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The effects of puma prey selection and specialization on less abundant prey in Patagonia

L. Mark Elbroch* and Heiko U. Wittmer

Wildlife, Fish, and Conservation Biology, 1088 Academic Surge, University of California, One Shields Avenue, Davis, CA 95616, USA (LME, HUW)
School of Biological Sciences, Victoria University of Wellington, P.O. Box 600, Wellington 6140, New Zealand (HUW)

* *Correspondent: lmelbroch@ucdavis.edu*

Populations of generalist foragers may in fact be composed of individuals that select different prey. We monitored 9 pumas (*Puma concolor*) in Chilean Patagonia using Argos–global positioning system (Argos-GPS) technology for a mean of 9.33 months ± 5.66 *SD*. We investigated 694 areas where puma location data were spatially aggregated, called GPS clusters, at which we identified 433 kill sites and 6 acts of scavenging. Pumas as a population specialized upon guanacos (*Lama guanicoe*), whereas only 7 of 9 individual pumas specialized upon guanacos. One puma specialized upon domestic sheep (*Ovis aries*) and 1 upon European hares (*Lepus europaeus*) in terms of numbers of prey killed. Male and female pumas selected different distributions of prey and pumas exhibited prey selection at both the individual and population level. Three of 9 pumas exhibited selection when we compared individual prey use to prey availability within individual pumas' home ranges. One puma selected endangered huemul (*Hippocamelus bisulcus*) and 2 selected sheep. When we compared individual prey use to prey use at the population level, 5 of 9 pumas differed from the population norm. Whereas pumas did not select huemul at the population level, 2 individuals did select huemul. Two individuals also selected domestic sheep, and the influence of these 2 pumas was substantial enough to result in a population-level effect. Our research highlights the need to determine whether pumas exhibit individual foraging variation throughout their range, the extrinsic factors associated with (and possibly influencing) such variation, and how pumas that select rare and less abundant species in multiprey systems impact recovering prey populations.

Key words: diet, European hare, global positioning system (GPS) cluster, guanaco, *Hippocamelus*, *Lama*, Patagonia, *Puma*, selection, specialization

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Animals can be categorized broadly as generalist or specialist foragers, although populations of generalist foragers may in fact be composed of individuals that select different prey (e.g., Estes et al. 2003; Matich et al. 2011; Woo et al. 2008). Predators exhibit prey selection when they consume a particular prey disproportionately to its availability (Estes et al. 2003; Knopff and Boyce 2007), or when they select a prey disproportionately to the population norm. Following Knopff and Boyce (2007), we differentiate prey *selection* from prey *specialization*, which describes the prey species composing the majority of a predator's diet. Based on these definitions, a predator can select one prey species and specialize on another.

Across taxa, individuals within many populations exhibit different prey selection (see Estes et al. 2003; Matich et al. 2011); yet, neither the theoretical implications of variable intraspecific prey selection nor the population-level consequences of predators selecting or specializing on a particular prey in multiprey systems are currently well understood (Estes et al. 2003; Pettorelli et al. 2011). Historically, biologists assumed that predator populations exhibited a "mean" foraging strategy on a "mean" prey representative of prey populations. Then they employed functional responses (Holling 1959) to model the foraging behavior of the "mean" predator with changes in the availability of "mean" prey, an approach that may underestimate or overestimate the effects of predators upon rare prey when there are specialist predators in the population (Pettorelli et al. 2011).

Generalist foraging in multiprey systems establishes scenarios for apparent competition between prey that share predators (Holt 1977), and apparent competition is a mechanism that can

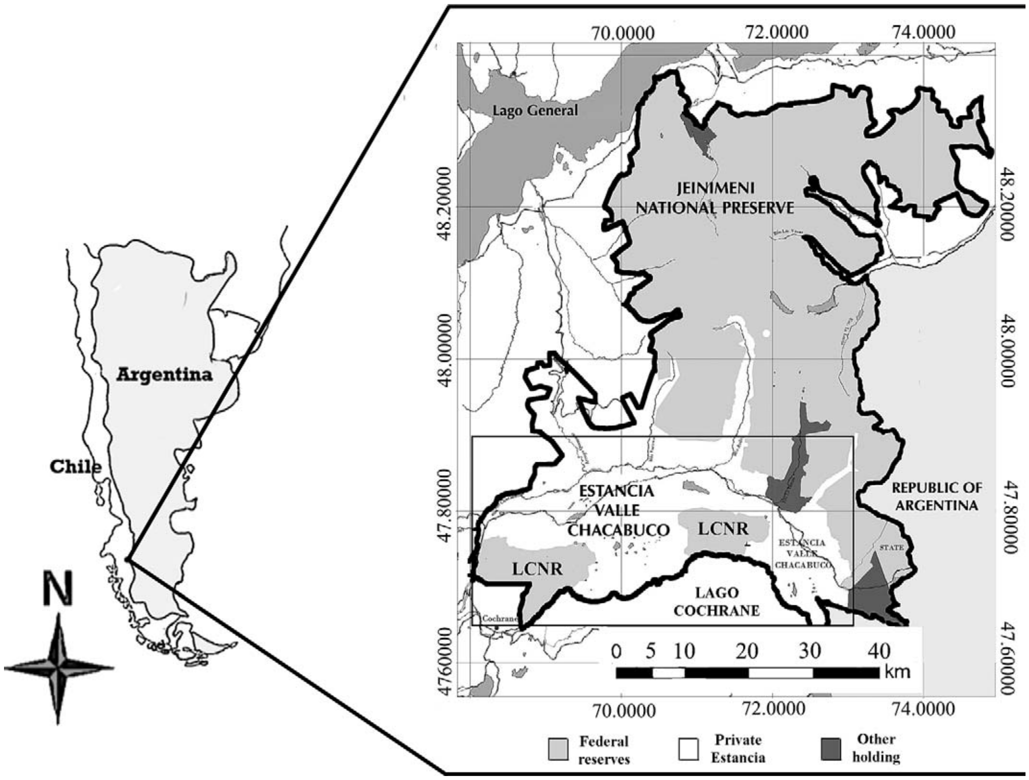

Fig. 1.—Location of study site in Chilean Patagonia. Inset illustrates land ownership across the area, and the thick black outline delineates the boundaries of the future Patagonia National Park. The smaller black rectangle delineates the actual study area in which we monitored pumas (*Puma concolor*). LCNR = Lago Cochrane National Reserve.

drive declines in rare species (DeCesare et al. 2010). In apparent competition, predators that prey on multiple prey can continue unsustainable predation on rare species because they are subsidized by alternative prey (DeCesare et al. 2010). Because different foraging specializations exhibited by different individuals may be taught to their offspring (Estes et al. 2003) and persist for years (Estes et al. 2003; Woo et al. 2008), the potential impact that relatively few, long-lived predators that either select or specialize on rare prey may have on rare species in natural systems is important both in theoretical and applied contexts. For example, Williams et al. (2004) estimated that a pod of 5 orcas (*Orcinus orca*) that specialized on sea otters (*Enhydra lutris*) could kill 8,500 otters each year. Further, they calculated that if just 4.4% of the estimated orca population surrounding the Aleutian archipelago (170 individuals) specialized on sea otters, then orcas could drive the entire Aleutian Islands population of sea otters to extinction in 3–4 months (Williams et al. 2004). Thus, research efforts that explore the influence of predators that select or specialize on rare prey on the viability of rare prey populations are critical (Pettorelli et al. 2011).

The puma (*Puma concolor*) is a large, solitary felid with the broadest geographic range of any terrestrial mammal in the Western Hemisphere (Sunquist and Sunquist 2002). Increasing evidence suggests that individual pumas exhibit varied prey selection (Knopff and Boyce 2007; Murphy and Ruth 2010), and that individual pumas that select or specialize on rare prey can severely affect the population viability of those prey (Festa-Bianchet et al. 2006; Ross et al. 1997; Sweitzer et al. 1997). For example, a single female puma killed 8.7% ($n = 11$) of adult bighorn sheep (*Ovis canadensis*) and 26.1% ($n = 6$) of the spring lambs in a small bighorn sheep population in a single year (Ross et al. 1997). Therefore, we tested whether individual pumas exhibited varied prey selection, and if so, whether selection by individuals differed from selection exhibited by the puma population as a whole. More importantly, we sought to determine how differences in individual- versus population-level selection influenced less abundant prey in natural systems.

An understanding of individual- versus population-level selection is essential to the management of pumas that select rare prey. In response to severe puma predation on rare species, conservation scientists continue to debate whether depredation permits, the removal of individual pumas that select or specialize on rare species, or wide-scale puma culling, either through direct action or indirectly through raising harvest quotas, is the best strategy to aid rare species recovery (Cougar Management Guidelines Working Group 2005; Robinson et al. 2008; Rominger 2007). When few individual pumas select rare prey, puma predation patterns at the population level will be subject to stochastic changes in the puma population (Festa-Bianchet et al. 2006); therefore, the removal of individual pumas that select rare prey rather than population-level management will be more effective in reducing predation on rare prey. In contrast, when many pumas select rare prey in proportion to their availability, management that targets individual pumas will be ineffective. Instead, population-level management will be the better strategy to reduce predation on rare prey.

Patagonia is a large (>1,000,000-km^2), sparsely populated region below latitude 39°S in southern Chile and Argentina, and an area in which the foraging ecology of pumas remains poorly understood (Walker and Novaro 2010). Nevertheless, puma–livestock conflict and puma predation on endangered huemul (*Hippocamelus bisulcus*) and recovering guanaco (*Lama guanicoe*) populations are of increasing conservation concern (Flueck 2009; Kissling et al. 2009; Walker and Novaro 2010; Wittmer et al., in press). In addition, puma diets in southern South America have primarily been documented in areas where prey are largely exotic, and based on scat analyses, with the identity of the predator species unconfirmed with genetic tests (Franklin et al. 1999; Iriarte et al. 1991; Novaro et al. 2000; Palacios et al. 2012; Rau and Jiménez 2002; Yáñez et al. 1986). Four of the 6 published studies on puma diets based on scat analyses in Patagonia reported that puma populations specialized on European hares (*Lepus europaeus*—Franklin et al. 1999; Novaro et al. 2000; Rau and Jiménez 2002; Yáñez et al. 1986). Of the 5 studies completed in areas actually inhabited by European hares, researchers reported that hares contributed ≥40% to puma diets (Franklin et al. 1999; Iriarte et al. 1991; Novaro et al. 2000; Rau and Jiménez 2002; Yáñez et al. 1986). Nevertheless, we must account for the fact that it is common to confuse the scats of different carnivore species (Elbroch et al. 2012; Farrell et al. 2000; Janečka et al. 2011). For example, Janečka et al. (2011) reported that in a study in which researchers targeted snow leopard (*Uncia uncia*) scats and used associated signs such as footprints and scrapes to facilitate positive identification, genetics later confirmed that 57% of 146 scats identified in the field as snow leopard were in fact red fox (*Vulpes vulpes*). Lacking the use of genetic tools required to identify puma scats, we suspect that researchers in previous studies on puma diets in Patagonia misclassified some fox scats as puma, thus biasing their findings toward small prey. Further, without genetic analyses, scat analysis does not allow researchers to assess the influence of individual specialist predators on rare prey species. The potential misidentification of scats and the need to calibrate prey and biomass remains found in scats using digestibility coefficients to estimate actual prey numbers killed (Ackerman et al. 1984; Gamberg and Atkinson 1988) may have cultured a distorted understanding of puma foraging ecology in southern South America. In order to better incorporate research on the diets of individual pumas and to provide alternative data to scat-based research, we decided to employ global positioning system (GPS) technology to study puma diets in Patagonia.

New and improving GPS technology has facilitated our understanding of the foraging ecology of large carnivores through increasing the detection probability of their kill sites in the field and allowing us to compare the variable diets of individuals (e.g., Cavalcanti and Gese 2010; Knopff et al. 2009). Dietary analyses based on GPS clusters, however, also have potential biases, and may miss or underestimate the contributions of small prey to puma energetics (Bacon et al. 2011). This is because pumas may not remain in place long enough to create a cluster when consuming small prey, or researchers may not locate the remains, if any exist. Nevertheless, we argue that investigating GPS clusters to study foraging ecology is particularly well suited to pumas and other solitary felids because felids often "pluck" and drop the fur of at least a portion of their prey, even mammals as small as hares (L. M. Elbroch, pers. obs.). In contrast, some canids scatter prey remains, or consume small prey more completely, so cluster analysis may prove less suited for studies of canid foraging ecology.

Here we report on the foraging ecology of individual pumas and a population of pumas as determined through GPS tracking of 9 animals (4 males and 5 females) in the future Patagonia National Park, Chilean Patagonia. We confirmed the identities of their prey by visiting potential "kill sites" identified by spatially clustered GPS locations (called GPS clusters—Anderson and Lindzey 2003). In our study area, native prey biomass exceeded that of nonnative species and the complete array of native large- and medium-sized vertebrates still coexisted on the landscape. The community included approximately 120 of the 1,000 endangered huemul still remaining in Chile (Jiménez et al. 2008), upon which the influence of puma predation remains of immediate conservation concern (Corti et al. 2010; Wittmer et al., in press), and 2,500 sheep (*Ovis aries*), a continued source of human–puma conflict across much of the puma's distribution in South America (Kissling et al. 2009).

Given the potential for variable prey selection by individual pumas to influence populations of rare and less abundant prey such as huemul and domestic sheep, we tested the following hypotheses. Because guanacos were the most abundant prey in our study area (Elbroch and Wittmer 2012), we hypothesized that contrary to earlier published accounts, individual pumas and pumas as a population would specialize on guanacos, and that male and female pumas would kill guanacos of equivalent health. We also hypothesized that pumas in Patagonia would exhibit foraging strategies similar to those in North America (Knopff and Boyce 2007; Ross et al. 1997), with individual pumas exhibiting preferences for different species of prey. We hypothesized that pumas as a population would select rare huemul, but that few individuals would do so. Further, we hypothesized that few pumas would select domestic sheep, but rather eat them in proportions equal to or less than expected given their availability in the study area. To test these hypotheses, we compared prey consumed by the puma population, as determined by investigating GPS clusters, with prey availability in the study area, as well as prey consumed by individual pumas with the distinctive prey availabilities within each of their respective home ranges, and with the proportions of different prey species selected by pumas as a population.

Materials and Methods

Study area.—Our study covered approximately 1,100 km^2 in the southern portion of Chile's Aysén District, immediately north of Lago Cochrane in central Chilean Patagonia (–72.2300°S, –47.12000°W; Fig. 1). It included the 69-km^2 Lago Cochrane National Reserve, the 690-km^2 private Estancia Valle Chacabuco, and approximately 440 km^2 of the 1,611-km^2 Jeinimeni National Reserve; these 3 areas will be combined into the future Patagonia National Park (http://www.conservacionpatagonica.org/). The land cover was characteristic of rugged Patagonia mountains and was a mixture of 3 dominant cover classes: open Patagonian steppe; high-elevation deciduous forests dominated by lenga (*Nothofagus pumilio*); and lower-elevation shrub communities dominated by ñirre (*N. antarctica*) interspersed with chaura (*Pernettya mucronata*) and calafate (*Berberis microphylla*) shrubs. The study area supported large numbers of native guanacos and a small population of endangered huemul (Elbroch and Wittmer 2012; Wittmer et al., in press). European hares were abundant in all habitats, especially in scrub communities, and approximately 2,500 sheep and 150 cows were kept in the eastern portion of the estancia. Culpeo foxes (*Lycalopex culpaeus*) and several scavenger birds, including Andean condors (*Vultur gryphus*), southern caracaras (*Caracara plancus*), Chimango caracaras (*Milvago chimango*), and black-chested buzzard eagles (*Geranoaetus melanoleucus*) were common. Beyond the borders of the future national park, sheep farming was the most common land use.

Captures and collar programming.—Our capture procedures adhered to guidelines approved by the American Society of Mammalogists (Sikes et al. 2011), and were approved by the independent Institutional Animal Care and Use Committee at the University of California, Davis. We captured pumas from March to September in 2008 and 2009, when locating them was facilitated by the presence of snow on the ground. When conditions were suitable, we traveled on horseback until fresh puma tracks were found, and used hounds to force pumas to retreat to either a tree or rocky outcrop where we could safely approach an animal. Pumas were anesthetized with ketamine (2.5–3.0 mg/kg) administered with a dart gun, and then lowered to the ground where they were administered medetomidine (0.075 mg/kg) by syringe. We fitted pumas with either an Argos-GPS collar (Argos collar, SirTrack, Havelock North, New Zealand; Tellus Collar, Televilt, Lindesberg, Sweden; or Lotek 7000saw, Lotek Wireless, Newmarket, Ontario, Canada) or very-high-frequency collar (SirTrack), the weights of which were <3% of adult female weights in the study area, and <2% of the weight of adult males. Once an animal was completely processed, the effects of the capture drugs were reversed with atipamezole (0.375 mg/kg), and pumas departed the capture sites on their own.

Collars were programmed to acquire GPS locations at 2-h intervals, and transmit data through an Argos uplink at 2- to 5-day intervals. Our most common programming was a 6-h Argos uplink every 3 days to relay GPS location data. Elbroch and Wittmer (2012) provide further details about the collars deployed in our study.

Field investigations.—Upon retrieval, location data were displayed and distances between consecutive puma locations were calculated in ArcGIS 9.1 (ESRI, Redlands, California). We defined GPS clusters (Anderson and Lindzey 2003) as any 2+ points within 150 m of each other, and CyberTracker-certified observers (Elbroch et al. 2011; Evans et al. 2009) conducted field investigations of any cluster where ≥1 GPS location was made during the hours of crepuscular light or periods of darkness. Observers located the areas associated with clusters using handheld Garmin Etrex and Venture models (Garmin International, Inc., Olathe, Kansas). We investigated every cluster, even those made completely within daylight hours, for the first 2 months of the project. Because the daytime clusters never revealed predation and required significant time to check (each puma would make 1–3 short daytime clusters per day), we chose not to investigate clusters with durations completely within daylight hours for the remainder of the project and to assume that they were day beds rather than kills. We did not include the day cluster investigations made early in the project in our analyses.

We used prey remains, including hair, skin, rumen or stomach, and bone fragments to identify prey species and the state of prey remains, including the location of bite marks and what had been eaten, were used to determine whether the puma had killed the animal or was scavenging. For ungulates, we marked the location of the rumen as the kill site with handheld Garmin GPS units (accuracy 5–10 m). For smaller prey, the stomach or intestines when they were available, or the largest collection of any remains, was marked as the kill site.

To help future researchers gauge what area they need to investigate while searching for prey remains, we measured the distance between kill sites marked with a handheld GPS in the field and the nearest puma GPS location associated with that kill. We defined the time until investigation as the number of days between the day the puma departed a GPS cluster and the day the site was investigated by an observer. If an observer visited a kill site that was still active or on the same day the puma departed the GPS cluster, the time until investigation was recorded as 0. We used logistic regression to test whether the time until investigation strongly indicated whether kill remains were found at a GPS cluster.

In addition, we opportunistically identified additional fresh kills by unmarked pumas by following tracks found in the field and following scavenging birds, particularly Andean condors and species of caracara. Kills were attributed to pumas only when tracks confirmed their presence at the site, and when bite marks, wounds, and signs of struggles indicated that they were not scavenging. We included these data in descriptive analyses of puma diets for our study area that dealt with pumas as a population, but not in the analyses of prey selection or specialization.

Prey indexes.—We counted numbers of prey killed and calculated biomass of prey to better reflect their energetic contributions to puma diets. The age of guanacos up to 24 months old were determined using tooth eruption sequences in the lower mandible (Raedeke 1979). We estimated the monthly weights of 1-year-old (chulengos) and 2-year-old guanacos using linear growth estimates, a birth weight of 12.7 kg, and 1-year and 2-year weights of 42 kg and 100 kg, respectively (Sarno and Franklin 1999). Guanacos $>$ 2 years of age were estimated to weigh 120 kg (Raedeke 1979). Guanacos $>$ 2 years of age were considered adults and their sex was determined by measuring the mass of a lower canine (Raedeke 1979).

The only data available for growth rates in huemul were an estimated birth weight of 5 kg (Flueck and Smith-Flueck 2005). Therefore, we applied growth allometry for the structurally similar mule deer (*Odocoileus hemionus*; 0.21 kg/day—Anderson and Wallmo 1984) to estimate weights of huemul $<$ 1 year old. We estimated weights of huemul 1–3 years old based on growth rates reported for mule and white-tailed deer (*O. virginianus*—Putnam 1988). We used a weight of 65 kg for adult huemul ($>$3 years—Iriarte Walton 2008). The ages of huemul up to 3.5 years old were estimated using tooth eruption sequences. The sex of huemul was determined using external morphology, including genitalia and antlers. For small prey, we assumed 4 kg for European hares (the mean weight of 30 specimens hunted by locals or killed by vehicles in our study area), 2 kg for Patagonian haired armadillos (*Chaetophractus villosus*—Iriarte Walton 2008), 9 kg for culpeo foxes (Iriarte Walton 2008), and 6.4 kg for upland geese (*Chloephaga picta*—Todd 1996).

Franklin et al. (1999) used punctures in the crania of guanacos to identify puma predation on guanacos in Torres del Paine National Park. To assess whether this method accurately estimated the number of guanacos killed by pumas, we carefully inspected the crania and mandibles from a subset of guanaco kills by pumas in our study area for tooth marks. We then quantified the percentage of skulls in each guanaco age class that held tooth marks that betrayed puma predation.

When possible, we estimated the relative health of adult guanacos and huemul from a field analysis of the bone marrow in a femur. The marrow was scored 1–3 on 2 characteristics, and these were summed to yield a scale of 2–6, with 2 reflecting very poor health and 6 reflecting good health. First the marrow was scored for color: 1 for red–brown, 2 for pink, or 3 for white. Second, we scored marrow for texture: 1 for very loose or runny or in extreme cases partly missing to 3 for firm. We employed an analysis of variance to assess whether male and female pumas killed guanacos of equivalent health.

Time of kills and duration of GPS clusters.—We defined the time of kill as the time of the 1st GPS location gathered by a puma collar within 150 m of a kill site. We defined the cluster length as the total hours from the 1st to the last GPS location within 150 m of the kill site, even when the puma moved farther from the kill site but returned while using the site.

Preferential prey selection.—We defined prey selection for the puma population as the killing of a prey species in greater proportions than expected given their availability. To do this, we used habitat-specific prey abundances (discussed below) as an index for prey availability. We used a chi-square goodness-of-fit test to determine 2nd-order resource selection (Johnson 1980; see Cavalcanti and Gese [2010] for an example with jaguars [*Panthera onca*]), and whether pumas as a population selected any of their 4 primary prey species (as determined from site investigations) in our study area in greater abundance than their availability would suggest. To account for variable samples among pumas, we divided the biomass killed for each prey type by each puma by the total biomass each killed before testing for 2nd-order resource selection.

Next, we used chi-square goodness-of-fit tests to determine 3rd-order resource selection (Johnson 1980). We did this by testing prey killed by individual pumas against 2 different indexes for prey availability. First, we used prey abundances as an index for prey availability to test whether individual pumas killed prey in proportions to their availabilities within each of their respective home ranges. Second, we used 2nd-order selection as an index for prey availability to test whether individual pumas selected prey in the same proportions selected by pumas as a population. When results of the chi-square tests were significant, we employed Bonferroni *Z*-tests to determine which prey proportions were statically different from expected (Byers et al. 1984).

We estimated prey densities in different habitats using program Distance 6.0 (Thomas et al. 2010), and these data were reported in Elbroch and Wittmer (2012). Program Distance determines detection probabilities of animals at different distances from transects, and then quantifies their densities. We applied the estimates of 6,550 guanacos, 120 huemul, 21,973 hares, and 2,500 sheep to our study area, and then multiplied these by specific prey weights described above to estimate available biomass. We used adult weights for all animals, except guanacos. During transect sampling for guanacos, the percent of 1st-year animals among mixed groups also was calculated (19%) and we multiplied this proportion by the weight of 6-month-old chulengos (27.3 kg) to reflect actual biomass on the landscape more realistically. For sheep, we used adult weights because nearly all the lambs were sold off each Christmas at 2 months of age.

Prey specialization.—We defined prey specialization as killing a prey in greater abundance than any other prey (Knopff and Boyce 2007), both at the population and individual levels. We quantified prey specialization in terms of numbers of prey killed, and total biomass of prey killed.

RESULTS

Prey indexes and GPS cluster characteristics.—We monitored 8 pumas using Argos-GPS technology (2 SirTrack and 6 Lotek 7000s), and 1 puma using the stored GPS data in the collar because its Argos capabilities failed (Telonics collar) for a mean of 9.33 months ± 5.66 *SD*. We investigated 694 GPS clusters, and located prey remains at 63.3% of these, including 433 kill sites and 6 scavenging sites. Kill sites were located on average 8 m ± 14.2 *SD* away from the nearest puma location data.

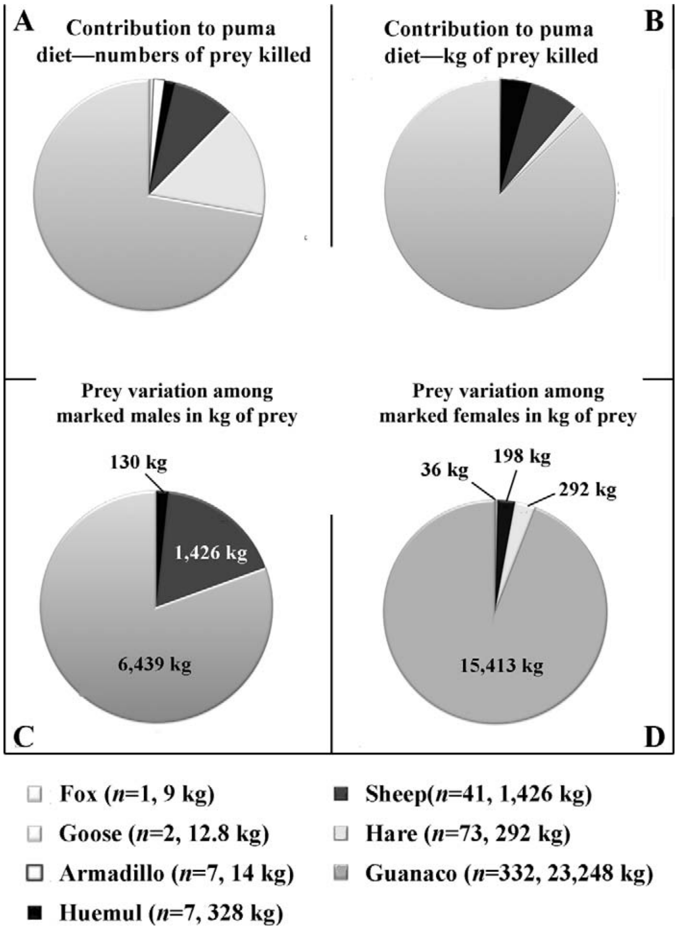

FIG. 2.—Prey indexes in terms of A) numbers of prey killed and B) kilograms of biomass killed for pumas (*Puma concolor*) as a population, and kilograms of prey killed by C) males and D) females in Chilean Patagonia, 2008–2009.

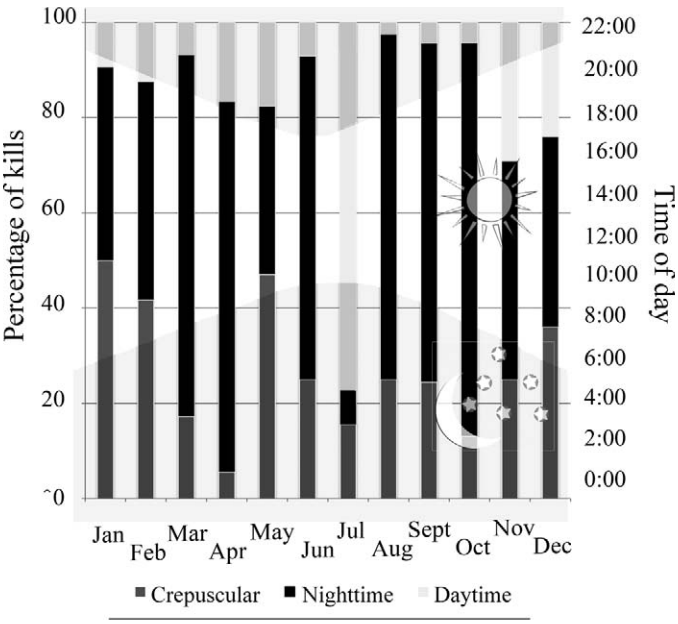

FIG. 3.—Percentage of puma (*Puma concolor*) kills made in Chilean Patagonia, 2008–2009, in 3 time categories by month of year. Backdrop and labels on the right side of the figure illustrate the hours of sunlight through the year.

We conducted field investigations of Argos-relayed GPS clusters within 11 days ± 12 *SD* (range, 0–78 days) of the time the puma left the area. We did not use the stored data in the malfunctioning collar in the analysis on time until investigation, because site investigations for this animal were conducted on average 792 ± 87 days (range, 650-945 days) after the puma had left the area. Probability of locating prey remains was inversely correlated with time until investigation ($r_s = 0.01$ $n = 609$, $P = 0.02$).

Prey animals included 350 ungulates and 83 small to medium-sized vertebrates (Figs. 2A and 2B). Sixty-four percent of kills were made at night, 26% during crepuscular hours, and 10% during the day (Fig. 3). The probability that observers would discover prey remains did not show a relationship with cluster length until 14 h, at which the probability of locating a kill increased with the duration of time a puma spent at a cluster: 2 h (42% yielded kills), 4 h (52%), 6 h (43%), 8 h (37%), 10 h (59%), 12 h (46%), 14 h (73%), 16 h (91%), and 18 h (98%). Kills were found 100% of the time at clusters > 18 h, with the exception of 2 large clusters created by females at den sites (196 h for F4 and 258 h for F5). In every case of scavenging, male 2 (M2) commandeered guanacos killed by marked females (4 from F3 and 2 from F4). We also identified 30 fresh guanacos killed by unmarked pumas (17 chulengos and 13 subadults and adults).

Male and female pumas selected prey differently ($\chi^2_6 = 123.38$, $n = 433$, $P < 0.0001$). Accounting for the age of prey and their variable weights, guanacos constituted 88.5% (96.6% for females and 79.3% for males), domestic sheep constituted 8.7% (0% for females and 19.1% for males), European hares constituted 1.9% (1.9% for females and 0% for males), and endangered huemul constituted 0.9% (1.3% for females and 1.6% for males) of total biomass killed by pumas (Figs. 2C and 2D). Guanacos were by far the primary prey of pumas at our study site, both in terms of numbers killed ($n = 332$) and biomass (23,248 kg; Figs. 2A and 2B).

Males and females killed guanacos of equivalent health ($F_{1,137} = 0.55$, $n = 138$, $P > 0.46$); the mean marrow index was 4.46 ± 1.31 *SD*. Of 139 adult guanaco kills for which sex could be determined reliably, 67 (48.2%) were female and 72 (51.8%) were male. Only 84 (87.5%) of 96 chulengos killed, 6 (60%) of 10 2nd-year guanacos, and 9 (25%) of 35 adult guanacos exhibited puma teeth marks on the head or mandible.

We documented 7 huemul killed by 2 marked pumas. M2 killed 2 adult females > 7 years old, both of which were unhealthy and exhibited porous, brown bone marrow (marrow scores of 2). F4 killed 5 huemul, including 1 fawn of unknown sex, 2 yearlings (1 male and 1 female), and a subadult male estimated to be 3.5 years old. All huemul killed by F4 exhibited healthy bone marrow.

The length of time pumas spent at a cluster increased with the estimated size of prey killed ($r_s = 0.23$, $n = 414$, $P < 0.0001$; Fig. 4), but the relationship showed considerable

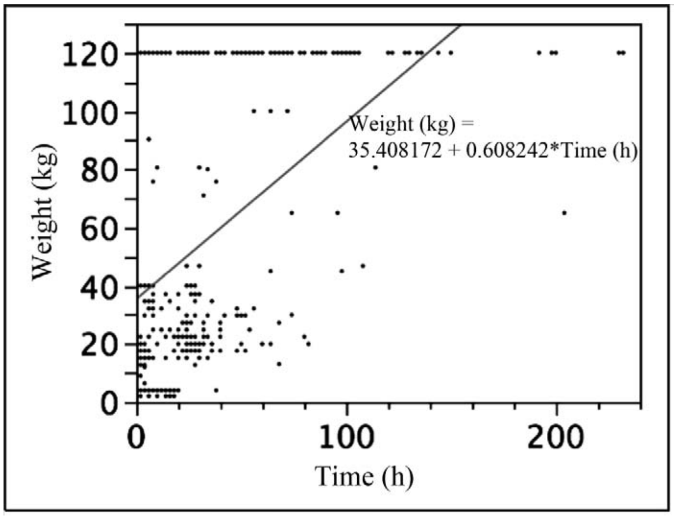

Fig. 4.—Regression analysis between weight of prey and length of global positioning system (GPS) cluster (h) for GPS-collared pumas (*Puma concolor*) in Chilean Patagonia, 2008–2009.

scatter. The heaviest prey (120 kg) were recorded at GPS clusters occupied as briefly as 2 h.

Preferential prey selection.—The population of pumas exhibited 2nd-order prey selection of domestic sheep and avoidance of European hares (Table 1). When comparing prey selection to prey availability, 1 puma selected huemul and 2 selected sheep (Table 1). When comparing individual prey use to the proportions selected by the population as a whole, 2 pumas selected sheep, 1 selected guanacos, 1 selected huemul, and 1 selected European hares (Table 2).

Prey specialization.—In terms of numbers of prey killed and biomass of prey killed, pumas as a population highly specialized upon guanacos. Individual pumas also specialized upon guanacos in terms of both number and biomass of prey killed, except in 2 cases. M4 specialized on domestic sheep in terms of both numbers and biomass. F5 specialized on European hares in terms of numbers of prey killed, but specialized on guanacos in terms of biomass killed.

Discussion

Our use of GPS technology to study puma foraging ecology provided radically different results than research reliant upon scat analysis previously reported for Patagonia. In areas inhabited by European hares, scat-based studies from Patagonia reported that hares comprised 40–52% of puma diets (Franklin et al. 1999; Iriarte et al. 1991; Novaro et al. 2000; Rau and Jiménez 2002; Yáñez et al. 1986), whereas we estimated that hares contributed only 1.9% to puma energetics in terms of biomass in our study area. Only females killed prey < 8 kg, and females killed all 73 hares we found. F5 was monitored for 95 days before we documented her 1st guanaco kill, a period before the birth of her 1st litter during which she killed 25 hares and 2 armadillos.

Table 1.—Prey selection by pumas (*Puma concolor*) as a population and by individual pumas determined by comparing observed diets (based on global positioning system cluster investigations in Chilean Patagonia, 2008–2009) versus expected diets (based upon available prey biomass in the environment) in terms of kilograms of prey for 4 prey species, and the results of Bonferroni *Z*-tests for significance. Significant results are marked with asterisks (**). Prey are guanacos (*Lama guanicoe*), European hares (*Lepus europaeus*), huemul (*Hippocamelus bisulcus*), and domestic sheep (*Ovis aries*).

<table>
<tr><th>Puma</th><th>No. kills</th><th>Diet</th><th>Guanaco</th><th>Hare</th><th>Huemul</th><th>Sheep</th></tr>
<tr><td>All pumas</td><td>423</td><td>Observed (%)</td><td>88.50</td><td>1.90</td><td>0.90</td><td>8.70</td></tr>
<tr><td></td><td></td><td>Expected (%)</td><td>88.60</td><td>8.50</td><td>0.50</td><td>2.30</td></tr>
<tr><td></td><td></td><td><i>Z</i> cutoff</td><td>2.475</td><td>2.475</td><td>2.475</td><td>2.475</td></tr>
<tr><td></td><td></td><td><i>Z</i>-value</td><td>|−0.06|</td><td>|−4.87|**</td><td>1.17</td><td>8.78**</td></tr>
<tr><td>M1</td><td>3</td><td>Observed (%)</td><td>100</td><td>0</td><td>0</td><td>0</td></tr>
<tr><td></td><td></td><td>Expected (%)</td><td>92.70</td><td>5.00</td><td>0</td><td>2.40</td></tr>
<tr><td></td><td></td><td><i>Z</i> cutoff</td><td>2.395</td><td>2.395</td><td>2.395</td><td>2.395</td></tr>
<tr><td></td><td></td><td><i>Z</i>-value</td><td>0.49</td><td>|−0.40|</td><td>—</td><td>|−0.27|</td></tr>
<tr><td>M2</td><td>25</td><td>Observed (%)</td><td>95.30</td><td>0</td><td>4.70</td><td>0</td></tr>
<tr><td></td><td></td><td>Expected (%)</td><td>90.40</td><td>8.90</td><td>0.70</td><td>0</td></tr>
<tr><td></td><td></td><td><i>Z</i> cutoff</td><td>2.395</td><td>2.395</td><td>2.395</td><td>2.395</td></tr>
<tr><td></td><td></td><td><i>Z</i>-value</td><td>0.83</td><td>|−1.56|</td><td>2.40</td><td>—</td></tr>
<tr><td>M3</td><td>78</td><td>Observed (%)</td><td>73.00</td><td>0</td><td>0</td><td>27.00</td></tr>
<tr><td></td><td></td><td>Expected (%)</td><td>80.60</td><td>16.50</td><td>0.20</td><td>2.70</td></tr>
<tr><td></td><td></td><td><i>Z</i> cutoff</td><td>2.475</td><td>2.475</td><td>2.475</td><td>2.475</td></tr>
<tr><td></td><td></td><td><i>Z</i>-value</td><td>|−1.70|</td><td>|−3.93|</td><td>|−0.40|</td><td>13.24</td></tr>
<tr><td>M4</td><td>16</td><td>Observed (%)</td><td>48.90</td><td>0</td><td>0</td><td>51.10</td></tr>
<tr><td></td><td></td><td>Expected (%)</td><td>66.40</td><td>8.30</td><td>1.00</td><td>24.30</td></tr>
<tr><td></td><td></td><td><i>Z</i> cutoff</td><td>2.475</td><td>2.475</td><td>2.475</td><td>2.475</td></tr>
<tr><td></td><td></td><td><i>Z</i>-value</td><td>|−1.48|</td><td>|−1.20|</td><td>|−0.40|</td><td>2.50</td></tr>
<tr><td>F1</td><td>40</td><td>Observed (%)</td><td>100</td><td>0</td><td>0</td><td>0</td></tr>
<tr><td></td><td></td><td>Expected (%)</td><td>94.70</td><td>5.30</td><td>0</td><td>0</td></tr>
<tr><td></td><td></td><td><i>Z</i> cutoff</td><td>2.200</td><td>2.200</td><td>2.200</td><td>2.200</td></tr>
<tr><td></td><td></td><td><i>Z</i>-value</td><td>1.50</td><td>|−1.50|</td><td>—</td><td>—</td></tr>
<tr><td>F2</td><td>16</td><td>Observed (%)</td><td>98.90</td><td>1.10</td><td>0</td><td>0</td></tr>
<tr><td></td><td></td><td>Expected (%)</td><td>89.40</td><td>9.10</td><td>1.50</td><td>0</td></tr>
<tr><td></td><td></td><td><i>Z</i> cutoff</td><td>2.395</td><td>2.395</td><td>2.395</td><td>2.395</td></tr>
<tr><td></td><td></td><td><i>Z</i>-value</td><td>1.23</td><td>|−1.11|</td><td>|−0.49|</td><td>—</td></tr>
<tr><td>F3</td><td>90</td><td>Observed (%)</td><td>99.30</td><td>0.70</td><td>0</td><td>0</td></tr>
<tr><td></td><td></td><td>Expected (%)</td><td>94.90</td><td>5.10</td><td>0</td><td>0</td></tr>
<tr><td></td><td></td><td><i>Z</i> cutoff</td><td>2.200</td><td>2.200</td><td>2.200</td><td>2.200</td></tr>
<tr><td></td><td></td><td><i>Z</i>-value</td><td>1.90</td><td>|−1.90|</td><td>—</td><td>—</td></tr>
<tr><td>F4</td><td>103</td><td>Observed (%)</td><td>93.40</td><td>2.50</td><td>4.20</td><td>0</td></tr>
<tr><td></td><td></td><td>Expected (%)</td><td>91.30</td><td>7.00</td><td>1.80</td><td>0</td></tr>
<tr><td></td><td></td><td><i>Z</i> cutoff</td><td>2.395</td><td>2.395</td><td>2.395</td><td>2.395</td></tr>
<tr><td></td><td></td><td><i>Z</i>-value</td><td>0.76</td><td>|−1.79|</td><td>1.83</td><td>—</td></tr>
<tr><td>F5</td><td>52</td><td>Observed (%)</td><td>85.80</td><td>14.20</td><td>0</td><td>0</td></tr>
<tr><td></td><td></td><td>Expected (%)</td><td>90.10</td><td>8.80</td><td>1.00</td><td>0</td></tr>
<tr><td></td><td></td><td><i>Z</i> cutoff</td><td>2.395</td><td>2.395</td><td>2.395</td><td>2.395</td></tr>
<tr><td></td><td></td><td><i>Z</i>-value</td><td>−1.04</td><td>1.37</td><td>−0.72</td><td>—</td></tr>
</table>

In terms of prey selection, pumas as a population selected sheep and depredated European hares less than expected based on availability. Contrary to our hypothesis, pumas as a population did not select huemul, but instead killed them in proportion to their availability in the study area. Individual pumas, however, exhibited varied prey selection. When we compared individual prey use to prey availability within each of their respective home ranges, only 3 of 9 pumas exhibited prey selection. When we compared individual prey use to prey use at the population level, 5 of 9 pumas exhibited prey

TABLE 2.—Prey selection by individual pumas (*Puma concolor*) in Chilean Patagonia, 2008–2009, determined by comparison of observed individual puma diets (% kg prey killed) with expected, defined as the proportions of prey depredated by pumas as a population (see Table 1) for 4 prey species, and the results of Bonferroni *Z*-tests for significance (*Z* cutoff of 2.475). Significant results are marked with asterisks (**). Prey are guanacos (*Lama guanicoe*), European hares (*Lepus europaeus*), huemul (*Hippocamelus bisulcus*), and domestic sheep (*Ovis aries*).

Puma	Diet	Guanaco	Hare	Huemul	Sheep
M1	Observed (%)	100	0	0	0
	Expected (%)	88.50	1.90	0.90	8.70
	Z-value	0.62	|−0.24|	|−0.17|	|−0.53|
M2	Observed (%)	95.30	0	4.70	0
	Expected (%)	88.50	1.90	0.90	8.70
	Z-value	1.07	−0.70	2.01	|−1.54|
M3	Observed (%)	73.00	0	0	27.00
	Expected (%)	88.50	1.90	0.90	8.70
	Z-value	|−4.29|**	|−1.23|	|−0.84|	5.73**
M4	Observed (%)	48.90	0	0	51.10
	Expected (%)	88.50	1.90	0.90	8.70
	Z-value	|−4.97|**	|−0.56|	|−0.38|	6.02**
F1	Observed (%)	100	0	0	0
	Expected (%)	88.50	1.90	0.90	8.70
	Z-value	2.28	|−0.88|	|−0.60|	|−1.95|
F2	Observed (%)	98.90	1.10	0	0
	Expected (%)	88.50	1.90	0.90	8.70
	Z-value	1.30	|−0.23|	|−0.38|	|−1.23|
F3	Observed (%)	99.30	0.70	0	0
	Expected (%)	88.50	1.90	0.90	8.70
	Z-value	3.21**	|−0.83|	|−0.90|	|−2.93|**
F4	Observed (%)	93.40	2.50	4.20	0
	Expected (%)	88.50	1.90	0.90	8.70
	Z-value	1.56	0.45	3.55**	|−3.13|**
F5	Observed (%)	85.80	14.20	0	0
	Expected (%)	88.50	1.90	0.90	8.70
	Z-value	|−0.61|	6.50**	−0.69	|−2.27|

selection that differed from the population norm. As we predicted, pumas as a population in our study area specialized strongly on guanacos in terms of both prey numbers and biomass killed. Several individual pumas, however, varied from the population in terms of their prey specialization.

In terms of numbers, huemul were rare prey in the system, and domestic sheep were approximately one-third as abundant as guanacos. Because pumas as a population did not select huemul, we might have assumed that pumas randomly and rarely killed huemul in the study area. Only when we looked at prey selection by individual pumas did it become clear that 2 of 6 individual pumas that overlapped with huemul selected them more often than expected. M2 killed only 2 huemul, yet his 370-km^2 fixed-kernel home range (Elbroch and Wittmer 2012), which was the largest in the study, made huemul a very rare commodity. This fact and the low number of kills recorded for this individual increased the significance of the disproportion between his prey selection and the prey availability in his home range. In contrast, F4, for which we recorded many kills, did not select huemul when we compared her prey selection with the availability of prey in her small, 98-km^2 fixed-kernel home range. Instead, she selected huemul when we compared her prey use against the proportions of prey used by pumas as a population. Both methods of determining prey selection identified individuals that selected rare prey and future research efforts should compare these methods to determine their strengths and weaknesses.

The puma population also included 1 sheep specialist, and an additional individual that selected domestic sheep but did not specialize on them. The effects of just 2 pumas selecting sheep resulted in a population-level effect: pumas in the study depredated sheep 3.8 times more than expected given their abundance. Perhaps the local sheep population was robust enough to absorb losses to 2 pumas that selected them, but the huemul population was not—the effects of current puma predation threaten the viability of huemul (Wittmer et al., in press). As has been observed in areas with small populations of bighorn sheep in North America (Festa-Bianchet et al. 2006; Ross et al. 1997), examination of our data suggests that pumas may or may not specialize on or select rare or less abundant prey, but when they do, the impacts of a small number of individuals may be profound.

Culling native predators to protect native prey species is controversial (Orians et al. 1997), as is predator removal to address livestock losses (Polisar et al. 2003). Nevertheless, when predators select rare prey, culling may be required to maintain or increase prey numbers. When it is a few individual predators that select rare prey, predation patterns exhibited by the predator population may be influenced by stochastic changes in the predator population. For this reason, targeted removal of predators that select rare prey effectively changes predation patterns exhibited by the predator population.

Examination of our data shows that few pumas selected huemul and sheep in Patagonia, and therefore, selective removal of individual pumas that are proven to select huemul or livestock is the best strategy to effectively change puma predation patterns on these prey. Population-level management, such as wide-scale culling, would prove ineffective in addressing puma predation on livestock and huemul in Patagonia, unless by chance those individual pumas that indeed do select for these prey species were removed in the process. Further, the nontargeted removal of pumas over areas $< 1{,}000$ km^2 has proven ineffective in reducing puma densities due to immigration from adjacent areas (Robinson et al. 2008). Thus, we conclude that the best strategy for pumas, huemul, and livestock owners is the removal of pumas proven to select rare prey, similar to the management of pumas that select livestock or bighorn sheep in the Sierra Nevada in California (Cougar Management Guidelines Working Group 2005; Ernest et al. 2002). In this way, both huemul and pumas will be able to persist in the future Patagonia National Park.

Important topics for further research in Patagonia include the influence of pumas on the demography of endangered huemul and recovering guanacos, and the importance of exotic species (hares and sheep) in subsidizing puma populations. More generally, our research highlights the need for further research to determine whether pumas exhibit individual foraging variation throughout their range, the extrinsic factors associated with (and possibly influencing) such variation, and how specialists on rare and less abundant species in multiprey systems impact recovering prey populations. Additionally, we need further research on, and a greater education about, how to manage predators that select or specialize on rare prey to the degree that they threaten local prey populations. Such knowledge will be essential in creating viable conservation strategies for both pumas and their prey, as well as aid us in understanding and mitigating livestock predation in areas where livestock overlap with native prey.

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