

Dietary composition, plasticity, and prey selection of Pallas's cats

STEVEN ROSS,* BARIUSHAA MUNKHTSOG, AND STEPHEN HARRIS

School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, United Kingdom (SR, SH)
Institute of Biology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia (BM)

* Correspondent: steve.ross@bristol.ac.uk

Dietary plasticity and diet composition of Pallas's cat (*Otocolobus manul*) was quantified in central Mongolia. Diet of Pallas's cat was assessed by scat analyses, and prey surveys were used to estimate prey availability. Prey selection was calculated using multinomial likelihood ratio tests. Analysis of 146 scats identified 249 prey items. Pallas's cats ate a broad range of small mammals, insects, birds, reptiles, and carrion, but Daurian pikas (*Ochotona dauurica*) were the most frequently consumed prey. Multinomial likelihood ratio tests indicated nonrandom selection of prey species. Pikas were selected disproportionately to their availability, and other more numerous prey items were used less than expected, indicating feeding specialization. Specialization on pikas appears to optimize energy intake per unit foraging by Pallas's cats, because pikas are 2–4 times larger than other small mammal prey. We argue that pika control programs in China and Mongolia potentially threaten Pallas's cat populations, because no other prey species could fill the niche occupied by the pika in terms of size and year-round availability. DOI: 10.1644/09-MAMM-A-342.1.

Key words: diet, Mongolia, niche specialization, *Otocolobus manul*, Pallas's cat, pika, selection

© 2010 American Society of Mammalogists

Optimal foraging theory predicts that when resources are abundant optimal foragers should specialize on prey that maximize energy return. As resource abundance declines, specialists should expand their diet to include less valuable prey items. Optimal foragers are therefore specialists when resources are abundant and generalists when resources are scarce (Pyke et al. 1977; Stephens and Krebs 1986). Specialization is an advantage in terms of increased feeding efficiency, because different food items have different foraging costs, capture strategies, and nutritional benefits. Specialization also can reduce dietary overlap and interspecific competition (Futuyma and Moreno 1988; MacArthur and Pianka 1966). However, one of the most common factors contributing to the vulnerability of a species is niche specialization (Boyles and Storm 2007; McKinney 1997), because specialization can lead to an increased dependence on specific resources, resulting in less flexibility to changes in the resource base (Harcourt et al. 2002). In contrast, generalist feeders are more plastic in their behavior and may switch foraging strategies more readily (O'Donoghue et al. 1998), allowing for adaptation to changes in the composition of available food resources. Thus, dietary specialization may relate to extinction risk because specialists are more sensitive to the loss of specific prey items (Laurance 1991; Siero and Arlettaz 1997), whereas generalists have more plasticity to changes in their resource base.

Pallas's cat (*Otocolobus manul*) is a small (3- to 5-kg) carnivore, sparsely distributed from the Caspian Sea to eastern Mongolia and most common in the grassland steppe regions of central Asia (Ross et al. 2008). It is currently listed as Near Threatened due to population declines from habitat fragmentation, consumptive hunting, and loss of its prey base due to rodent and pika (*Ochotona* spp.) control programs (Clark et al. 2006; Ross et al. 2008). Pikas and rodents have been targeted as pests by poisoning campaigns in China, Mongolia, and Russia because they are believed to compete with livestock for forage and to contribute to grassland degradation, and can serve as vectors for the plague (Clark et al. 2006; Smith et al. 1990; Smith and Xie 2008; Winters 2006). In China some pika populations were reduced to <5% of their precontrol densities (Lai and Smith 2003). In Mongolia poison bait campaigns to control small mammal numbers have occurred in all provinces (Clark et al. 2006; Winters 2006); control of rodents is also ongoing in Russia (Shilova and Tchabovsky 2009). Because of its rarity and secretive nature, little is known about the ecology of Pallas's cat, its diet, or the potential impacts of pika and rodent control programs.

We investigated the feeding niche of Pallas's cat to gauge its plasticity to anthropogenic disturbances to its prey base. We predicted that Pallas's cats would be generalists because



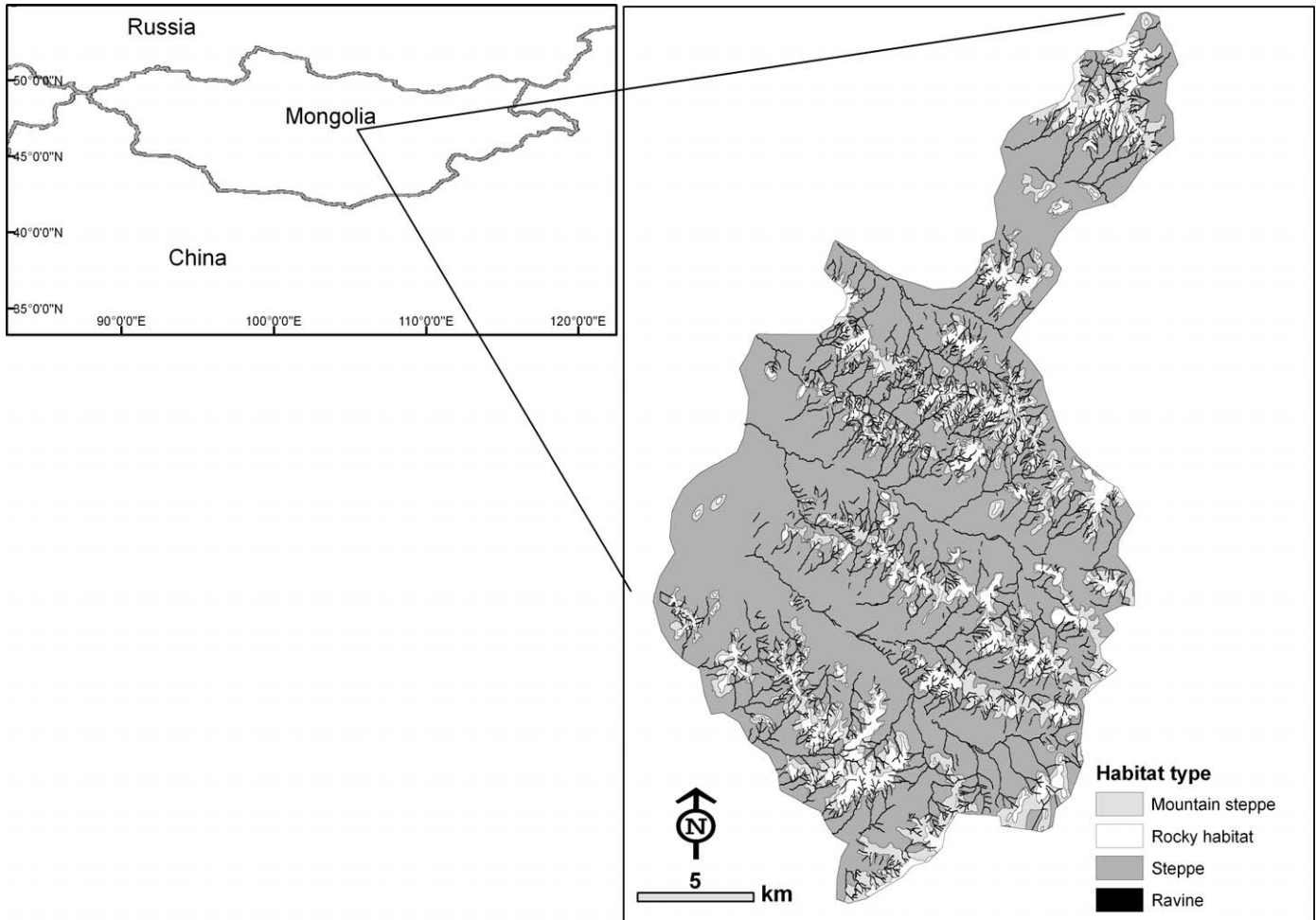


FIG. 1.—Location and habitat of the study area in central Mongolia.

of the high degree of seasonal variation and unpredictable prey base within their range (Heptner and Sludskii 1992; Korpimäki and Krebs 1996; Stephens and Krebs 1986). The objectives of our study were to quantify seasonal variation in the diversity of diet and prey consumption as a measure of dietary plasticity; to test the prediction that Pallas's cats are generalist feeders by quantifying prey consumption in proportion to the availability of prey species, thereby measuring prey selection; and to better understand the underlying sensitivity of Pallas's cats to disturbances to their prey base.

MATERIALS AND METHODS

Study site and population.—Data presented in this study were collected between June 2006 and October 2007 from a population of Pallas's cats within a 418-km² area in the Hustain Nuruu National Park buffer zone in central Mongolia (47°47'N, 106°01'E; Fig. 1). Altitude was 1,200–1,680 m and the climate was continental. During the study mean annual temperature was -1.2°C , with highs of 38°C and lows of -43°C . Annual precipitation was 165 mm, with more than 80% falling in summer. Two seasons were recognized based on average daily temperature. In summer (15 April–14

October) average daily temperature was typically above 0°C , whereas in winter (15 October–14 April) average daily temperature was typically below 0°C . Topography consisted of rounded mountains with rocky crests formed by wind and frost erosion. Heavy summer precipitation formed numerous dry ravines that dissected the landscape. Four habitat types (steppe, mountain steppe, rocky, and ravine habitats) were separated based on differences in topography, substrate, and vegetation (Ross 2009). All habitat boundaries were mapped (Fig. 1) using a global positioning system (Garmin Inc., Olathe, Kansas) attached to the handlebars of an off-road motorcycle (Honda XR, Honda Motorcycle Co., Ltd., Tokyo, Japan).

Potential mammalian prey species included ground squirrels (*Spermophilus undulatus*), Mongolian gerbils (*Meriones unguiculatus*), Russian dwarf hamsters (*Phodopus campbelli*), Chinese striped hamsters (*Cricetulus barabensis*), Brandt's voles (*Lasiopodomys brandtii*), Siberian jerboas (*Allactaga sibirica*), Daurian pikas (*Ochotona dauurica*), and mountain voles (*Alticola semicanus*; these were confined to areas with rocky cover). Larger mammals included Siberian marmots (*Marmota sibirica*), Tolai hares (*Lepus tolai*), and Daurian hedgehogs (*Mesechinus dauuricus*). Steppe runners (*Eremias trauchi*), numerous birds, beetles, and grasshoppers also were present. Domestic livestock (horses, sheep, and goats) used the

study area during winter but due to their large size were unlikely to be preyed upon by Pallas's cats, although dead livestock were available as carrion and young sheep and goats were potential prey.

Prey availability.—Rodent surveys were undertaken each season on 15 permanently marked, 500-m-long, randomly placed line transects. Live traps (7.6 × 8.9 × 22.9-cm; H. B. Sherman Traps Inc., Tallahassee, Florida) were placed at 10-m intervals along each transect (i.e., 50 per transect), prebaited for 24 h, and set for 48 h (2 trap nights). Traps were checked a minimum of twice per 24 h. The survey boundary, indicating coverage of line transects, was calculated using three 9 × 9 trapping grids, with 10-m trap spacing, within each of the 4 available habitats. Small mammals caught within grids were marked individually, using nontoxic marker pens, and distance between 1st capture and recapture calculated. Average habitat-specific recapture distance was then used to delineate the survey boundary width of the trap line. The index of captures per 100 traps described by Nelson and Clark (1973) was modified by incorporating the survey boundary, so that rodent density was calculated as: rodents/ha = $(A \times 100/TU) \times (S \times L/10,000)$, where A is number of individual small mammals caught, S is survey boundary (m), L is length of transect (m), and TU is trapping units corrected for sprung traps by subtraction of half a trap unit per sprung trap, and calculated as $P \times i \times N$, where P is number of trapping intervals, i is length of trapping interval (24 h), and N is number of traps.

Because Daurian pikas did not consistently enter Sherman traps, we used pellet-group sign surveys to estimate pika abundance (Cassini and Galante 1992; Marques et al. 2001) on the same transects used for estimates of rodent densities. Pellet groups in a 10-m-wide strip centered on the transect line were dispersed with a brush, and 24 h later the number of new pellet groups were counted in 10 × 10-m sections corresponding to trap spacing. Because Afghan pikas (*Ochotona rufescens*) produce a mean of 4.13 pellet groups during their diurnal activity periods (Matsuzawa et al. 1981), we assumed that 4.13 pellet groups equaled 1 pika. We used a survey boundary equal to the radius of 80% home-range core areas (32 m) for Daurian pikas; this was used during daily activity (Wang et al. 2000) and corresponded to our sample period. Pika density was calculated as: pika/ha = $(pg/4.13) \times (S \times L/10,000)$, where pg is pellet groups counted, S is survey boundary (m), and L is length of transect (m). We believe pika sign surveys adequately represented actual pika density but took precautions while simulating prey selection to prevent estimation errors influencing our results. Trapping and handling techniques complied with guidelines of the American Society of Mammalogists (Gannon et al. 2007) and were approved by the University of Bristol's Ethics Committee (Investigation UB/05/010).

Pallas's cat diet.—Scat samples were collected from known Pallas's cat latrines identified using telemetry of radiocollared cats. Scat analysis was used to reconstruct Pallas's cat diet using an established protocol (Reynolds and Aebischer 1991). Summer and winter diets were considered separately, and

samples collected within 10 days of seasonal boundaries were excluded from analyses. Reference collections of skulls, teeth, bones, and guard hairs from the study area were used to identify prey items in scats. Guard hairs were imprinted on a film of nail varnish on a glass microscope slide to provide a reference collection of hair scale patterns (Day 1966). Scats were oven dried at 60°C to constant weight, soaked in water and detergent for 48 h, and passed through a 5- μ m sieve. Microscopic and macroscopic fractions were separated, dried, identified, and weighed (Reynolds and Aebischer 1991). All small mammals were identified to species and insects and feathers to family.

Prey selection.—To analyze selection we grouped prey into 3 functional forms: Daurian pikas; steppe rodents (Mongolian gerbils, Brandt's voles, Chinese striped hamsters, and ground squirrels); and mountain voles. Prey groups reflected size, because pikas are 2–4 times the size of steppe rodents and mountain voles, and habitat differences, because only mountain voles are found in rocky habitats. We omitted species of birds, insects, and other items from the analyses, because their densities could not be estimated reliably, and they were minor components of Pallas's cat diet.

To make statistical inferences on selectivity, the sample of scats containing each prey item was compared to expected numbers of scats containing that prey using multinomial likelihood ratio tests based on the null hypothesis of random, nonselective prey killing by predators (Karanth and Sunquist 1995). We assumed that prey species i has a population density d_i , and that a single kill of species i typically results in λ_i scats. Under the null hypothesis of nonselection, proportion of scats identified to species i is expected to be $\pi_i = d_i \lambda_i / \sum_i d_i \lambda_i$ (Karanth and Sunquist 1995; Link and Karanth 1994). We estimated densities of available prey (d_i) as described above. Scat output (λ_i) from each prey was estimated using the daily energy expenditure of 16 Pallas's cats measured using field metabolic rate (S. Ross, University of Bristol, pers. comm.) and assuming that Pallas's cats gained 16.42 kJ of metabolizable energy (ME) per gram of prey eaten; that is, the same ME that bobcats (*Lynx rufus*) gain from microtine rodents, as measured by Powers et al. (1989) using oxygen bomb calorimetry. Thus, we estimated the numeric equivalents of each of the 3 prey classes required to balance daily energy needs as $Pr = FMR/(ME \times DM)$, where Pr is number of prey eaten per day to balance energy, ME is metabolizable energy per gram of prey (kJ), DM is dry mass of individual prey items, and FMR is field metabolic rate (kJ/day). Scat output (λ_i) then was calculated using fresh prey to fecal output values calculated for bobcats (Golley et al. 1965).

We conducted analyses with the software SCATMAN (Hines and Link 1994) using our estimates of d_i , λ_i , and the frequency of occurrence of the 3 prey categories in scats. When >1 prey item occurred in a scat, each was given an equal contribution to frequency (2 items were assigned 0.5 each—Karanth and Sunquist 1995). We ran the analyses assuming prey availability only within habitats used by Pallas's cats (mountain steppe, rocky, and ravine habitats—

Ross 2009) and again assuming all habitats and prey were available to cats. We estimated chi-square significance levels using a parametric bootstrapping procedure designed to reduce type 1 error rates in likelihood ratio tests using 1,000 iterations (Link and Karanth 1994). Since pika density estimates were a potential source of error, we assessed the risk of type 1 errors due to imprecise pika density estimates. Because errors could have occurred on either side of density estimates, we lowered and increased pika density in simulations and noted the fold-increase or decrease at which results changed from significant to nonsignificant selection, or vice versa, thus indicating the level of confidence in our results. We also allowed for errors in scat production rates by specifying variability at 40% of the mean level (Hines and Link 1994).

Statistical analyses.—Dietary composition is presented as frequency of occurrence (FO) estimated by the formula $FO = (f_i/\text{total number of scats}) \times 100$, where f_i is the number of scats in which item i appears. We also present the percentage occurrence (PO) of food items as $PO = (\text{number of occurrences}) \times (100/\text{total number of items})$. Cumulative dietary diversity was plotted against number of scats analyzed (k) to determine whether an asymptote had been reached and hence the diet of Pallas's cats in the study area had been sampled adequately. Cumulative diversity was calculated using the formula $h_k = M_k HB_k - (M_{k-1} HB_{k-1}/M_k - M_{k-1})$, where HB_k is cumulative diversity in the k th scat calculated using the Brillouin index, and M_k is cumulative number of prey items found in the k th scat sample (Magurran 1988). Contingency table analysis was used to determine differential use of food items between summer and winter using a G -test (Sokal and Rohlf 2000). The Shannon index ($H = -\sum(n_i/n) \times \ln(n_i/n)$), where n_i is number of individuals of taxon i , and Simpson's index ($D = \sum(n_i/n)^2$), were used to estimate trophic diversity, and were calculated using the frequency of occurrence of prey items (Magurran 1988). We tested for seasonal differences in diet diversity using a Shannon diversity t -test on seasonal frequency of occurrence data within the software PAST (Hammer et al. 2001). Prey biomass data were analyzed using Kruskal–Wallis 1-way analysis of variance using the transect as the sample unit. We used Mann–Whitney U -tests with Bonferroni corrections for multiple comparisons to make post hoc pairwise comparisons of prey biomass in each habitat. We did not test rodent density against pika density because of the different survey methods used to estimate rodent and pika densities. All statistical tests employed an alpha level of 0.05.

RESULTS

Scat analyses.—We identified 249 prey items in 146 scats. Small mammals accounted for 85.5% of prey items (Table 1). The most frequently consumed small mammals were Daurian pikas, Mongolian gerbils, and mountain voles. Insects, in particular beetles and grasshoppers, were eaten frequently, particularly in winter. Birds were eaten only occasionally; most were passerines, with 1 Daurian partridge (*Perdix*

daurica) and 1 unidentified Falconiformes species. Daurian hedgehogs and Tolai hares were rarely eaten. Reptiles were rarely observed in the study area and were consumed infrequently. Two marmots and 2 domestic goats were consumed; because of their size, we suspect they were eaten as carrion. Several nonfood items were recorded, and all scats contained a small amount of Pallas's cat hair from grooming. Ticks from grooming, vegetation ingested incidentally when eating prey, parasitic worms, and parasite eggs also were recorded. Cumulative dietary diversity (h_k) reached an asymptote at about 70–80 scats, indicating that an adequate sample had been obtained to enable valid seasonal comparisons.

Small mammal density.—A total of 2,865 individual rodents were captured in 10,106 trap nights (Table 2). Mongolian gerbils accounted for 67.4% of individuals captured, Chinese striped hamsters 14.6%, mountain voles 9.1%, Russian dwarf hamsters 4.9%, Brandt's voles 3.6%, and ground squirrels 0.4% of captures. Rodent abundance data were extremely variable because of the patchy distribution of colonies. Rodent density did not differ between habitats during summer ($H_3 = 4.86$, $P = 0.18$) or winter ($H_3 = 0.37$, $P = 0.94$; Table 2). Summer rodent density was higher ($U_1 = 940.00$, $P < 0.005$) than winter density. Pika density differed among habitats in summer ($H_3 = 8.60$, $P = 0.03$) but not in winter ($H_3 = 3.95$, $P = 0.27$). In summer, pika density was higher in mountain steppe ($U_1 = 14.00$, $P = 0.02$) and ravines ($U_1 = 7.00$, $P = 0.03$) than rocky habitats; other habitats did not differ in pika density (Table 2). Pika density did not differ between seasons ($U_1 = 1767.50$, $P = 0.99$).

Seasonal variation in diet.—Frequency of occurrence of pikas was higher ($G_1 = 4.67$, $P = 0.03$) in summer than winter, and the frequency of occurrence of insects (grouped) was higher ($G_1 = 3.95$, $P = 0.05$) in winter than summer, despite insects being either dead or dormant in winter (Table 1). We observed no significant differences ($t_1 = 1.59$, $P = 0.11$) in dietary diversity between seasons (Table 3).

Prey selection.—Estimated number of field-collectable scats produced by Pallas's cat after eating 1 prey item were calculated as 0.43 for pikas, 0.17 for steppe rodents, and 0.12 for mountain voles. Multinomial likelihood ratio tests indicated that Pallas's cats nonrandomly selected prey species in summer ($\chi^2_2 = 237.3$, $P < 0.005$) and winter ($\chi^2_2 = 32.7$, $P < 0.005$). In summer and winter pikas were highly selected ($P < 0.005$) and steppe rodents used less than expected ($P = 0.03$); mountain voles also were used less than expected ($P = 0.02$) during summer (Table 4). Significant selection for pikas was maintained after simulating a 7.2-fold increase in pika density in summer and a 1.8-fold increase in winter; decreasing pika density only increased the power of pika selection. Simulations indicated that results were robust to substantial errors in pika density estimates, with a low risk of type 1 error in selection. Selection patterns also remained consistent when all habitats were made available rather than only those known to be used by Pallas's cats (Table 4).

TABLE 1.—Frequency of occurrence (FO) and percent occurrence (PO) of prey items recorded in Pallas's cat scats in summer and winter in central Mongolia between June 2006 and October 2007.

Prey items	Summer			Winter		
	<i>n</i>	FO	PO	<i>n</i>	FO	PO
Small mammals						
Daurian pika (<i>Ochotona dauurica</i>)	59	71.1	39.6	30	47.6	30.6
Mongolian gerbil (<i>Meriones unguiculatus</i>)	29	34.9	19.5	23	36.5	23.5
Mountain vole (<i>Alticola semicanus</i>)	26	31.3	17.5	15	23.8	15.3
Brandt's vole (<i>Lasiopodomys brandtii</i>)	7	8.4	4.7	7	11.1	7.1
Chinese striped hamster (<i>Cricetulus barbensis</i>)	6	7.2	4.0	2	3.2	2.0
Ground squirrel (<i>Spermophilus undulatus</i>)	1	1.2	2.0	0	0.0	0.0
Medium-sized mammals						
Tolai hare (<i>Lepus tolai</i>)	0	0.0	0.0	2	3.2	2.0
Daurian hedgehog (<i>Mesechinus dauuricus</i>)	2	2.4	1.3	0	0.0	0.0
Reptiles						
Steppe runner (<i>Eremias strauchi</i>)	3	3.6	2.0	0	0.0	0.0
Birds						
Passerines	5	6.0	3.4	3	4.8	3.1
Galliformes	0	0.0	0.0	1	1.6	1.0
Falconiformes	1	1.2	0.7	0	0.0	0.0
Insects						
Coleoptera—beetles	6	7.2	4	8	12.7	8.2
Orthoptera—grasshoppers	3	3.6	2	6	9.5	6.1
Carrion						
Goat, sheep	1	1.2	0.7	1	1.6	1.0
Marmot	0	0.0	0.0	2	3.2	2.0
Nonfood items, accidental ingestion						
Vegetation	24			11		
Parasite eggs	10			25		
Parasitic worms	3			7		
Ticks	4			2		
Grooming hairs	83			63		

DISCUSSION

Although Pallas's cats used a broad range of food items, small mammals formed the majority of the diet, and pikas were highly selected. Previously unreported prey items included insects, carrion, reptiles, Daurian hedgehogs, and a large bird of prey. Only 2 small mammal species, Siberian jerboas and Russian dwarf hamsters, were not eaten; both are nocturnal. Observed activity peaks of Pallas's cats suggest that they are crepuscular (Ross 2009), and the diet of Pallas's cat indicated that they are mainly crepuscular or diurnal hunters.

Seasonal differences in Pallas's cat diet included a significant increase in insect consumption and a decrease in

pika consumption during winter. Because insects were either dead or dormant in the subzero winter conditions, their increased use was not due to chance encounters. Pallas's cats were actively seeking insects and able to locate caches of frozen grasshoppers or the hibernation sites of beetles. Similarly, corsac (*Vulpes corsac*) and red (*V. vulpes*) foxes in southern Mongolia regularly consumed insects during winter, presumably by excavating them from underground sites (Murdoch et al. 2010). The observed reduction in pika consumption during winter could be explained by a decrease in pika availability. Although differences in pika numbers were not detected between seasons, inclement weather and use of underground food stores decrease the amount of time pikas spend on the surface in winter (Sokolov et al. 2009), resulting in decreased availability to predators. Lack of reptiles, ground

TABLE 2.—Summer and winter mean rodent and pika density (individuals/ha \pm SE) in central Mongolia between June 2006 and October 2007.

Habitat	Summer density		Winter density	
	Rodents	Pikas	Rodents	Pikas
Steppe	14.03 \pm 0.76	0.93 \pm 0.25	2.36 \pm 0.73	0.86 \pm 0.21
Mountain steppe	9.90 \pm 0.31	0.74 \pm 0.26	2.07 \pm 0.87	0.40 \pm 0.11
Rocky	7.09 \pm 0.25	0.00 \pm 0.00	1.57 \pm 0.51	0.11 \pm 0.05
Ravine	14.50 \pm 0.77	1.31 \pm 0.44	5.47 \pm 5.11	0.35 \pm 0.13

TABLE 3.—Pallas's cat dietary diversity in summer and winter using the Shannon (*H*) and Simpson (*D*) indices of diversity in central Mongolia between June 2006 and October 2007.

Diversity index	Summer	Winter
Shannon (<i>H</i>)	1.84	2.01
Simpson (<i>D</i>)	0.76	0.8

TABLE 4.—Results of multinomial likelihood ratio tests for summer and winter prey selection by Pallas's cats in central Mongolia between June 2006 and October 2007, with prey available from habitats used by Pallas's cats and from all habitats, showing observed (O) and expected (E) use of prey categories and *P*-values assuming variability in scat production rates at 40% of the mean level.

Prey group	Habitats used by Pallas's cats						All habitats available to Pallas's cats					
	Summer			Winter			Summer			Winter		
	O	E	<i>P</i>	O	E	<i>P</i>	O	E	<i>P</i>	O	E	<i>P</i>
Pikas	54.0	9.29	***	40.2	18.2	***	54.0	10.2	***	40.2	29.9	*
Mountain voles	17.1	29.6	*	17.2	25.2	NS	17.1	26.1	NS	17.2	22.1	NS
Steppe rodents	29.0	61.2	***	42.6	56.7	*	29.0	63.8	***	42.6	47.9	NS

*** *P* < 0.005; * *P* < 0.05, NS = nonsignificant.

squirrels, and Daurian hedgehogs in winter diets of Pallas's cat was due to the dormancy of these species.

Although we predicted that Pallas's cat would be a generalist species, several aspects of its diet indicated that it is a dietary specialist, exploiting pikas regardless of their availability or the availability of other potential prey (Pyke et al. 1977; Stephens and Krebs 1986). Pallas's cats used pikas disproportionately to their availability in both seasons, and our results indicated that selection for pikas was robust to potential errors in our estimates of pika density. Pallas's cats further conformed to expectations for a specialist (Pyke et al. 1977) by increasing selection for pikas in summer when they were more available. Despite a 7-fold increase in rodent density during summer, Pallas's cat did not redirect predation to more abundant prey species. Pallas's cats in the study area therefore behaved as pika specialists, but with a facultative ability to use a broad range of prey. Our results agree with observations of Pallas's cat in other parts of its range, which also suggest pikas are highly favored as prey (Heptner and Sludskii 1992; Sunquist and Sunquist 2002).

Prey selection should be nonrandom if the intrinsic values of prey types differ (Stephens and Krebs 1986). Assuming all consumed prey had similar handling times, pikas probably were most preferred because of their comparatively high biomass. In terms of daily energy requirements of Pallas's cats, approximately 2.4 adult pikas/day would be required in comparison to 5.5–8.5 adult rodents/day. Specialization on pikas therefore reduces the number of prey items required to meet energy requirements and optimizes energy intake per unit foraging. Thus, pikas are an optimal prey item for Pallas's cats in energetic terms.

Dietary specialization is believed to contribute to the vulnerability of a species to environmental change (Boyles and Storm 2007; Harcourt et al. 2002; McKinney 1997), but the range of prey species taken by Pallas's cats demonstrated a degree of dietary flexibility that may reduce the costs of specialization. Nevertheless, Pallas's cats are potentially susceptible to fluctuation of preferred prey. Reduction in pika density caused by control programs could affect fitness of Pallas's cats by decreasing foraging efficiency and reducing energy intake.

Although accurate and updated information is difficult to obtain, small mammal poisoning campaigns will continue on the steppes of central Asia (Xin 2008). Poisoning occurred in

late 2006 and early 2007 in China and in 2004 in Mongolia (Harris 2010; Winters 2006). Control programs designed to reduce or eliminate pika populations potentially could affect survival of Pallas's cat because no other prey species fills the niche occupied by the pika in terms of size and year-round availability (Smith et al. 1990). However, declines in local Pallas's cat populations might go unrecorded because they live at low population densities and are difficult to survey (Ross 2009). In addition, pest control methods are rarely species-specific (Arthur et al. 2007; Olea et al. 2009); thus, they have the potential to reduce all small mammal prey populations and give little chance of predator adaptation. Further work is needed to quantify the impact of small mammal control programs on Pallas's cat populations and other members of the carnivore guild.

ACKNOWLEDGMENTS

We thank the Leverhulme Trust, Panthera/Wildlife Conservation Society Kaplan Award, the Royal Zoological Society of Scotland, the Royal Geographic Society, the Small Cat Conservation Alliance, the Dulverton Trust, and the Cincinnati Zoo and Botanical Gardens for funding; the Ministry of Nature and the Environment of Mongolia and the Mongolian Academy of Sciences for providing permissions; N. Galsandorj, G. Jimsran, and B. Dandarmaa for assistance in the field; B. Harvey for help with scat analyses; and 2 referees for their constructive comments.

LITERATURE CITED

- ARTHUR, A. D., R. P. PECH, Z. Y. JIEBU, AND H. LIN. 2007. Grassland degradation on the Tibetan Plateau: the role of small mammals and methods of control. Australian Center for International Agricultural Research Technical Reports 67:1–35.
- BOYLES, J. G., AND J. J. STORM. 2007. The perils of picky eating: dietary breadth is related to extinction risk in insectivorous bats. *PLoS ONE* 2(7):e672.
- CASSINI, M. H., AND M. L. GALANTE. 1992. Foraging under predation risk in the wild guinea pig—the effect of vegetation height on habitat utilization. *Annales Zoologici Fennici* 29:285–290.
- CLARK, E. L., ET AL. (COMPS. AND EDS.). 2006. Summary conservation action plans for Mongolian mammals. Regional Red list series. Vol. 2. Zoological Society of London, London, United Kingdom (in English and Mongolian).
- DAY, M. G. 1966. Identification of hair and feather remains in the gut and faeces of stoats and weasels. *Journal of Zoology (London)* 148:201–217.

- FUTUYMA, D. J., AND G. MORENO. 1988. The evolution of ecological specialization. *Annual Review of Ecology and Systematics* 19:207–233.
- GANNON, W. L., R. S. SIKES, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 88:809–823.
- GOLLEY, F. B., G. A. PETRIDES, E. L. RAUBER, AND J. H. JENKINS. 1965. Food intake and assimilation by bobcats under laboratory conditions. *Journal of Wildlife Management* 29:442–447.
- HAMMER, Ø., D. A. T. HARPER, AND P. D. RYAN. 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4(1):art. 4. http://palaeo-electronica.org/2001_1/past/issue1_01.htm. Accessed 15 September 2009.
- HARCOURT, A. H., S. A. COPPEO, AND S. A. PARKS. 2002. Rarity, specialization and extinction in primates. *Journal of Biogeography* 29:445–456.
- HARRIS, R. B. 2010. Rangeland degradation on the Qinghai-Tibetan plateau: a review of the evidence of its magnitude and causes. *Journal of Arid Environments* 74:1–12.
- HEPTNER, V. G., AND A. A. SLUDSKII. 1992. Mammals of the Soviet Union. Vol. 2, part 2. Carnivora (hyaenas and cats). Smithsonian Institution Libraries and the National Science Foundation, Washington, D.C.
- HINES, J. E., AND W. A. LINK. 1994. SCATMAN. United States Geological Survey Patuxent Wildlife Research Center, Patuxent, Maryland.
- KARANTH, K. U., AND M. E. SUNQUIST. 1995. Prey selection by tiger, leopard and dhole in tropical forests. *Journal of Animal Ecology* 64:439–450.
- KORPIMÄKI, E., AND C. J. KREBS. 1996. Predation and population cycles of small mammals: a reassessment of the predation hypothesis. *BioScience* 46:754–764.
- LAI, C. H., AND A. T. SMITH. 2003. Keystone status of plateau pikas (*Ochotona curzoniae*): effect of control on biodiversity of native birds. *Biodiversity Conservation* 12:1901–1912.
- LAURANCE, W. F. 1991. Ecological correlates of extinction proneness in Australian tropical rain forest mammals. *Conservation Biology* 5:79–89.
- LINK, W. A., AND K. U. KARANTH. 1994. Correcting for overdispersion in tests of prey selectivity. *Ecology* 75:2456–2459.
- MACARTHUR, R. H., AND E. R. PIANKA. 1966. On optimal use of a patchy environment. *American Naturalist* 100:603–609.
- MAGURRAN, A. E. 1988. Ecological diversity and its measurement. Croom Helm, London, United Kingdom.
- MARQUES, F. F. C., ET AL. 2001. Estimating deer abundance from line transect surveys of dung: sika deer in southern Scotland. *Journal of Applied Ecology* 38:349–363.
- MATSUZAWA, T., M. NAKATA, AND M. TSUSHIMA. 1981. Feeding and excretion in the Afghan pika (*Ochotona rufescens rufescens*), a new laboratory animal. *Laboratory Animals* 15:319–322.
- MCKINNEY, M. L. 1997. Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annual Review of Ecology and Systematics* 28:495–516.
- MURDOCH, J. D., T. MUNKHZUL, S. BUYANDELGER, R. P. READING, AND C. SILLERO-ZUBIRI. 2010. Seasonal food habits of corsac and red foxes in Mongolia and the potential for competition. *Mammalian Biology* 75:36–44.
- NELSON, L., AND F. W. CLARK. 1973. Correction for sprung traps in catch/effort calculations of trapping results. *Journal of Mammalogy* 54:295–298.
- O'DONOGHUE, M., S. BOUTIN, C. J. KREBS, G. ZULETA, D. L. MURRAY, AND E. J. HOFER. 1998. Functional responses of coyotes and lynx to the snowshoe hare cycle. *Ecology* 79:1193–1208.
- OLEA, P. P., ET AL. 2009. Lack of scientific evidence and precautionary principle in massive release of rodenticides threatens biodiversity: old lessons need new reflections. *Environmental Conservation* 36:1–4.
- POWERS, J. G., W. W. MAUTZ, AND P. J. PEKINS. 1989. Nutrient and energy assimilation of prey by bobcats. *Journal of Wildlife Management* 53:1004–1008.
- PYKE, G. H., H. R. PULLIAM, AND E. L. CHARNOV. 1977. Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology* 52:137–154.
- REYNOLDS, J. C., AND N. J. AEBISCHER. 1991. Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the fox *Vulpes vulpes*. *Mammal Review* 21:97–122.
- ROSS, S. 2009. Providing an ecological basis for the conservation of the Pallas's cat (*Otocolobus manul*). Ph.D. dissertation, University of Bristol, Bristol, United Kingdom.
- ROSS, S., J. D. MURDOCH, D. MALLON, J. SANDERSON, AND A. BARASHKOVA. 2008. *Otocolobus manul*. In IUCN 2008. 2008 IUCN Red list of threatened species. www.iucnredlist.org. Accessed 30 September 2009.
- SHILOVA, S. A., AND A. V. TCHABOVSKY. 2009. Population response of rodents to control with rodenticides. *Current Zoology* 55:81–91.
- SIERRO, A., AND R. ARLETTAZ. 1997. Barbastelle bats (*Barbastella* spp.) specialize in the predation of moths: implications for foraging tactics and conservation. *Acta Oecologia* 18:91–106.
- SMITH, A. T., N. A. FORMOZOV, R. S. HOFFMANN, Z. CHANGLIN, AND M. A. ERBAJEVA. 1990. The pikas. Pp. 14–60 in Rabbits, hares and pikas: status survey and conservation action plan (J. C. Chapman and J. E. C. Flux, eds.). IUCN, Gland, Switzerland.
- SMITH, A. T., AND Y. XIE. 2008. A guide to the mammals of China. Princeton University Press, Princeton, New Jersey.
- SOKAL, R. R., AND F. J. ROHLF. 2000. Biometry: the principles and practice of statistics in biological research. 3rd ed. W. H. Freeman and Company, New York.
- SOKOLOV, V. E., E. YU. IVANITSKAYA, V. V. GRUZDEV, AND V. G. HEPTNER. 2009. Lagomorphs—mammals of Russia and adjacent regions. Science Publishers, Enfield, New Hampshire.
- STEPHENS, D. W., AND J. R. KREBS. 1986. Foraging theory. Princeton University Press, Princeton, New Jersey.
- SUNQUIST, M., AND F. SUNQUIST. 2002. Manul. Pp. 219–224 in Wild cats of the world (M. Sunquist and F. Sunquist, eds.). University of Chicago Press, Chicago, Illinois.
- WANG, M., W. ZHONG, AND X. WAN. 2000. A study of home range of Daurian pika (*Ochotona daurica*) through telemetry. *Acta Theriologica Sinica* 20:116–122.
- WINTERS, A. M. 2006. Rodenticide use and secondary poisoning risks to non-target wildlife in central Mongolia. M.S. thesis, Michigan State University, East Lansing.
- XIN, H. 2008. China's environmental challenges: a green fervor sweeps the Qinghai-Tibetan Plateau. *Science* 321:633–635.

Submitted 14 October 2009. Accepted 5 February 2010.

Associate Editor was Jonathan Jenks.