

Feeding ecology of the Patagonia puma in southernmost Chile

Ecología trófica del puma de la Patagonia
en el extremo sur de Chile

J. AGUSTIN IRIARTE^{1, 3}, WARREN E. JOHNSON²,
and WILLIAM L. FRANKLIN²

¹ Center for Latin American Studies, University of Florida, Gainesville, FL 32611;

² Department of Animal Ecology, Iowa State University, Ames, IA 50011;

³ DIPROREN, Servicio Agrícola y Ganadero, Av. Bulnes 259, Of. 704, Santiago

ABSTRACT

The feeding ecology of the Patagonia puma (*Felis concolor patagonica*) was studied in Torres del Paine National Park, Chile, by analyzing seasonal and yearly variation in 590 prey items found in 405 puma feces from 1982 to 1988. Mammalian species accounted for 92% of all prey items in feces. European hares (*Lepus capensis*) were the most preyed-upon vertebrate, representing 50% of the items found in feces. Guanacos (*Lama guanicoe*) made up 32% of prey items and accounted for 47% of the total biomass consumed by pumas. From 1982 to 1988, the proportion of guanaco remains in puma feces increased from 9% to almost 30% of total prey items, paralleling an increase in the guanaco population from 670 to 1,300 individuals in the study area. The only livestock species found in the puma diet was sheep (*Ovis aries*), representing 5% of the total number of prey found in feces. Small- and medium-sized prey may be important alternative prey in areas where large prey are less abundant.

Key words: *Felis concolor*, Chile, food habits, prey selection.

RESUMEN

La ecología trófica del puma de la Patagonia (*Felis concolor patagonica*) fue estudiada en el Parque Nacional Torres del Paine, Chile, haciendo un análisis estacional y anual de 590 presas encontradas en 405 fecas entre 1982 y 1988. El 92% de los restos en las fecas correspondían a mamíferos. La liebre europea (*Lepus capensis*) fue la presa más común en la dieta, representando el 50% del total de los ítemes de presas. El guanaco (*Lama guanicoe*) representó el 32% de los ítemes y el 47% de la biomasa total consumida por el puma. De 1982 a 1988, los restos de guanacos en las fecas de puma aumentaron de 9% hasta casi 30% del número total de presas, paralelamente a un aumento en la población de guanacos de 670 a 1.300 individuos en el área de estudio. La única especie de ganado encontrado en la dieta del puma fue la oveja (*Ovis aries*), representando el 5% del número total de presas encontradas en las fecas. Las presas pequeñas y medianas parecen ser alternativas importantes en áreas donde las presas grandes no son abundantes.

Palabras claves: *Felis concolor*, Chile, dieta, selección de presa.

INTRODUCTION

The puma has the most extensive range of any terrestrial mammal in America, covering more than 100 latitudinal degrees from the Strait of Magellan to Canada's Yukon. As might be expected from its widespread distribution, pumas occupy diverse habitats and consume a variety of prey. The literature on puma diet in the temperate and subtropical areas of North America has been reviewed by Goldman (1946), Young (1946), Dixon (1982), Anderson (1983), and Currier (1983). In

the Neotropics, however, pumas have been studied in considerably less detail (see Iriarte *et al.* 1991 for a review).

Although much of the available information on pumas in Chile is anecdotal (Pritchard 1902, Osgood 1943, Housse 1953, Miller & Rottmann 1976), recent studies indicate that the puma is a major predator of several species in Chile, including pudu (*Pudu pudu*, Courtin *et al.* 1980), guanaco (*Lama guanicoe*, Wilson 1984), Chilean huemul (*Hippocamelus bisulcus*), Upland Goose (*Chloephaga picta*), Lesser Rhea (*Pterocnemia pennata*), and livestock (Courtin *et al.* 1980, Yáñez *et al.* 1986). Only the most general aspects of puma feeding

ecology in Chile are known, and how the puma's diet is related to availability, distribution, age, and sex ratios of prey is poorly understood. Yáñez *et al.* (1986) conducted a study of puma food habits from feces collected from 1983 to 1984 in Torres del Paine and the surrounding sheep ranches, but related the results only to differences in the distribution of sheep. One of the objectives of our study is to expand on this earlier study by examining between-year differences in puma food habits. Because of the increasing abundance of guanaco, one of the common prey items, food habits of pumas in parts of southern Chile may have changed during the last 10 years. Another objective is to estimate seasonal variations in puma diet and to determine whether pumas take prey in proportion to its availability. Torres del Paine is an ideal place for this study because of the high density of pumas and because the relatively open terrain is conducive to obtaining estimates of prey availability.

STUDY AREA

The study was conducted at Torres del Paine National Park (51°03'S, 72°55'W) in the XII Administrative Region of Chile (Fig. 1). The 240,000-ha Park extends westward from the desert-grasslands of Patagonia, through the eastern Andean foothills, to glaciated mountains and continental ice fields. Elevations range from 100 to 3,000 m. Steppe biome composed of pampa characteristic of the southern part of South America occurs below 500 m (Texera 1973; Pisano 1973, 1974; Ortega & Franklin 1988; Johnson & Franklin 1991).

We separated our data into 3-month periods based on climate and ecology of the wildlife. Winter (June-August), is dry, less windy, and relatively cold (mean daily July temperature is 0.2°C). Summer (December-February) is windy, rainy, and relatively warm (January mean daily temperature is 12.6°C) (temperature records from 1985 to 1987 at Park head quarters). Spring and fall are intermediate seasons weatherwise.

This portion of the southern Chilean Patagonia has a high diversity of mammalian species (Johnson *et al.* 1990). Large native prey species were guanaco (mean adult weight = 120 kg), Upland Goose (3.7 kg), and Lesser Rhea (16 kg) (Miller and Rottmann 1976; Raedecke 1979). Introduced prey species were domestic sheep (44 kg), young cattle (80 kg), horses (250 kg), and European hare (3.4 kg). Other potential prey items included the Geoffroy's cat (*Felis geoffroyi*, 4.5 kg), culpeo fox (*Pseudalopex culpaeus*, 7.5 kg), gray fox (*P. griseus*, 4.5 kg), and Patagonia skunk (*Conepatus humboldti*, 3.5 kg) (Fuller *et al.* 1987, W.E. Johnson unpubl. data). Several native cricetine rodents were also potential minor prey (see Iriarte *et al.* 1990).

The study was conducted in two adjacent areas with different guanaco densities (Fig. 1). The area of high guanaco density (9,500 ha) contained most of the Park's guanacos. It was open terrain and included 1,000 ha of a major sheep ranch at the border of the Park. The area of low guanaco density (10,000 ha) had more dense vegetative cover, was bordered by two sheep ranches, and included portions of a cattle ranch.

METHODS

Sixty-three fecal samples were collected opportunistically from 1982 to 1983 and 342 from 1985 to 1988 (103 in 1985, 86 in 1986, 62 in 1987, and 81 in 1988). Estimated age, location, date, and size were recorded for each feces; time since deposition was estimated by comparison with those of known age. We were confident that collected feces were from pumas. The only potential misidentification was culpeo fox feces which were noticeably smaller, more twisted, and darker, and Lesser Rhea, which contained exclusively plant material (mainly grasses). Because of the movement patterns of pumas in the study area and their small average home ranges (mean = 6,900 ha, W.E. Johnson, unpubl. data), we assumed that most of the feces contained prey killed within the same area.

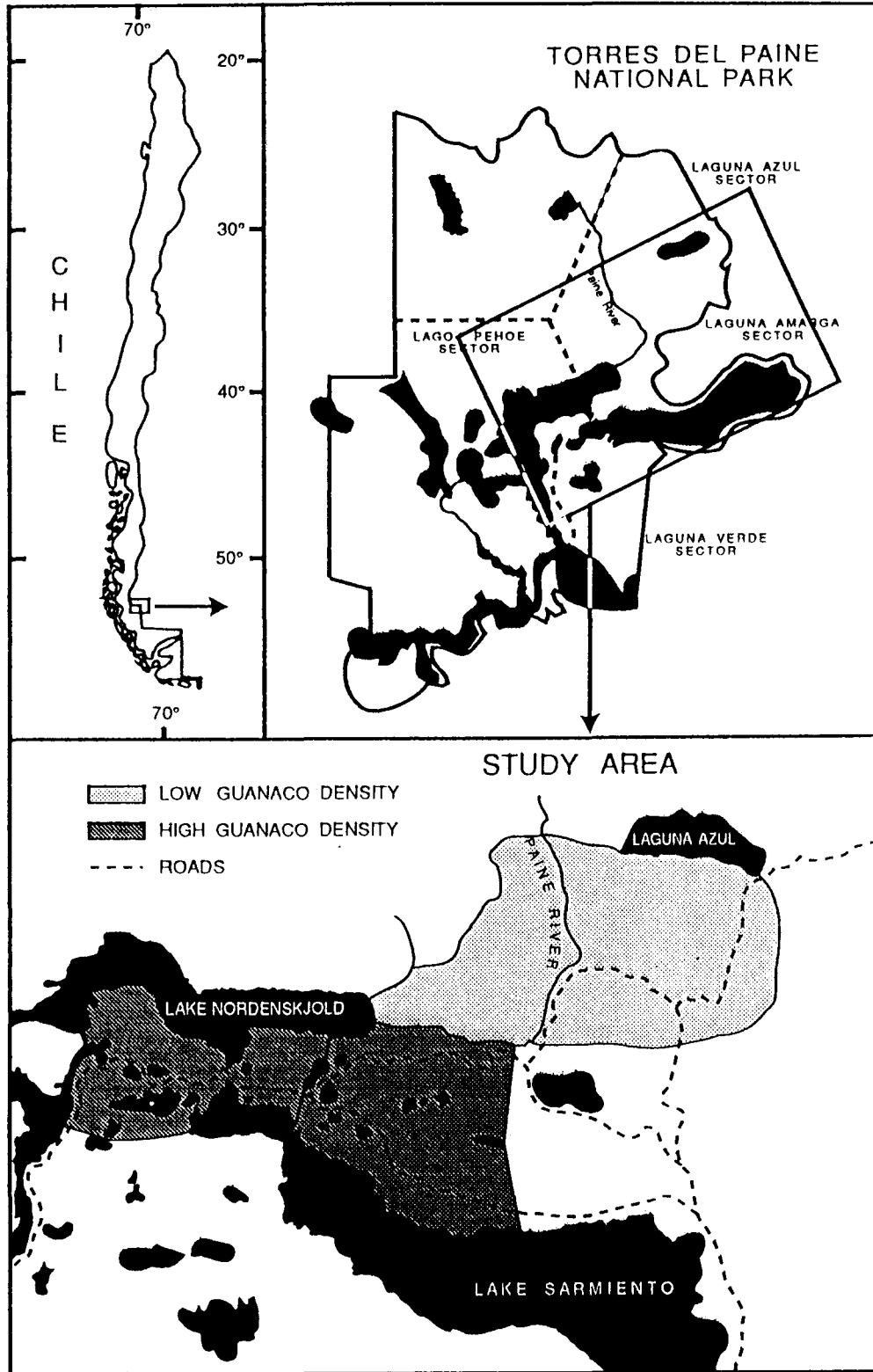


Fig. 1: Location of the two sections of the study area in Torres del Paine National Park, Chile.

Ubicación de los dos sectores de estudio en el Parque Nacional Torres del Paine, Chile.

Feces collected in 1982, 1983, 1985, and 1986 were rinsed, sifted, and the contents identified by point-frame analysis (Johnson & Hansen 1977). Feces collected in 1987 and 1988 were air-dried and the major components were separated (Ackerman *et al.* 1984). Hard parts (bones, teeth, nails, hair, and feathers) were compared with reference specimens for identification to species level for mammals and family level for birds. Percent numerical occurrence (number of times a prey taxa is found as percentage of the total) was used for comparisons between seasons, years, and sections of the study area. Frequency of occurrence (percentage of total feces in which an item was found) was used to calculate relative biomass consumed and relative number of individuals consumed (Ackermann *et al.* 1984).

Number of solid, field-collectable feces has been shown to be inversely related to prey size for large carnivores such as wolves (*Canis lupus*) (Floyd *et al.* 1978) and pumas (Ackerman *et al.* 1984). We therefore calculated relative percent biomass consumption and relative numbers of prey consumed by pumas following Ackerman *et al.* (1984). The equation $C = 1.98 + 0.035W$, where C is the correction factor and W is the mean prey weight, corrects for the underrepresentation of large prey items in the feces. The average biomass of the vertebrate prey eaten by pumas was estimated by the geometric mean weight of vertebrate prey (MWVP) in the puma diet (Jaksic & Braker 1983).

Seasonal variation in diet was examined by comparing only feces of known age ($n = 307$). Yearly variation was determined by comparing feces from 1 September to 31 August for each year. The proportion of feces from each season varied between years, but because there was no significant difference in diet between seasons ($\chi^2 = 16.2$, $df = 12$, $P = 0.18$), we did not adjust the data to ensure that the seasons were equally represented. We used Chi-square analysis to test for differences in prey frequency distributions, categorizing prey items as sheep, guanaco, European hare, birds, or other. When testing between the two sections of the study

area we compared the individual Chi-square values of each prey category with Bonferroni comparisons to examine influence of the items (Johnson & Wichern 1982: 197). Individual Chi-square scores with $P < 0.01$ ($\alpha = 0.05/\text{no. of categories}$) were considered significant.

To compare puma food habits with prey abundance, the density of guanacos, European hare, birds, carnivores, and sheep were estimated for the area of high guanaco density from June 1987 to July 1988. Guanacos were counted along five 8– to 12-km routes. We assumed these were total counts because of the open terrain and the habituation of the guanacos to people. Numbers of adult, yearling, and juvenile guanacos from eight censuses were averaged and multiplied by the average weight of each age class to estimate total available guanaco biomass. Adults were assumed to weigh 120 kg, yearlings 80 kg, and juveniles 30 kg (Raedecke 1979, Defosse *et al.* 1981).

European hare densities were estimated from four random 1.5– km transects sampled monthly from June 1987 to May 1988. Monthly data were combined to obtain an estimate of density and standard error for the year using Program TRANSECT (Burnham *et al.* 1980). Mean weight of European hares was estimated from 109 hares shot on a neighboring ranch. Sheep densities were obtained from neighboring ranchers. Minimum number of waterbirds from the families Anatidae, Podicipedidae, Phoenicopteridae, and Rallidae was estimated monthly by a total count on 16 of 64 seasonal, semi-permanent, and permanent ponds and lakes (Garay *et al.* 1991). Monthly surveys were averaged to obtain an estimate for the year. Minimum numbers of Lesser Rhea were determined from the mean number seen during the guanaco censuses.

The density of gray and culpeo foxes and Patagonia hog-nose skunks was estimated from telemetry data. We estimated a density of 1 fox/km² by dividing the portion of the study area used by each species by its average home-range size as indexed from radiotelemetry relocations and assuming there were two foxes per

home-range (W.E. Johnson, unpubl. data). We estimated a density of 1.6 skunk km² by extrapolating the results of Fuller *et al.* (1987) and Johnson *et al.* (1988) on the western end of the study area to the appropriate habitat in the whole area.

Puma predation on these species was assessed from 99 feces with identifiable prey items collected from 1985 to 1988 in the high-guanaco density area. Because rodents were a minor part of the diet of the puma, they were not used in this comparison.

The influence of differences in prey availability on prey selection was also examined by comparing contents of feces from each of the two areas with the relative densities of guanacos and European hares available in each section. Hare densities in the area of low guanaco density were estimated from six random line transects totaling 9 km using program TRANSECT (Burnham *et al.* 1980). Guanaco densities were determined from two censuses conducted on October 1987 and March 1988 along two 14-km routes.

RESULTS

Seasonal and Yearly Variation of Puma Diet

During the 6-year study, 590 individual prey items were found in 405 puma feces (Table 1). Mammalian species accounted for 92% of the prey items by number and birds the remaining 8%. European hares represented 50% of the prey items, guanacos 23%, and sheep 5%. The most common remains of birds in the feces were of the two largest and most abundant species in the study area, the Upland Goose (5%) and Lesser Rhea (1%). Puma hairs were found in three feces and were considered to result from grooming because puma bones were not found. Plant and rock material were present in 6% and 1% of the puma feces, respectively. Guanacos contributed 47% and European hares 40% of the total biomass consumed by pumas (Table 2). Small rodents represented < 3% of the total vertebrate prey by percent numerical occurrence and only 0.03% by biomass.

There were no significant differences in numerical occurrence of prey categories among seasons ($\chi^2 = 16.2$, $df = 12$, $P = 0.18$). There was, however, a significant difference among years ($\chi^2 = 38.3$, $df = 16$, $P = 0.001$). The frequency of guanacos in puma feces increased from 9% in 1982 to 29% in 1988 (Table 3). European hares remained at an almost constant level of numerical occurrence (yearly average = 53%) and birds were most important in the diet in 1982-83 (22%), when guanaco numerical occurrence was the lowest. Mean weights of vertebrate prey in puma feces from 1985 to 1988 were almost twice those of 1982 (Table 3).

Prey Abundance and Puma Predation

An average of $1,108 \pm 46$ guanacos ($\bar{X} \pm SE$) or $11.7/\text{km}^2$ occupied the high-density section ($74 \pm 4\%$ adults, $7 \pm 2\%$ yearlings, and $19 \pm 2\%$ juveniles). European hare densities were estimated at $45.6 \pm 8.7/\text{km}^2$, sheep at $1.1/\text{km}^2$, and Upland Goose and Lesser Rhea at $5.3/\text{km}^2$. The relative biomass of European hare and guanaco consumed by puma appeared to be different from the relative biomass available, with the European hare contributing more biomass to the diet of the puma than expected from their abundance, and the guanaco less (Table 4). A comparison between relative numbers of vertebrate prey available with relative numbers consumed also revealed that pumas appeared to prey on European hares more, and on guanacos less, than expected from their estimated abundance alone. In the area of high guanaco density, pumas fed on 13 European hares for every guanaco.

There was no significant difference in estimated European hare densities between the two sections of the study area (45.6 ± 8.7 versus 57.5 ± 11.2 , $z = 0.84$, $P = 0.20$), but there were significantly more guanacos in the area of high-guanaco density ($1,108 \pm 46$ versus 158 ± 8 , $z = 20.3$, $P < 0.001$). The proportion of prey items in feces from the two sections of the study area was significantly different

TABLE 1

Seasonal percent numerical occurrence of prey items in 405 feces of the Patagonia puma collected in Torres del Paine National Park, Chile, 1982-1988

Porcentaje numérico de presencia estacional de restos de presa en 405 fecas del puma de la Patagonia colectadas en el Parque Nacional Torres del Paine, Chile, 1982-1988

Prey items	Sep-Nov	Dec-Feb	Mar-May	Jun-Aug	Unknown	Total
Artiodactyla						
<i>Lama guanicoe</i>	35.4	26.8	19.2	26.5	15.6	23.1
<i>Ovis aires</i>	4.6	6.2	4.0	3.6	7.8	5.4
Total ungulates	40.0	33.0	23.2	30.1	23.4	28.5
Carnivora						
<i>Pseudalopex culpaeus</i>	0	1.8	0.8	0	0.6	0.8
<i>Canepatus humboldti</i>	0	0.6	0.8	1.2	0.6	0.8
Unidentified	3.1	1.8	0	1.2	0.6	1.2
Total carnivores	3.1	4.2	1.6	2.4	1.8	2.8
Lagomorpha						
<i>Lepus capensis</i>	40.0	48.8	64.8	47.0	49.8	50.5
Rodentia						
<i>Auliscomys micropus</i>	0	1.2	1.6	0	0	0.8
<i>Phyllotis darwini</i>	0	0.6	0.8	0	0	0.4
<i>Reithrodon physodes</i>	0	0	0.8	0	0	0.4
Unidentified	1.5	0	0.8	2.4	3.3	1.2
Total rodents	1.5	1.8	4.0	2.4	3.3	2.8
Unidentified mammals	10.8	8.6	3.2	12.0	4.6	7.2
Total mammals	95.9	96.4	96.9	93.9	82.9	91.8
Birds						
<i>Chloephaga picta</i>	3.1	1.8	2.4	6.0	8.0	4.8
<i>Pterocnemia pennata</i>	1.5	0.6	0	0	2.6	1.2
Unidentified birds	0	1.2	0.8	0	6.5	2.2
Total birds	4.6	3.6	3.2	6.0	17.1	8.2
Total Vertebrates (n)	65	162	125	83	155	590
Total Feces (n)	46	114	95	61	89	405

($\chi^2 = 22.36$, $df = 5$, $P < 0.001$). Prey items contributing most to the differences between the two areas were European hares ($\chi^2 = 8.3$, $P < 0.001$) and guanacos ($\chi^2 = 11.8$, $P < 0.001$). The proportion of European hare in the puma feces was greater in the low-density guanaco section while the occurrence of guanaco remains in the feces was more frequent where guanaco densities were highest.

DISCUSSION

Puma food habits in Torres del Paine were similar to those of pumas throughout

North and South America in that mammalian species were the major food source (Iriarte *et al.* 1991). The European hare and guanaco, the most locally abundant medium- and large-sized mammalian species, were the most common prey consumed at Torres del Paine. Livestock was not a large part of the diet, but the low incidence of predation on sheep by pumas in Torres del Paine National Park might reflect low densities of sheep rather than avoidance of livestock. Yáñez *et al.* (1986) found that sheep remains were more common in puma feces collected on sheep ranches than in feces collected inside the

TABLA 2

Percent biomass contributed by different prey items to the diet of the Patagonia puma, estimated from prey remains in 405 feces collected in Torres del Paine National Park, Chile, 1982-1988. Unidentified remains were not used in this analysis

Porcentaje de biomasa aportada por diferentes presas a la dieta del puma de la Patagonia. Estimación basada en los restos de presas en 405 fecas colectadas en el Parque Nacional Torres del Paine, Chile, entre 1982-1988. Los restos no identificados no fueron usados en este análisis.

Prey species	Frequency of occurrence %	Weight ^a kg	Correction factor ^b kg/sample	Relative biomass consumed %	Relative number consumed %
<i>Lepus capensis</i>	70.9	3.35	2.10	39.5	81.3
<i>Lama guanicoe</i>	32.8	97.0	5.38	46.8	3.3
<i>Ovis aries</i>	6.2	44.0	3.52	5.8	0.9
Carnivores	3.5	5.2	2.16	2.0	2.6
Birds	10.0	5.9	2.19	5.8	6.7
Rodents	3.2	0.04	0.04	0.03	5.2

^a Weights from Markham (1971), Miller and Rottmann (1976), Raedecke (1979), and Fuller *et al.* (1987); assuming equal numbers of culpeo fox, gray fox and skunk in diet, and using a weighted average by occurrence in diet for Upland Goose and Lesser Rhea.

^b From Floyd *et al.* (1978) and Ackerman *et al.* (1984).

^c No correction factor.

TABLE 3

Annual percent numerical occurrence of prey in feces of the Patagonia puma in Torres del Paine National Park, 1982-1988

Porcentaje numérico de presencia anual de presas en fecas de puma de la Patagonia colectadas en el Parque Nacional Torres del Paine, Chile, 1982-1988

Prey items	1982-83	1984-85	1985-86	1986-87	1987-88
Artiodactyla					
<i>Ovis aries</i>	6.4	6.8	5.1	5.3	2.4
<i>Lama guanicoe</i>	9.1	22.0	25.3	26.1	29.4
Subtotal	15.5	28.8	30.4	31.4	31.8
Carnivora					
<i>Pseudalopex sp.</i>	0.8	0.7	1.0	1.0	0.8
<i>Conepatus humboldti</i>	0	0	2.0	1.0	0
Unidentified	0.7	1.4	2.0	1.0	0.8
Total carnivores	1.5	2.1	5.0	3.0	1.6
Lagomorpha					
<i>Lepus capensis</i>	54.8	48.5	53.5	50.0	57.1
Rodentia					
<i>Auliscomys micropus</i>	0	0	0	1.0	0
<i>Oryzomys longicaudatus</i>	0	0	1.0	0	0.8
<i>Reithrodon physodes</i>	0	0	0	0	0.8
<i>Phyllotis darwini</i>	0	0	0	0	0.8
Unidentified	2.5	0.7	1.0	2.1	1.6
Total rodents	2.5	0.7	2.0	3.1	4.0
Unidentified mammals	3.6	17.5	4.0	7.3	0.8
Total mammals	77.9	97.6	94.9	94.8	95.3

Prey items	1982-83	1984-85	1985-86	1986-87	1987-88
Birds					
<i>Chloephaga picta</i>	11.1	1.5	2.0	5.2	4.0
<i>Pteroctemia pennata</i>	4.0	0	2.0	0	0
Unidentified	7.0	0.7	1.0	0	0.8
Total birds	22.1	2.2	5.0	5.2	4.8
Total Vertebrates (n)	108	132	99	96	126
Total Feces (n)	63	94	72	65	97
Mean weight of vertebrate prey (kg)	16.4	32.4	31.2	32.2	32.9

TABLE 4

Relative biomass and minimum numbers of puma vertebrate prey in the high-density guanaco section (9,500 ha) from June 1987 to May 1988 compared with relative biomass and number of individuals consumed as determined from puma scats

Biomasa relativa y número mínimo relativo de las especies de vertebrados en el sector de alta densidad de guanacos (9.500 ha) de junio 1987 a mayo 1988, comparado con la biomasa relativa y el número relativo de individuos consumidos determinado a través de fecas de puma

Species	Available		Consumed	
	Biomass %	Number %	Biomass %	Number %
<i>Lama guanicoe</i>	82.2	17.6	58.6	6.1
<i>Lepus capensis</i>	11.1	68.8	26.0	77.5
Carnivores	1.0	3.9	3.5	6.7
Birds	2.2	8.0	4.8	8.1
<i>Ovis aries</i>	3.5	1.7	7.1	1.6

Park. The impact of puma predation on sheep is also greater than indicated by the proportion of sheep in feces. On the ranch within the area of high guanaco density, pumas killed an average of four sheep per hunting bout ($n = 12$), and at times, as many as 15, although they only fed on parts of these (Iriarte 1988).

Although 500 cattle (< 200 of these were calves) often were in the study area, pumas did not prey on them. This is generally similar to findings in North America where only in a few places, such as in British Columbia, Nevada, and Utah, have remains from cattle made up to 9% of the items in the puma feces (Robinette *et al.* 1959, Spalding & Lesowski 1971).

In the area of high guanaco density pumas appeared to feed on a proportionally greater biomass and number of European

hares than expected on the basis of their relative abundances. A number of hypotheses could be proposed to explain this phenomenon, including the hunting tactics of pumas, relative probability of encounter and ease of capture, higher annual reproductive rate, and the reproductive chronology of European hares.

Predation of European hares is probably also influenced by pumas' ability to obtain other prey items, especially guanacos. Yearly and locational differences in puma food habits demonstrated the influence of prey availability on prey selection. For example, in the area where guanacos were more common, pumas preyed on 13 European hares to every guanaco, compared to the whole study area where the ratio was 25 to 1 (Table 4). Pumas have also responded to increasing numbers of guanacos on a long-term basis as guanacos

regain their historical status as the region's major large herbivore. A 94% increase from 670 to 1,300 guanacos from 1982 to 1988, due to increased protection by Park guards (W. L. Franklin, unpubl. data), was accompanied by a rise in the occurrence of guanaco remains in puma feces from 9% to 30% and a increase in MWVP from 16 to 33 kg. European hare remained important in the puma diet throughout the 7-year period, maintaining an almost constant level of numerical occurrence as prey (average for the period = 53%). Since the European hare was introduced to South America 90 years ago (Miller & Rottman 1976, Grigera & Rapoport 1983), it has obviously become an important prey species of the puma, demonstrating the ability of pumas to prey opportunistically. Puma predation on a large number of European hares may also have increased the potential competition with other prey species such as the Geoffroy's cat, culpeo fox, and Black-chested Eagle (*Geranoaetus melanoleucus*) which also prey heavily on the European hare (Iriarte *et al.* 1990; Johnson & Franklin 1991; W.E. Johnson, unpubl. data).

In addition to increasing in numbers, prey can be more available to pumas by becoming more vulnerable. For example, guanacos accounted for the greatest proportion of the pumas' diet in spring, when the guanacos were born and yearlings were

expelled from their family groups. These are periods of increased exposure and mortality for guanacos (W. L. Franklin, unpubl. data). From spring through fall, as the number of European hares raised during their reproductive season and guanacos become less vulnerable, the proportion of European hare in puma feces increased, and guanaco decreased.

Pumas appear to have benefitted from the creation of Torres del Paine National Park, both directly and indirectly. In addition to providing the puma increased protection, the number of guanacos, the pumas' principal large prey species, has increased since the Park's creation. The presence of a predictable source of prey species within a relatively small area probably contributes to the relatively high density of pumas in the area. Further studies are needed, however, to determine the full impact that fluctuations in prey availability may have on puma food habits and ultimately on puma population dynamics.

ACKNOWLEDGMENTS

We thank C.N. Caviedes, J.F. Eisenberg, F.M. Jaksic, K.H. Redford, J. Robinson and M.E. Sunquist for their constructive criticisms on the paper. We thank G. Arribillaga, F. Barrientos, G. Bundell, S. Catir, T. Fuller, G. Garay, J. González, O. Guíneo, K. Harms, J. Hoffman, R. Lawrence, A. Phillips, P. Ricci, G. Santana, and J. Toro for their cooperation in our field research. We thank the Chilean National Park and Forest Service (CONAF) for their assistance, and K.A. Johnson for helping

TABLE 5

Percent numerical occurrence of prey in puma feces collected in low and high guanaco density areas from 1982 to 1988 in Torres del Paine National Park, Chile

Porcentaje numérico de presas de puma en áreas de alta y baja densidad de guanacos en fecas de puma colectadas de 1982 a 1988 en el Parque Nacional Torres del Paine, Chile

Prey species	High guanaco density	Low guanaco density	All Combined
<i>Lepus capensis</i>	39.0	61.6	45.2
<i>Lama guanicoe</i>	33.6	12.1	27.7
<i>Ovis aries</i>	7.3	7.1	7.3
Rodents	3.1	7.1	4.2
Carnivores	3.1	0	2.2
Unidentified mammals	8.1	3.0	6.7
Birds	5.8	9.1	6.7
Total Vertebrates (n)	259	99	358
Total Feces (n)	162	64	226

start this project. The study was funded by grants from the National Geographic Society (Grant No. 3581-87), Patagonia Research Expedition (Iowa State University), the Organization of American States, and the National Wildlife Federation. J.A. Iriarte was supported by the Program for Studies in Tropical Conservation of the University of Florida and W.E. Johnson by an International Telephone and Telegraph Corporation Fellowship. This project was conducted under a research agreement (Proyecto Puma) between Iowa State University and CONAF. This is Journal Paper No. J-13898 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Project No. 2519.

LITERATURE CITED

- ACKERMANN BB, FG LINDZEY & TP HEMKER (1984) Cougar food habits in southern Utah. *Journal of Wildlife Management* 48: 147-155.
- ANDERSON AE (1983) A critical review of literature on puma (*Felis concolor*). Colorado Division of Wildlife Special Report 54: 1-91.
- BURNHAM KP, DR ANDERSON & JL LAAKE (1980) Estimation of density from line transect sampling of biological populations. *Wildlife Monographs* 72: 1-202.
- COURTIN SL, NV PACHECO & WD ELDRIDGE (1980) Observaciones de alimentación, movimientos y preferencias de hábitat del puma en el Isote Rupanco. *Medio Ambiente (Chile)* 4: 50-55.
- CURRIER MJP (1983) *Felis concolor*. *Mammalian Species* 200: 1-7.
- DEFOSSE AM, JL GARRIDO, OJ LAPORTE & L DUGA (1981) Cría de guanacos en cautividad. Variación de su crecimiento y calidad de su lana. *Centro Nacional Patagónico (Argentina)* 45: 1-17.
- DIXON KR (1982) Mountain lion (*Felis concolor*). In Chapman, JA & GA Feldhamer (eds) *Wild animals of North America: biology, management and economics*. John Hopkins University Press.
- FLOYD TJ, LD MECH & PA JORDAN (1978) Relating wolf scat content to prey consumed. *Journal of Wildlife Management* 42: 528-532.
- FULLER TK, WE JOHNSON, WL FRANKLIN & KA JOHNSON (1987) Notes on the Patagonian hog-nosed skunk (*Conepatus humboldti*) in southern Chile. *Journal of Mammalogy* 68: 864-867.
- GARAY G, WE JOHNSON & WL FRANKLIN (1991) Relative abundance of aquatic birds and their use of wetlands in the Patagonia of southern Chile. *Revista Chilena de Historia Natural*. En 64: 127-137.
- GOLDMAN EA (1946) Classification of the races of the puma, part 2. In Young SP & EA Goldman (eds) *The puma, mysterious American cat: 177-302*. The American Wildlife Institute, Washington, D.C.
- GRIGERA DE & EH RAPOPORT (1983) Status and distribution of the European hare in South America. *Journal of Mammalogy* 64: 163-166.
- HOUSE R (1953) *Animales salvajes de Chile*. Ediciones de la Universidad de Chile, Santiago.
- IRIARTE JA (1988) Feeding ecology of the Patagonia puma (*Felis concolor patagonica*) in Torres del Paine National Park, Chile. M.A. Thesis, University of Florida, Gainesville.
- IRIARTE JA, WL FRANKLIN & WE JOHNSON (1990) Diets of sympatric raptors in southern Chile. *Journal of Raptor Research* 24: 41-36.
- IRIARTE JA, WL FRANKLIN, WE JOHNSON & KH REDFORD (1991) Biogeographic variation of food habits and body size of the American puma (*Felis concolor*). *Oecologia* 85: 185-190.
- JAKSIC FM & HE BRAKER (1983) Food-niche relationships and guild structure of diurnal birds of prey: competition versus opportunism. *Canadian Journal of Zoology* 61: 2230-2241.
- JOHNSON MK & RAM HANSEN (1977) Comparison of point frame and hand separation of coyote scats. *Journal of Wildlife Management* 41: 310-320.
- JOHNSON RA & DW WICHERN (1982) Applied multivariate statistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey.
- JOHNSON WE & WL FRANKLIN (1991) Feeding and spatial ecology of the Geoffroy's cat in the southern Patagonia. *Journal of Mammalogy* 72: 815-820.
- JOHNSON WE, WL FRANKLIN & JA IRIARTE (1990) The mammalian fauna of the northern Chilean Patagonia: a biogeographical dilemma. *Mammalia* 54: 457-469.
- JOHNSON WE, TK FULLER, G ARRIBILLAGA, WL FRANKLIN & KA JOHNSON (1988) Seasonal changes in activity patterns of the Patagonian hog-nosed skunk (*Conepatus humboldti*) in Torres del Paine National Park, Chile. *Revista Chilena de Historia Natural* 61: 217-221.
- MILLER SD & J ROTTMANN (1976) Guía para el reconocimiento de mamíferos chilenos. Editora Nacional Gabriela Mistral, Santiago.
- ORTEGA IM & WL FRANKLIN (1988) Feeding habitat utilization and preference by guanaco male groups in the Chilean Patagonia. *Revista Chilena de Historia Natural* 61: 209-216.
- OSGOOD WH (1943) The mammals of Chile. *Field Museum of Natural History, Zoological Series* 30: 1-268.
- PISANO E (1973) La vida en los parques nacionales de Magallanes. *Monografías del Instituto de la Patagonia (Chile)* 6: 1-64.
- PISANO E (1974) Estudio ecológico de la región continental sur del área andino patagónica. II. Contribución a la fitogeografía de la zona del Parque Nacional Torres del Paine. *Anales del Instituto de la Patagonia (Chile)* 5: 59-104.
- PRICHARD H (1902) Field notes upon some of the larger mammals of Patagonia made between September 1900 and June 1901. *Proceedings of the Zoological Society (London)* 1: 272-277.
- RAEDECKE KJ (1979) Population dynamics and socioecology of the guanaco (*Lama guanicoe*) of Magallanes, Chile. Ph.D. dissertation, University of Washington, Seattle.
- ROBINETTE WL, JS GASHWILER & OW MORRIS (1959) Food habits of the cougar in Utah and Nevada. *Journal of Wildlife Management* 23: 261-273.
- SPALDING DJ & J LESOWSKI (1971) Winter food of the cougar in south-central British Columbia. *Journal of Wildlife Management* 35: 378-381.
- TEXERA W (1973) Distribución y diversidad de mamíferos y aves en la provincia de Magallanes. *Historia geológica de los géneros de mamíferos nativos terrestres*. *Anales del Instituto de la Patagonia (Chile)* 4: 1-3.

- WILSON P (1984) Puma predation on guanacos in Torres del Paine National Park, Chile. *Mammalia* 48: 515-522.
- YANÉZ JL, JC CARDENAS P GEZELLE & FM JAKSIC (1986) Food habits of the southernmost mountain lions (*Felis concolor*) in South America: natural versus livestocked ranges. *Journal of Mammalogy* 67: 604-606.
- YOUNG SP (1946) History, life habits, economic status and control. Part 1. In Young SP & EA Goldman (eds) *The puma, mysterious American cat*: 1-173. The American Wildlife Institute, Washington, D.C.