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Ecology of the Patagonia puma *Felis concolor patagonica* in southern Chile

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Abstract

The ecology of the Patagonia puma was studied in Torres del Paine National Park, Chile. Thirteen pumas were captured from 1986 to 1989 and equipped with radio transmitters. During the winter of 1988 there was one puma per 17 km^2 in the 200 km^2 study area. Home ranges varied from 24 to 107 km^2. Female home ranges overlapped with those of other males and females extensively, but male ranges overlapped each other for only short time periods. Seven adult pumas had home ranges extending outside the park boundaries and at least three preyed on sheep. Guanacos *Lama guanicoe*, especially young animals, were the puma's most important prey item by biomass, but European hares *Lepus capensis* were preyed upon more than expected relative to available biomass. Of 731 guanaco skulls collected from 1979 to 1988, 33% showed clear evidence of having been killed by pumas. Over the past decade puma numbers are believed to have increased in the park, perhaps in response to an increase in guanaco numbers and continued protection. With decreased hunting pressure and harassment by horses and dogs, pumas have habituated to people and are being observed more often by park visitors.

Keywords: Puma; Ecology; Human conflict; Patagonia; Chile

1. Introduction

The puma *Felis concolor* has the widest distribution of any terrestrial mammal in the Americas. In Chile, three subspecies of pumas are commonly recognized, *F. c. puma* in the arid Atacama desert and altiplano of northern Chile, *F. c. araucanus* in the Central Valley, and *F. c. patagonica* in the Patagonia steppe and Andean foothills (Cabrera, 1957; Hornacki et al., 1982; Currier, 1983). Throughout its range the puma is commonly associated with forested areas or in dryer more-open regions, such as the pampas of southern South America, it frequents locations with increased topographic relief and vegetative cover (Miller, 1980; Olrog and Lucero, 1981; Andrews, 1982; Nowell and Jackson, 1996).

Historically, important native prey of the Patagonia puma included the guanaco *Lama guanicoe*, lesser rhea *Pterocnemia pennata*, pudu *Pudu pudu*, and huemul *Hippocamelus bisulcus* (Courtin et al., 1980; Miller, 1980; Yañez et al., 1986). With the introduction of domestic sheep *Ovis aries* into southern Chile in 1877, and their increase to two million by 1916, they also became important prey (Miller, 1980) and pumas have been killed by ranchers. In 1927, Wolffsohn (in Miller, 1980: 309) noted that on one estancia (ranch) in southern Chile, 84 pumas were killed in a single year by the use of traps, dogs, rifles, and poison (also see Hudson, 1917).

Although land-clearing, agriculture, forestry, and grazing have altered and fragmented areas of suitable puma habitat in southern South America (Lubchenco et al., 1991), large tracts still remain. Puma populations in the open pampas have been reduced by hunting (Miller, 1980), but puma densities remain high in the adjacent forested and more-mountainous areas (Miller, 1980;

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Franklin, 1991). Thus, although pumas have been extirpated from some areas of the Patagonia (Novaro, 1991), they are still an important cause of depredation on sheep, cattle and goats and continue to be killed by ranchers and bounty hunters (see Bellati and von Thungen, 1990; Bellati, 1992; Bruggers and Naccagnini, 1994).

In Chile, pumas are protected by law, but hunting continues. Torres del Paine National Park in southern Chile was created in 1959 and expanded in 1975. Park administrators sought to manage the park and its wildlife as a complete, functioning ecosystem while ranchers, interested in protecting their livelihood, viewed the park as a refuge from which pumas could attack livestock and then retreat to safety.

Little is known of the Patagonia puma. Wilson (1984) described the impact of pumas on guanacos during the winter in Torres del Paine, and Yañez et al. (1986) documented puma food habits during two seasons of the year. The overall goal of the present study was to assess the ecology and predator–prey relationships of the Patagonia puma in Torres del Paine National Park, especially as related to its conservation biology. Our objectives were to (1) estimate puma population density, (2) document their movements, home range sizes, activity patterns, and habitat use, (3) compare puma food habits with prey availability, and (4) describe the impact of pumas on the guanaco population and local sheep ranches.

2. The study area

Year-round field studies were conducted in Torres del Paine National Park (51°3'S, 72°55'W), Ultima Esperanza, Chile (Fig. 1) from January 1986 to December 1989. Supplementary information was collected in the five previous and five subsequent years. The 240,000-ha park extends westward from the desert-grasslands of Patagonia through the eastern Andean foothills to glaciated mountains. Elevations range from 100 to 300 m. The steppe biome occurs at elevations below 500 m (Pisano, 1974).

The steppe grassland was characterized as a xeric pre-Andean shrub association. The dominant species of this association in the park is "mata barrosa" *Mulinum spinosum* a spiny, dome-shaped shrub, characteristic of the thin, rocky upland, and rapidly draining soils. Other important shrub species are "senecio" *Senecio patagonicus*, "calafate" *Berberis buxifolia*, "mata negra" *Verbena tridens* and "paramela" *Adesmia boronoides*. The woodland areas are dominated by two medium-sized

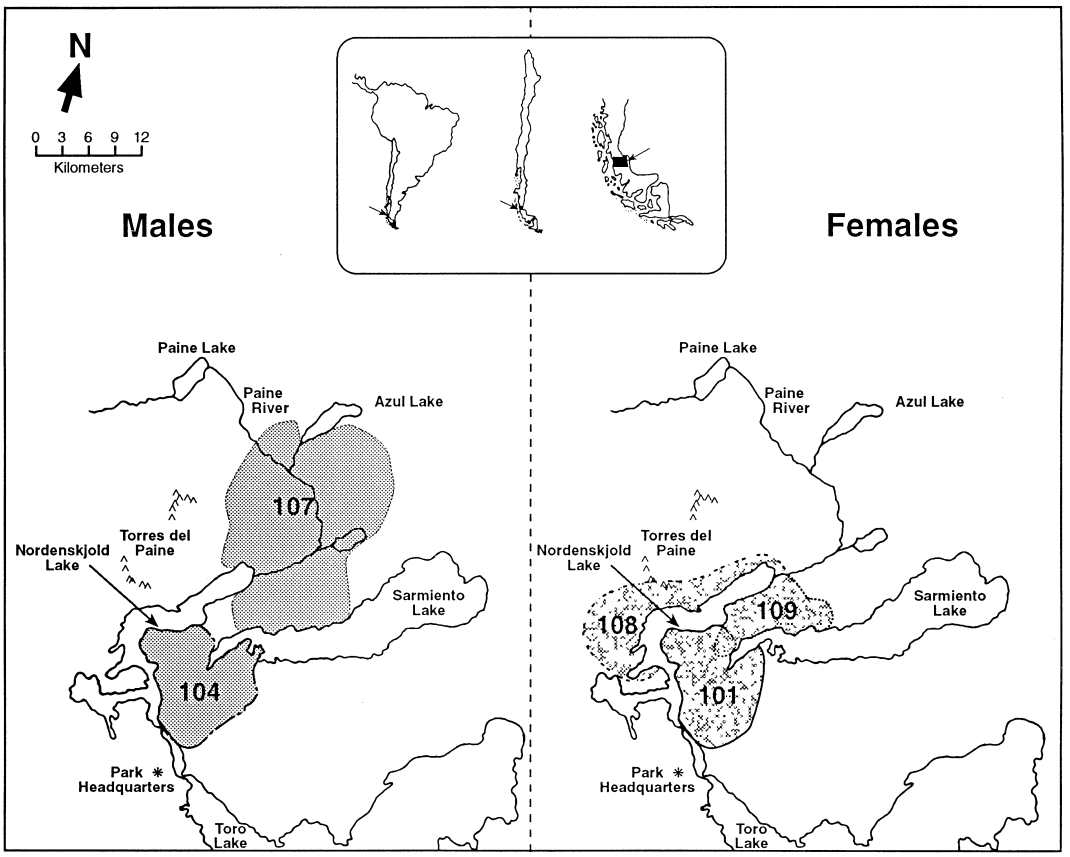

Fig. 1. Location of Torres del Paine National Park in southern Chile and home ranges of radio-collared Patagonia pumas at Torres del Paine National Park, 1986–1988. Females: adults 101 and 108 and juvenile 109. Males: adults 104 and 107.

tree species, ''nirre'' *Nothofagus antarctica* and ''lenga'' *N. pumilio* (Texera, 1973; Pisano, 1974; Ortega and Franklin, 1988).

Prey available to the puma include the guanaco, European hare *Lepus capensis*, upland goose *Chloephaga picta*, lesser rhea, and domestic sheep. Potential competitors of the puma include Geoffrey's cat *Felis geoffroyi*, culpeo fox *Dusicyon culpaeus*, chilla fox *D. griseus*, Patagonia skunk *Conepatus humboldti*, and several raptor species (Fuller et al., 1987; Johnson et al., 1988; Iriarte et al., 1990a; Johnson and Franklin, 1991, 1994a,b).

The study area extended from Lago (Lake) Toro in the south to the park boundaries near Lago Paine in the north, and from Lago Pehoe in the west to Chinas River in the east (Fig. 1) and included portions of five private ranches. We concentrated our efforts on a 200-km^2 core study-area located in the center of the park between Lagos Sarmiento, Pehoe, Nordenskjold, and Azul. This area included the 4000 ha ''Peninsula'' (Ortega and Franklin, 1988), where 90% of the parks guanacos were located. Numerous corridors (see Beier, 1993) were available for movement of pumas into and out of the area.

3. Methods

3.1. Capture and telemetry

Pumas were captured from 1986 to 1988, primarily during winter (June–August) when light snow and mild wind improved tracking conditions. Pumas were bayed in trees, caves, or on cliffs by trained hunting dogs (Hornocker, 1970) and immobilized with a mixture of ketamine hydrochloride (11 mg/kg) and xylazine hydrochloride (1.5 mg/kg) administered intramuscularly by a Telinject® blowgun. Each cat was sexed, aged (Ashman et al., 1983), weighed, measured, tagged in both ears with numbered plastic eartags, and fitted with a motion-sensitive radio-collar (164 MHz; Advanced Telemetry Systems, MN).

Daytime locations were obtained randomly once or twice a week using a Yagi-three-element antenna and were recorded on aerial photos. When possible, individuals were located within 50 m to accurately determine habitat characteristics. We also obtained night locations, but the rough terrain and the difficulty of approaching pumas without disturbing them made this impractical. Habitat was classified as trees <3 m, >3 m, trees mixed with shrubs, shrubs, or cliffs and rocky slopes. Habitat density was categorized based on the percentage of canopy cover as either high (75–100%), medium (26–74%), or low (0–25%).

Diel cycles in activity patterns were assessed by monitoring radio-collared cats from prominent hills in relation to changing day lengths. Percentage activity was calculated for dawn (defined as the hour before and after sunrise), day, dusk (the hour before and after sunset), and night. Samples of activity were taken randomly during 4–12 h observation periods, and no more than one sample per individual was taken per hour.

Minimum home ranges were described by the minimum convex polygon technique (Mohr, 1947) for periods when we were relatively certain we knew the general movement patterns of individual pumas. Because we calculated home range primarily using daytime locations, and because terrain features often made it difficult to accurately triangulate study animals, our estimates of home range sizes were probably low.

We calculated minimum densities of pumas in the core study area based upon known radio-collared individuals in the area plus the number of unmarked pumas frequenting the area as estimated by visual sightings and snow tracking. We also calculated frequency of visual sightings from September 1990 to October 1993.

3.2. Prey

We determined puma prey by analyzing scat and stomach contents of samples collected during preliminary (1982–1983, $n=63$ scats) and intensive (1987–1988, $n=342$ scats and 6 stomachs) study periods. Methods of field scat collection and analysis, adjustment for under representation of items in scats from large prey, seasonal variation analysis, and estimating prey abundance are discussed in detail elsewhere (Iriarte, 1988; Johnson et al., 1990; Garay et al., 1991; Iriarte et al., 1991). European hare densities were estimated from four random 1.5-km transects sampled monthly from June 1987 to May 1988 and using the program TRANSECT (Burnham et al., 1980).

3.3. Relationship with the guanaco

Guanaco censusing began in Torres del Paine National Park in 1975 by park guards (Ortega and Franklin, 1995). During the following 14 years, 55 guanaco censuses were conducted in the Peninsula area by park personnel and our research staff. Size and composition of male, family, mixed, and female groups and the numbers of solo males were recorded. Animals were classified by sex and age as adult males, adult females, yearlings (12–24 months), and chulengos (juveniles <12 months). To compare puma predation on guanacos, portions of the study area with an average year-round density of <10 guanacos/km^2 were classified as low density and areas with >10 guanacos/km^2 as high density.

We located fresh guanaco carcasses in the field by observing circling Andean condors *Vultur gryphus* and concentrations of crested caracaras *Polyborus plancus*. Dead guanacos were classified as ''puma kills'' if there were large tooth marks (puma canine size) on the

throat, skull and/or neck, broken large bones, or if the carcass was covered by plant debris. We categorized guanaco skulls collected from 1978 to 1988 by sex (size of the canines), age (tooth wear and replacement) (Raedeke, 1978, 1979; Wheeler, 1982; Puig and Monge, 1983), and evidence of having been killed by pumas (Shaw, 1979).

4. Results

4.1. Captures, population density, sightings

We captured 13 pumas: three adult males and three adult females (>24 months-old), and four male and three female subadults during the 4-year study. Adult males weighed significantly more than females (76 versus 48 kg; $t = 5.23$, d.f. = 5, $p = 0.002$) and tended to be larger (Table 1).

During the winter of 1988 five radio-collared adult pumas (two males and three females) were in the study area, resulting in a minimum density of 2.5 pumas/100 km^2. On the basis of tracks and visual sightings, we determined there to be at least one additional adult male, one adult female, and five kittens (<6 months old) in a 200 km^2 area, which when combined with marked animals resulted in a density of 6 pumas/100 km^2.

In the 1970s observations of pumas in the park were rare. In the early 1980s pumas were occasionally seen at night near cabins or in the headlights of vehicles, but rarely during the day. In the mid to late 1980s the number of day and nighttime sightings of pumas by field researchers, park staff, and tourists increased dramatically and continued to increase into the early 1990s. In October 1995, nine individuals were sighted in one day and reports indicated that there were probably as many as 12 pumas in the 40 km^2 Peninsula study area, which was equivalent to 30 pumas/100 km^2 or 1/3.3 km^2 (Hugh Miles, pers. comm.).

4.2. Activity, habitat use, and home range

Pumas were most active at dawn (52% of the times monitored, $n = 61$), and were slightly less active at dusk (44%, $n = 109$) and at night (43%, $n = 313$). During daylight hours pumas were active in 25% of the 949 telemetered observations. Pumas were found primarily in areas with trees (54% of the relocations) and areas of high cover density (64%) (Table 2). When active, pumas increased their use of areas with bushes, grass, rocks, and cliffs (53% compared with 36% when not active), and their use of areas of low and medium canopy density (46% compared with 34%).

Minimum home ranges for females ranged from 27 to 107 km^2 and for males from 24 to 100 km^2 (Table 3). Female home ranges overlapped temporally and spatially with other females and extensively with males (Fig. 1). Males overlapped with each other for only short periods of time at the edges of their home ranges, and in each instance seemed to be associated with changes in home range occupancy or a female possibly in heat. From March 1987 to January 1990 three adult males (males 107, 104, 112) replaced each other in the occupancy of a portion of the study area. Seven of eight adult pumas we radio tracked had home ranges that extended beyond the park boundaries and three were known to have preyed on sheep.

4.3. Prey

Mammals and birds accounted for 92 and 8% of the prey items counted in 405 puma scats. European hares

Table 1
Patagonia puma body-weights (kg) and measurements (mm) for four adult males (including one in captivity) and four adult females (including one shot by hunters) (mean ± SE)

Sex	*n*	Body mass	Body length	Tail	Head
F	4	47.5 ± 6.4	1265 ± 84	745 ± 51	254 ± 32
M	4	75.8 ± 8.7	1372 ± 74	778 ± 23	291 ± 13

Table 2
Percentage of habitat use by pumas in Torres del Paine National Park, Chile, as determined from 111 telemetry relocations. Percentage of canopy cover classifed as low (0–25%), medium (26–74%) and high (75–100%)

Habitat type	Habitat density			
	Low	Medium	High	Total
Trees >3 m tall	0.9	5.4	37.8	44.1
Trees <3 m tall	0	0	9.9	9.9
Trees and shrubs	0	0	17.8	23.3
Shrubs	1.8	4.5	9.0	15.3
Grassland	5.4	5.4	0.9	11.7
Cliffs and rocks	9.9	2.7	0.1	2.6
Total	18.0	18.0	64.0	100.0

Table 3
Summary of yearly home ranges of 8 pumas in Torres del Paine National Park as described by the minimum convex polygon method, based upon pumas collared with telemetry transmitters (*n* = the number of times located)

Animal	Sex	Age	Time period	*n*	km^2
101	F	Ad	6/86–6/87	38	66
103	F	Juv	9/86–3/87	26	27
108	F	Ad	5/88–10/88	27	75
109	F	Juv	7/88–6/89	46	107
104	M	Ad	4/87–10/88	36	100
107	M	Ad	2/88–7/88	58	97
111	M	Ad	8/87–4/88	26	53
112	M	Ad	3/89–1/90	37	24

represented 51%, guanacos 23%, sheep 5%, upland goose 5%, rodents 3%, and lesser rhea 1%. There was no difference in the numerical occurrence of prey categories by seasons of the year ($\chi^2 = 16.2$, d.f. = 12, $p = 0.18$), but it was significantly different among years ($\chi^2 = 38.3$, d.f. = 16, $p = 0.001$). This difference was due to an increase from 9 to 29% in the frequency of guanaco remains in puma scats between 1982–1983 and 1987–1988.

Numbers of guanacos in the high-density area averaged 1108 ± 46 ($x \pm$ S.E.) between 1983 and 1988. Mean density of prey species was 45.6 ± 8.7 European hare/km^2, 11.7 guanacos/km^2 (74 ± 4% adults/km^2, 7 ± 2% yearlings/km^2, 19 ± 2% chulengos/km^2), 5.3 upland goose and lesser rhea/km^2, and 1.1 sheep/km^2. European hares were the most numerous prey of pumas (Fig. 2), but in terms of biomass (Fig. 3), guanacos (59%) were the most important food source. However, European hares were preyed on more and guanacos less than expected relative to their estimated biomass availability (Fig. 3). In the Peninsula, the area of high guanaco density, pumas fed on an estimated 13 European hares for every one guanaco.

From 1975 to 1988 the guanaco population increased from 97 to 1276 animals. There was no difference in the proportion of guanacos in each age classes from 1981 to 1988, averaging in 1988 70% adults, 21% chulengos and 9% yearlings. Of 731 guanaco skulls collected from 1979 to 1988, 33% showed clear evidence of having been killed by pumas (Table 4). More were killed in winter and spring (63%) and in areas of high guanaco density ($\chi^2 = 37.02$, d.f. = 2, $p = 0.0001$), but almost equal numbers of both sexes were taken ($n = 70$ skulls,

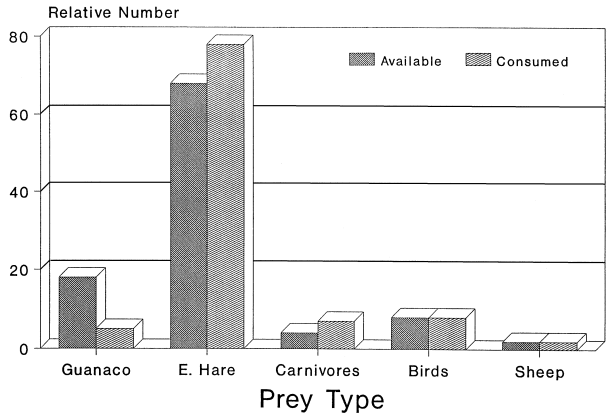

Fig. 2. Relative numbers of individual prey consumed by Patagonia pumas compared with the relative number of prey available in Torres del Paine National Park, Chile, 1982–1983 and 1987–1988 (see Iriarte, 1991).

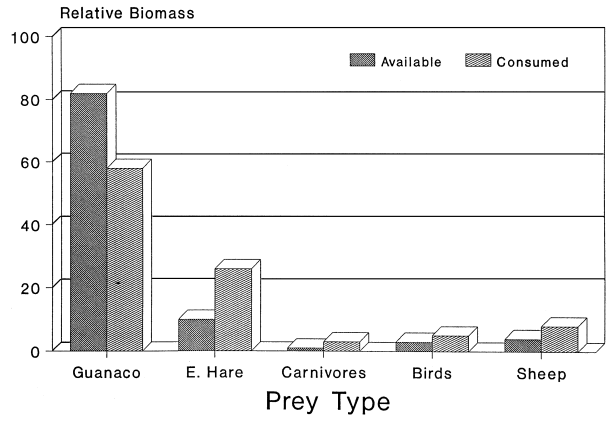

Fig. 3. Relative biomass of prey consumed by Patagonia pumas compared with the relative biomass of prey available in Torres del Paine National Park, Chile, 1982–1983 and 1987–1988 (see Iriarte 1991).

Table 4
Age in months of 731 guanaco skulls collected in the Peninsula of Torres del Paine National Park, Chile, from May 1978 to July 1988. See text for methods of aging and determination of puma kills

	Puma kills		Non-puma kills		Total	
Age	*n*	%	*n*	%	*n*	%
1–10	115	47.3	189	38.6	304	41.6
11–20	28	11.5	84	17.4	112	15.3
21–30	19	7.8	33	6.9	52	7.1
31–40	5	2.1	20	4.1	25	3.4
41–50	19	7.8	31	6.8	50	6.8
51–60	16	6.6	60	12.4	76	10.4
61–70	5	2.1	8	1.6	13	1.8
71–80	5	2.1	5	1.0	10	1.4
81–90	1	0.4	13	2.6	14	1.9
91–100	12	4.9	13	2.6	25	3.4
101–110	1	0.4	4	0.9	5	0.7
111–120	5	2.1	11	2.2	16	2.2
121–130	2	0.8	6	1.2	8	1.1
131–140	1	0.4	1	0.2	2	0.3
141–150	6	2.5	8	1.6	14	1.9
151–160	3	1.2	2	0.4	5	0.7
Total	243	100.0	488	100.0	731	100.0

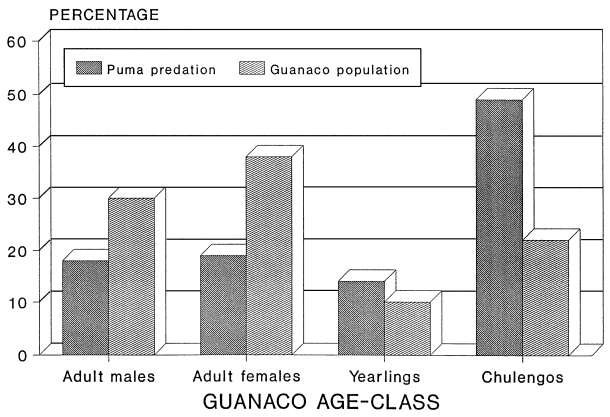

Fig. 4. Proportion of guanaco adult males, adult females, yearlings (12–24 months), and chulengos (juveniles < 12 months) killed by pumas (skulls collected 1978–1988) compared with the average proportion of guanacos present (censuses 1975–1988) in Torres del Paine National Park, Chile.

49% males and 51% females). Fifty-nine percent of their skulls were chulengos and yearlings (1–20 months old) and relative to their availabilities, chulengos were preyed upon about four times as much as adults (Fig. 4).

5. Discussion

Puma ecology and movement patterns have been well studied in temperate and subtropical areas of North America (Anderson, 1983; Currier, 1983; Hansen, 1992). In the Neotropics the puma is relatively unstudied, however; most research has focused on food habits (Yañez et al., 1986; Emmons, 1987; Iriarte et al., 1990b) or spatial distribution based on the presence of tracks or feces (Rabinowitz and Nottingham, 1986). The only exception was the pioneering work of Schaller and Crawshaw (1980) who monitored a male puma by radio-telemetry for two months in the Pantanal region of southern Brazil (also see Schaller, 1983). The Patagonia puma showed many of the characteristics and behavioral patterns of North American subspecies (see Hansen, 1992). However, as would be expected for a species with such a wide geographical distribution, there were some important contrasts with North American populations that were probably related to environmental differences, such as prey availability.

Numbers and sightings of pumas have dramatically increased since the expansion and improved management of Torres del Paine National Park in 1975. During this time livestock and hunters were nearly excluded, and guanacos and other prey increased within the park. Coinciding with these management changes, remarkable shifts in behavior occurred in this puma population. Pumas throughout their range are classically elusive, secretive, and extremely wary of people. However, over the past two decades many of the pumas in Torres del Paine have become more habituated to people. They often do not flee when encountered in the field at close distances, and often are observed in apparently normal activities such as hunting, feeding, resting, and mating. Several pumas have approached field workers or tourists within 5–15 m with no apparent aggression. To date there has only been one documented puma attack on humans in the park, when a young puma killed (and fed upon) a tourist fishing along an isolated trout stream.

5.1. Activity and home range

Daily activity patterns of pumas in Chile were remarkably similar to those reported for pumas in Utah (Ackerman, 1982) and Idaho (Seidensticker et al., 1973). Puma activity levels in Torres del Paine were generally low, reflecting the puma's feast-and-fast feeding habits and the high percentage of large prey items in their diet, in this case, the guanaco. When an adult guanaco was killed, the 110 kg carcass was generally fed on for several nights.

Estimates of puma home range size in Torres del Paine National Park were substantially smaller than most of the areas reported by Anderson (1983) for North America, but were comparable to those found in California (Kutilek et al., 1980). Puma density was also higher than in most of the studies reviewed by Anderson (1983), and was similar to or greater than California (Sitton, 1972) and Colorado (Currier, 1983) estimates. Small home range size and high puma density were probably due to the park's high concentration of guanacos and European hares, which together made up 87% of the biomass consumed by pumas (Iriarte et al., 1991).

5.2. Relationship to Patagonia guanaco

Our finding that pumas in Torres del Paine selectively preyed on juveniles was in contrast to North American studies where pumas have shown a preference for adult mule-deer *Odocoileus hemionous* (Robinette et al., 1959; Spalding and Lesowski, 1971, Dixon, 1982), and adult male elk *Cervus canadensis* (Hornocker, 1970). Guanacos were dragged away from the kill site into denser vegetation and/or covered with plant material and debris. This was probably an attempt to hide the carcasses from local scavengers. Pumas in the park returned to a carcass to feed 1–2 times per day, but in North America (Hornocker, 1970; Anderson 1983) they typically return 5–7 times per day.

Our estimate that one-third of the guanaco skulls (all age classes) that we examined were from individuals killed by pumas was probably low. Pumas often kill guanacos by a bite to the throat, thus leaving the skull undamaged. In addition, skulls of young animals are probably more difficult to find since they can be easily broken, eaten, and/or scattered.

5.3. Relationship of pumas to sheep ranches

Home ranges of seven of eight pumas extended outside the park and at least three of these preyed periodically on sheep. Two males left the park weekly at dusk to prey on sheep and returned by dawn. These pumas were using the park as a refuge, that might otherwise have been hunted by ranchers. However, the presence of hunters within the park also demonstrated that park boundaries did not completely deter poachers. Likewise, pumas that left the park were highly vulnerable to hunting, either outside the park or after having been tracked back into the park. Within a 2 year period, two of our 11 radio-collared pumas were killed by hunters, and we suspect at least 2–3 others that suddenly disappeared were also killed.

Most radio-tracked pumas occasionally left the park to prey on sheep, but livestock was not an important

source of food overall for park pumas. Yañez et al. (1986) also found that sheep remains were more common in puma scats collected outside the park than within it. Yet, despite the average low level of sheep remains we found in puma scats (10% for five areas), pumas appeared to have a major impact on the economies of local ranches. Several sheep were usually killed by pumas at one time, with only a few being fed upon. The owner of an adjacent ranch that had 4000–5000 sheep during the study period estimated that his average annual loss to puma depredation was 300–500 sheep, or several thousand dollars (Juan Goic, pers. comm.). He believed occasional hunting of pumas was an economic necessity to stay in business.

6. Conclusions, policy implications, and perspectives

The lessons being learned about puma ecology in Torres del Paine National Park can potentially be extrapolated to other parts of Patagonia with similar prey bases. The park has been important to the recovery and protection of this puma population and the associated assemblage of wildlife. However, it has also set the stage for conflict between this large predator and sheep ranching. For almost a 100 years this region was dominated by large corporate ranches, some units with as many as several hundred thousand sheep. Hunters were employed to kill as many pumas as possible. In the past 25 years agrarian reform has led to a reduction in the average size of ranches and full-time puma hunters have essentially disappeared. However, by some accounts, some individuals may still kill as many as 50–75 pumas a year, especially during snowy winters when pumas are easily tracked.

Torres del Paine National Park is a bastion of wildlife biodiversity surrounded by a landscape dominated by ranching. However, tension between livestock producers and pumas will continue as long as landowners view the park as a threat to their way of life and livelihood. Several factors may eventually help ease these tensions, however. First, in response to a dramatic increase in tourism to the park, three of the surrounding ranches have expanded into the hotel and ecotourism business and are shifting away from traditional sheep ranching. Second, in response to depressed prices for wool and sheep meat worldwide, and perhaps to economic losses associated with puma depredation, ranches in the region are shifting increasingly from sheep to cattle. Depredation on cattle has not been a significant problem thus far in this region.

Because of the puma's abundance and habituation to people in Torres del Paine, the park offers an unmatched setting for better understanding the inter-relationships of a large mammalian predator and its prey. We recommend that the park administration continue to foster and encourage the protection of the puma and that they continue to support research on its impact on other wildlife and its relationship with people.

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