. Phillips, N. H. Schumaker, and D. W. Smith. 2003. Impacts of landscape change on wolf restoration success: planning a reintroduction program based on static and dynamic spatial models. Conservation Biology 17:536–548.

Caswell, H. 2001. Matrix population models: construction, analysis and interpretation. 2nd ed. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.

Cooley, H. S., R. B. Wielgus, G. M. Koehler, H. S. Robinson, and B. T. Maletzke. 2009. Does hunting regulate cougar populations? A test of the compensatory mortality hypothesis. Ecology 90:2913–2921.

Cuéllar, E., L. Maffei, R. Arispe, and A. Noss. 2006. Geoffroy's cats at the northern limit of their range: activity patterns and density estimates from camera trapping in Bolivian dry forests. Studies on Neotropical Fauna and Environment 41:169–177.

Dale, V. H. 1997. The relationship between land-use change and climate change. Ecological Applications 7:753–769.

Doak, D. 1995. Source–sink models and the problem of habitat degradation: general models and applications to the Yellowstone grizzly. Conservation Biology 9:1370–1379.

Donadio, E., and S. Buskirk. 2006. Diet, morphology, and interspecific killing in Carnivora. American Naturalist 167:524–536.

Edwards, G. P., N. de Preu, B. J. Shakeshaft, I. V. Crealy, and R. M. Paltridge. 2001. Home range and movements of male feral cats (*Felis catus*) in a semiarid woodland environment in central Australia. Austral Ecology 26:93–101.

Elder, W. 1952. Failure of placental scars to reveal breeding history in mink. Journal of Wildlife Management 16:110.

Estes, L. D., et al. 2014. Using changes in agricultural utility to quantify future climate-induced risk to conservation. Conservation Biology 28:427–437.

Foreman, G. E. 1997. Breeding and maternal behaviour in Geoffroy's cats *Oncifelis geoffroyi*. International Zoo Yearbook 35:104–115.

Fuller, T., W. Berg, and D. Kuehn. 1985. Survival rates and mortality factors of adult bobcats in northcentral Minnesota. Journal of Wildlife Management 49:292–296.

Gaona, P., P. Ferreras, and M. Delibes. 1998. Dynamics and viability of a metapopulation of the endangered Iberian lynx (*Lynx pardinus*). Ecological Monographs 68:349–370.

Gill, C., and E. Rissmann. 1997. Female sexual behavior is inhibited by short- and long-term food restriction. Physiology and Behavior 61:387–394.

Ginzburg, L. R., S. Ferson, and H. R. Akçakaya. 1990. Reconstructability of density dependence and the conservative assessment of extinction risk. Conservation Biology 4:63–70.

Guevara, J., et al. 2009. Range and livestock production in the Monte Desert, Argentina. Journal of Arid Environments 73:228–237.

Haines, A. M., L. I. Grassman, and M. E. Tewes. 2004. Survival of adult leopard cats *Prionailurus bengalensis* in Thailand. Acta Theriologica 49:349–356.

Haines, A. M., M. E. Tewes, and L. L. Laack. 2005. Survival and sources of mortality in ocelots. Journal of Wildlife Management 69:255–263.

Haines, A. M., M. E. Tewes, L. L. Laack, J. S. Horne, and J. H. Young. 2006. A habitat-based population viability analysis for ocelots (*Leopardus pardalis*) in the United States. Biological Conservation 132:424–436.

Hayward, M. W., G. J. Hayward, D. Druce, and G. I. H. Kerley. 2009. Do fences constrain predator movements on an evolutionary scale? Home range, food intake and movement patterns of large predators reintroduced to Addo Elephant National Park, South Africa. Biodiversity and Conservation 18:887–899.

Heisey, D., and T. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. Journal of Wildlife Management 49:668–674.

Heller, N. E., and E. S. Zavaleta. 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. Biological Conservation 142:14–32.

Hornocker, M., and T. Bailey. 1986. Natural regulation in three species of felids. Pp. 211–220 in Cats of the world: biology, conservation, and management (S. D. Miller and D. D. Everett, eds.). National Wildlife Federation, Washington, D.C.

Intergovernmental Panel on Climate Change. 2001. Glossary of terms used in the IPCC third assessment report. www.ipcc.ch/glossary/index.htm. Accessed 15 October 2010.

Jaksic, F. M. 2001. Ecological effects of El Niño in terrestrial ecosystems of western South America. Ecography 24:241–250.

Jedrzejewski, W., B. Jedrzejewska, H. Okarma, K. Schmidt, A. N. Bunevich, and L. Milkowski. 1996. Population dynamics (1869–1994), demography, and home ranges of lynx in Bialowieza Primeval Forest (Poland and Belarus). Ecography 19:122–138.

Johnson, W., and W. Franklin. 1991. Feeding and spatial ecology of *Felis geoffroyi* in southern Patagonia. Journal of Mammalogy 72:815–820.

Kamler, J., and P. Gipson. 2000. Home range, habitat selection, and survival of bobcats, *Lynx rufus*, in a prairie ecosystem in Kansas. Canadian Field Naturalist 114:388–394.

Kelly, M., et al. 1998. Demography of the Serengeti cheetah (*Acinonyx jubatus*) population: the first 25 years. Journal of Zoology (London) 244:473–488.

Kemp, P. 1989. Seed bank and vegetation processes in deserts. Pp. 257–281 in Ecology of seed soil banks (M. Leck, V. Parker, and R. Simpson, eds.). Academic Press, New York.

Kerley, L. L., J. M. Goodrich, D. G. Miquelle, E. N. Smirnov, H. B. Quigley, and M. G. Hornocker. 2002. Effects of roads and human disturbance on Amur tigers. Conservation Biology 16:97–108.

Knick, S. 1990. Ecology of bobcats relative to exploitation and a prey decline in southeastern Idaho. Wildlife Monographs 108:3–42.

Konecny, M. J. 1989. Movement patterns and food habits of four sympatric carnivore species in Belize, Central America. Pp. 243–264 in Advances in Neotropical mammalogy (K. H. Redford and J. F. Eisenberg, eds.). Sandhill Crane Press, Gainesville, Florida.

Laack, L. L., M. E. Tewes, A. H. Haines, and J. H. Rappole. 2005. Reproductive life history of ocelots *Leopardus pardalis* in southern Texas. Acta Theriologica 50:505–514.

Labraga, J. C., and R. Villalba. 2009. Climate in the Monte Desert: past trends, present conditions, and future projections. Journal of Arid Environment 73:154–163.

Lambert, C., et al. 2006. Cougar population dynamics and viability in the Pacific Northwest. Journal of Wildlife Management 70:246–254.

Lindstrom, E. 1981. Reliability of placental scar counts in the red fox (*Vulpes vulpes* L.) with special reference to fading of the scars. Mammal Review 11:137–149.

Litvaitis, J. A., J. F. Beltrán, M. Delibes, S. Moreno, and R. Villafuerte. 1996. Sustaining felid populations in humanized landscapes. Journal of Wildlife Research 1:292–296.

Lucherini, M., T. G. Oliveira, and G. Acosta. 2008. *Leopardus geoffroyi*. In IUCN Red list of threatened species. Version 2013.2. www.iucnredlist.org. Accessed 7 December 2013.

Mace, R. D., and J. S. Waller. 1998. Demography and population trend of grizzly bears in the Swan Mountains, Montana. Conservation Biology 12:1005–1016.

Mawdsley, J. R., R. O'Malley, and D. S. Ojima. 2009. A review of climate-change adaptation strategies for wildlife management and biodiversity conservation. Conservation Biology 23:1080–1089.

Murray, B. G. 1967. Dispersal in vertebrates. Ecology 48:975–978.

Novaro, A., M. Funes, and S. Walker. 2005. An empirical test of source–sink dynamics induced by hunting. Journal of Applied Ecology 42:910–920.

Olson, T., and F. Lindzey. 2002. Swift fox survival and production in southeastern Wyoming. Journal of Mammalogy 83:199–206.

Otali, E., and J. S. Gilchrist. 2004. The effects of refuse feeding on body condition, reproduction, and survival of banded mongooses. Journal of Mammalogy 85:491–497.

Palomares, F., E. Revilla, J. Calzada, N. Fernández, and M. Delibes. 2005. Reproduction and predispersal survival of Iberian lynx in a subpopulation of the Doñana National Park. Biological Conservation 122:53–59.

Pereira, J. A., N. G. Fracassi, and M. M. Uhart. 2006. Numerical and spatial responses of Geoffroy's cat (*Oncifelis geoffroyi*) to prey decline in Argentina. Journal of Mammalogy 87:1132–1139.

Pereira, J. A., et al. 2010. Causes of mortality in a Geoffroy's cat population—a long-term survey using diverse recording methods. European Journal of Wildlife Research 56:939–942.

Pereira, J. A., et al. 2011. Population density of Geoffroy's cat in scrublands of central Argentina. Journal of Zoology (London) 283:37–44.

Pereira, J. A., R. S. Walker, and A. J. Novaro. 2012. Effects of livestock on the feeding and spatial ecology of Geoffroy's cat. Journal of Arid Environments 76:36–42.

Pessino, M. E. M., J. H. Sarasola, C. Wander, and N. Besoky. 2001. Respuesta a largo plazo del puma (*Puma concolor*) a una declinación poblacional de la vizcacha (*Lagostomus maximus*) en el desierto del Monte, Argentina. Ecología Austral 11:61–67.

Pia, M., M. López, and A. Novaro. 2003. Effects of livestock on the feeding ecology of endemic culpeo foxes (*Pseudalopex culpaeus smithersi*) in central Argentina. Revista Chilena de Historia Natural 76:313–321.

Pollock, K., S. Winterstein, C. Bunck, and P. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7–15.

Poole, K. 1994. Characteristics of an unharvested lynx population during a snowshoe hare decline. Journal of Wildlife Management 58:608–618.

Poole, K. 1997. Dispersal patterns of lynx in the Northwest Territories. Journal of Wildlife Management 61:497–505.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.

Pulliam, H. R. 1996. Sources and sinks: empirical evidence and population consequences. Pp. 45–69 in Population dynamics in ecological space and time (O. E. Rhodes, R. K. Chesser, and M. H. Smith, eds.). University of Chicago Press, Chicago, Illinois.

Quinn, N., and J. Thompson. 1987. Dynamics of an exploited Canada lynx population in Ontario. Journal of Wildlife Management 51:297–305.

Roff, D. 1975. Population stability and the evolution of dispersal in a heterogeneous environment. Oecologia 19:217–237.

Ruth, T. K., M. A. Haroldson, K. M. Murphy, P. C. Buotte, M. G. Hornocker, and H. B. Quigley. 2011. Cougar survival and source–sink structure on Greater Yellowstone's northern range. Journal of Wildlife Management 75:1381–1398.

Sikes, R. S., W. L. Gannon, and the Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the care and use of wild mammals in research. Journal of Mammalogy 92:235–253.

Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? Biological Conservation 83:247–257.

Slough, B., and G. Mowat. 1996. Lynx population dynamics in an untrapped refugium. Journal of Wildlife Management 60:946–961.

Sunquist, M. E., and F. Sunquist. 2002. Wild cats of the world. University of Chicago Press, Chicago, Illinois.

Walther, G. R., et al. 2002. Ecological responses to recent climate change. Nature 416:389–395.

White, G., and R. Garrott. 1990. Analysis of wildlife radiotracking data. Academic Press, New York.

Williams, B., M. Conroy, and J. Nichols. 2002. Analysis and management of animal populations. Modeling, estimation, and decision making. Academic Press, New York.

Woodroffe, R., and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. Science 280:2126–2128.

Ximénez, A. 1975. *Felis geoffroyi*. Mammalian Species 54:1–4.

Yanosky, A., and C. Mercolli. 1994. Notes on the ecology of *Felis geoffroyi* in northeastern Argentina. American Midland Naturalist 132:202–204.

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