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Authors: Holmes, Brian R., and Laundré, John W.

Source: Wildlife Biology, 12(2) : 201-209

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/0909-6396(2006)12[201:UOOEAF]2.0.CO;2

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Use of open, edge and forest areas by pumas *Puma concolor* in winter: are pumas foraging optimally?

Brian R. Holmes & John W. Laundré

Holmes, B.R. & Laundré, J.W. 2006: Use of open, edge and forest areas by pumas *Puma concolor* in winter: are pumas foraging optimally? - Wildl. Biol. 12: 201-209.

Optimal foraging theory predicts that an animal should optimize its time spent in food patches based on resource levels and, if preyed on by another species, predation risk. In large mammal predator-prey systems, previous studies have suggested that prey do consider predation risk when foraging and tend to avoid high-risk areas. In contrast, if large mammalian predators are trying to optimize their foraging, we predict that they should select these high-risk areas because such areas represent higher predation success. For pumas *Puma concolor* in south-eastern Idaho, previous work showed that edges of forests were the most successful hunting areas for mule deer *Odocoileus hemionus* compared to open and forest areas. We tested the prediction that pumas should optimize their foraging strategies by selecting edge areas during periods of movement. We followed puma tracks in the snow and recorded for every 20 m whether the pumas had been in an edge, open or forest area. We used a resource selection function and composition analysis to test if pumas were preferentially selecting edge areas over open or forested areas. Based on the resource selection function, pumas were four times more likely to use edge than open areas, but used edge and forest areas equally. Results of the composition analysis indicated that pumas also used edge areas significantly more than open but similar to forest areas. As pumas were selecting edge areas and avoiding open areas to forage, these results indicated that pumas may be foraging optimally. However, the equal use of edge and forest areas did not support our predictions, and we discuss possible explanations of these results.

Key words: Idaho, mule deer, Odocoileus hemionus, optimal foraging, Puma concolor, resource selection

Brian R. Holmes, Department of Biological Sciences, Idaho State University, Pocatello, ID 83201, USA - e-mail: amy_brian@onewest.net*
John W. Laundré, Instituto de Ecologia, A.C., Centro Regional Durango, Km 5 Carr. Durango-Mazatlan, 34100 Durango, Dgo. Mexico - e-mail: launjohn@hotmail.com

**Present address: Bureau of Land Management, Pocatello Field Office, 4350 Cliffs Drive, Pocatello, Idaho 83204, USA*

Corresponding author: John W. Laundré

Received 19 November 2003, accepted 26 November 2004

Associate Editor: Anthony P. Clevenger

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Optimal foraging theory, beginning with papers published by Emlen (1966) and MacArthur & Pianka (1966), attempts to explain the foraging behaviour of animals in terms of long-term fitness (see Pyke et al. 1977, Krebs et al. 1983, Pyke 1984, Stephens & Krebs 1986 for reviews). According to Pyke et al. (1977), optimal foraging theory research can be placed into four main categories: 1) optimal diet, or which food type to eat, 2) optimal patch choice, or where to feed, 3) optimal allocation of time to different patches, or how long to forage, and 4) optimal patterns and speed of movements, or where to go next. However, most optimal foraging studies have investigated herbivores and their plant food or mobile predators consuming behaviourally inert, relatively immobile prey (Brown et al. 1999). This has changed recently with research on mammalian predator-prey systems where the predator and prey are both mobile and behaviourally sophisticated (Corbett & Newsome 1987, MacCracken & Hansen 1987, Thompson & Colgan 1990, Kotler et al. 1994, Brown et al. 1999, Altendorf et al. 2001). In 2-player predator-prey systems, Edwards (1983), Kotler et al. (1994), and recently Altendorf et al. (2001) and Laundré et al. (2001) demonstrated that moose *Alces alces* cows with calves, ibex *Capra ibex*, mule deer *Odocoileus hemionus*, and elk *Cervus elaphus* do incorporate predation risk and alter foraging patterns or vigilance levels in response to wolves *Canis lupus*, leopards *Panthera pardus* and pumas *Puma concolor*.

Little information exists, however, from the perspective of the predator in these 2-player systems. Based on optimal foraging theory, a highly mobile predator should alter its hunting strategy to improve predation success, specifically relative to habitat selection. Powell (1994) in his study of fisher *Martes pennanti* preying on porcupine *Erethizon dorsatum* found that fisher altered their foraging patterns in response to prey behaviour and hunting success and concluded that they were foraging optimally. Relative to pumas, Hornocker (1970) speculated that, as predators of stealth, they could only make kills under conditions that enabled them to closely approach their prey before attacking. Logan & Irwin (1985) inferred that at least some of these conditions were vegetative cover and terrain. Laing (1988) concluded that 'cover' was the resource pumas should be selecting and that the physical characteristics of this resource which allowed prey detection, surveillance while stalking, and a close approach were essential for them to make a kill. There is evidence that pumas do select for this type of resource (Seidensticker et al. 1973, Ashman et al. 1983, Logan & Irwin 1985, Laing 1998, Murphy 1988, Koehler & Hornocker 1991) and that hunting success of pumas is related to the structural characteristics of local vegetation (Jalkotzy et al. 2000, Laundré & Hernández 2003). However, the two factors of resource selection and hunting success have not been combined to test the hypothesis that pumas forage optimally, i.e., that pumas primarily select habitats where hunting success is high and avoid habitats with low success.

Data from our study area suggest that forest edges provide the necessary structural components for successful hunting by pumas in winter. Of 52 sites where pumas killed deer, 38 (73%) occurred in edge, three (6%) in open, and 11 (21%) in forest areas (Laundré & Hernández 2003). Laundré & Hernández (2003) concluded that use of edge areas allowed a puma to observe deer out in the open and to ambush deer as they moved between open and forest patches. In terms of optimal foraging theory, edge areas are high-opportunity areas for pumas and high-risk areas for deer. Altendorf et al. (2001) tested this prediction on deer in our study area and demonstrated that in most habitats deer do perceive the higher risk in edge areas by using them less than open areas, and they also change their foraging behaviour when in edge areas.

Our study approaches the same idea, but from the perspective of the predator. If pumas are more successful at killing deer in edge areas, then consistent with optimal foraging theory, we predict that pumas should hunt disproportionately more in edge areas than in open or forest areas, even if deer spend more time in open areas. The purpose of our study was to test this prediction with the main assumption that except for periods of mating, pumas will move through all habitat types in such a way that they are ready to take advantage of an opportunity to make a kill and, thus, can be considered to be hunting (Beier et al. 1995). If puma selection of edge, forest or open areas is not significantly different from availability of these habitat types, this would refute the hypothesis that pumas are foraging optimally.

Methods

Study area

Our study was conducted in the winters (September- February) of 1996-1998 in various small mountain ranges located in two areas near the towns of Pocatello and Malta, Idaho, USA (Fig. 1). The areas consisted of a landscape mosaic of mountains with elevations of 1,500-3,100 m a.s.l. surrounded by lower elevation valleys. The total size of each of the study areas, including valleys, was approximately 2,000 km^2. Actual area of mountainous habitat was approximately 850 km^2 in

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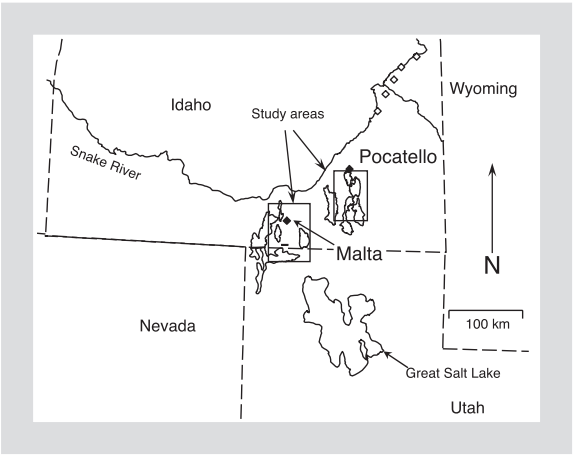


Figure 1. Location of the two study sites in southeastern Idaho and northwestern Utah. The approximate size and shape of the mountain ranges in the areas are indicated.

Malta and 1,000 km^2 in Pocatello. The mountains consisted primarily of public lands managed by the United States Forest Service (Caribou and Sawtooth National Forests), and the Bureau of Land Management (Burley and Pocatello Field Offices). Private land was interspersed throughout the area, primarily in the valleys, and was used for agricultural purposes and livestock grazing. The majority of the mountain ranges were accessible year-round by 4-wheel drive vehicle, snow machine, horseback and foot. Mean annual precipitation averaged approximately 30 cm, mainly in the form of winter snow. Summers were hot and dry, with daytime temperatures of 28-35°C. Winters were cold and windy, with daytime temperatures of -10 to 4°C.

In both study areas the mountains were mosaics of forest and open habitat patches. At higher elevations (2,000-3,000 m a.s.l.), the dominant tree species were Douglas-fir *Pseudotsuga menziensii*, quaking aspen *Populus tremuloides* and subalpine fir *Abies lasiocarpa*. Major tree species at lower elevations (1,500-2,300 m a.s.l.) included mixed forests of pinyon pine *Pinus edulis* (in the Malta study area), Utah juniper *Juniperus osteosperma*, Rocky Mountain juniper *J. scopulorum*, curlleaf mountain-mahogany *Cercocarpus ledifolius*, and Rocky Mountain maple *Acer glabrum*. The dominant shrub in the open areas of the mountains was big sagebrush *Artemisia tridentata*.

Pumas were the only large predator in the area. They preyed almost exclusively on mule deer with only incidental predation on porcupine, hares *Lepus* spp. and bobcat *Lynx rufus* (Holmes 2000; J.W. Laundré, pers. obs.). Puma densities in the area over the study period ranged within 2.0-3.1 pumas/100 km^2 of usable habitat (Holmes 2000, Laundré & Clark 2003). The radio-collared animals used in our study were captured and collared as part of an Idaho Fish and Game puma pilot study (Pocatello; Holmes 2000) and a larger long-term study of puma ecology and behaviour (Malta; Laundré & Hernández 2003). The primarily one predator-one prey system in the highly fragmented habitat of the study areas provided ideal conditions to test the prediction of our study.

Defining the resource

Based on the results of Laundré & Hernández (2003), we categorized the resources from which pumas should be selecting as open areas, forest edges and forest interiors. These classifications can be quite subjective, so we standardized them by defining specific criteria for each. Typically, open areas were areas covered by shrubs or grasses (usually less than one meter in height), few if any, trees and where observer visibility was generally unobstructed for > 25 m in all directions. Edge areas were zones of transition between forest and open patches where observer visibility was generally good in two directions. We set an edge width arbitrarily at 40 m: all areas ≤ 15 m into an adjacent forest patch and ≤ 25 m into an adjacent open area were classified as edge (Fig. 2). Based on ocular estimations, we assumed that at > 15 m from the edge boundary into the forest, visibility into the adjacent open area was too limited for a puma to easily observe deer. We chose a distance of ≤ 25 m from the edge boundary into the open because published data suggested that a puma at the edge boundary would be unlikely to successfully make a kill if it initiated a predation attempt on a deer at a position > 25 m away (Young 1946, Robinette et al. 1959, Wilson 1984, Beier et al.

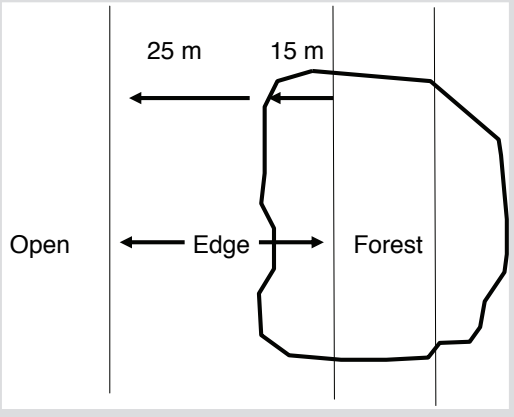


Figure 2. Designation of open, edge and forest areas in this study. Open areas were considered to be > 25 m from a forest edge. Edge areas were defined as a band ≤ 25 m into the open and ≤ 15 m into the adjacent forest. Forest areas were all wooded areas > 15 m from the edge.

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1995). In some cases, locations with alternate hiding cover (e.g. large rock formations), or widely-spaced trees that obscured visibility so much so that they obviously could not be classified as open, were classified as edge-like. We treated edge-like areas the same as edge for all analyses. Forests were stands of trees or shrubs (tall enough to measure a diameter-at-breast-height) where observer visibility was obscured in all directions. A forest patch had to be > 30 m across in all directions or by definition, we classified it as edge (e.g. an observer at its center would be within 15 m of an open area; see Fig. 2). Although our categorization of open, edge, and forest areas was subjective, a quantitative structural difference between them did exist; the mean distance between trees (± SE) in our study area was significantly greater in the edge (6.9 ± 0.6 m) than in the forest (3.7 ± 0.4 m; Altendorf 1997).

Availability of open, edge and forest areas

We measured availability (% open, edge and forest area) separately for each side of eight drainages (three in the Pocatello area and five in the Malta area) where puma tracks were followed. Drainage characteristics varied from fairly wide with a gentle slope to narrow with rather steep slopes. Each drainage had a road that followed its main direction. For each drainage, we drove the length of the road and measured its length to the nearest 0.16 km (0.1 mile) by the vehicle odometer. The starting point for most roads was the private land/public land boundary. We divided the total road length into 0.16 km (0.1 mile) increments and then randomly chose 10 increments as the starting points for line transects, using separate sets of random starting points for each side of the drainage. At each starting point, we walked the line transects for 1.0 km (or to the top of the ridge defining the drainage, whichever came first) at a compass bearing approximately perpendicular to the main direction of the drainage. As pumas in our study areas rarely paralleled roads extensively but crossed them and proceeded up the opposite side of the drainage, we assumed that this system of sampling would provide the best estimate of resource availability of the areas used by the pumas. Beginning at the starting point and every 20 m thereafter (determined by pacing), the observer recorded the point as being in open, edge or forest areas. We hiked 10 transects on each side of all except two drainages. Nine transects were hiked on each side of one drainage and six on each side of another, short drainage. To evaluate the adequacy of using 10 transects to estimate the percentages of open, edge and forest available we compared the running mean of the percentages of open, edge and forest areas against the number of transects hiked.

Puma use of open, edge and forest areas

During the winter, we located puma tracks opportunistically by driving the access roads of the drainages, and deliberately by walking in on radio-collared pumas. This method of following tracks found opportunistically and selection of a variety of different collared animals helped ensure we collected data from a representative sample of the population. In most cases, we did not follow more than one set of tracks for a given animal at the same time or in the same area. Thus track sets were separated in time and space and do not represent pseudo-replicated samples. Additionally, except for one occasion when a set of two similar-sized tracks were followed, all track sets were of individual adult animals, which eliminated the influence of mating behaviour on our data. As pumas rarely move during the day (Beier et al. 1995; J.W. Laundré, unpubl. data), we assumed that all track sets represented movements made approximately (± 1 hour) between sunset and sunrise. Additionally, based on the uniformity of the track spacing we found (J.W. Laundré, pers. obs.) and the fact that pumas rarely travel faster than 2 km/hour (Beier et al. 1995, Laundré 2005), we assumed that possible differences in travel velocity among habitat types was minimal. When following tracks of radio-collared pumas or tracks that appeared to have been made recently, we usually went in the opposite direction of the track to avoid influencing the animal's movements. If a kill site was found, we excluded tracks around the site. However, we included one set of tracks leading to and from the kill site. Similar to the availability transects, we recorded occurrence of open, edge or forest every 20 m along the travel path of the puma. Tracks were followed as long as possible (up to approximately two km), or until they were no longer discernable or left the drainage.

For radio-collared pumas, we combined all the track sets for individual animals. For track sets of unknown pumas, we gave them an identity based on the area where they were tracked and then treated these track sets as individual samples.

Statistical analyses

We used two different analyses to test the hypothesis that pumas were using edge areas significantly more than open or forest areas. The first was a resource selection function analysis (Manly et al. 1993). The resource selection function gives the probability that a resource of category i (edge, open or forest) would be the next one selected if each resource category could be offered equally. For this analysis, we treated each side of a drainage where tracks were followed as an individual experimental unit because of obvious vegetative differences

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between opposing slopes of a drainage. In this analysis, it made no difference whether the tracks were of known or unknown pumas, because data from track points were merely samples of the drainage-side experimental units. However, we considered only track sets with ≥ 20 track points, here defined as resource units, for this analysis. Additionally, if an individual puma traveled on both sides of a drainage during one travel bout, two 'sets' of tracks would contribute to the data set, one for each side of the drainage.

Depending on the study design, different equations are used to generate the resource-selection function (Manly et al. 1993). Because each of the 13 separate drainage sides where tracks were followed were treated as an experimental unit, we used the following equation (Manly et al. 1993:66) to generate a resource-selection function (w_i) for each resource type i (open, edge and forest):

$$\hat{w}_i = u_{i+} / \sum_{j=1}^{n} \hat{\pi}_{ij} u_{+j}$$

In addition to w_i, n is the number of drainage-sides, u_{i+} is the total number of points (resource units) from the puma tracks for resource category i; π_{ij} is the proportion of resource units of type i available in the j^{th} drainage (based on the random transects) and u_{+j} is the total number of resource units recorded from the puma tracks in the j^{th} drainage. To standardize each w_i, we added them together and divided each one by the total, so the sum across all resource categories equaled one (Manly et al. 1993:40). We estimated the standard error of w_i with the formula from Manly et al. (1993:67).

We calculated Bonferroni confidence intervals (Manly et al. 1993:50, Holmes 2000) for w_i for each category to determine preference, avoidance and significance between resource categories. We tested if selection occurred by calculating a log-likelihood chi-squared statistic for each drainage side (Manly et al. 1993:66). The sum of the log-likelihood chi-squared statistics was then an overall test for selection.

For the second analysis, we used the program Resource Selection (Leban 1999) to perform compositional analysis (Aebischer et al. 1993) with individual pumas as the experimental unit. In compositional analysis, data matrices of log-transformed ratios (Aitchison 1986) of proportional used and available resource categories across all individuals are constructed. A difference matrix is then created by subtracting corresponding components of the use and availability matrices. The null hypothesis is that the difference matrix is zero. To test the null hypothesis for significance, first Wilk's lambda (Λ) is computed from two residual matrices constructed from the difference matrix. Lambda is then used to compute a test statistic which approximates a chi-square distribution. If habitat use is found to be significantly non-random, then the habitats are ranked in order of preference based on comparisons of the mean and standard deviation of the log ratio differences over all individuals. Finally, depending on data normality, paired t-tests or randomization tests were used to determine significance between ranked habitats (Aebischer et al. 1993).

For the compositional analysis, we averaged track sets that were likely those of the same unknown puma as a single sample. For animals tracked in ≥ 2 different drainages, we weighted availability of resource types by the proportion of track points in each drainage and then summed for a total estimate of availability.

Results

Resource availability

Although we measured availability for each side of eight different drainages, we only used data from 13 sides of those eight drainages because we did not want to use availability from areas where pumas were not tracked. For the 13 drainage sides, we used 5,466 data points to evaluate availability for an average of 420 data points per drainage side (SD = 105.0). Over the last three transects hiked (8th, 9th and 10th) in each of 12 of the drainage sides, the changes in the cumulative percent of open, edge and forest were < 2.0%. Based on these results, we concluded that 9-10 random transects per drainage side were adequate to estimate the percentages of open, edge and forest habitat available. In one drainage (Charleston southwest) we only hiked six transects and the cumulative change between the last two transects averaged 4.0 % for the three habitat types. Although this was slightly higher than for 10 transects, we believe it did not affect the significance of our final results. The percent availability for each habitat type for the 13 drainages is listed in Table 1.

Resource selection function

We followed tracks on 13 sides of eight different drainages. We used 42 sets of tracks (≈ 44 km total length) from 12 different pumas to generate the resource selection functions. The log-likelihood chi-squared tests indicated that pumas did not use habitats in proportion to their availability. Of the 13 tests, 10 were significant at $\alpha = 0.05$, and the total log-likelihood chi-squared for the 13 drainages was $\chi^2_L = 582.2$, df = 46, $P < 0.001$ (see

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Table 1. Proportions of open, edge and forest habitat types used and available for the 13 drainage areas in the southeastern Idaho and south-central Idaho/northern Utah study areas during 1997-1999, and the corresponding resource-selection function (RSF) for each habitat category. RSF_{RAW} and RSF_{STD} refer to the unstandardized and standardized resource-selection function accordingly.

	Open		Edge		Forest	
Location	Used	Available	Used	Available	Used	Available
1miS	0.21	0.36	0.49	0.40	0.30	0.25
ClCrS	0.29	0.50	0.39	0.35	0.32	0.15
ClCrN	0.05	0.05	0.23	0.14	0.71	0.81
KelsawN	0.00	0.38	0.13	0.44	0.87	0.17
KelsawS	0.11	0.32	0.80	0.40	0.10	0.28
CharlestonSW	0.07	0.21	0.19	0.25	0.74	0.54
WDryN	0.04	0.21	0.86	0.66	0.11	0.13
WDryS	0.06	0.47	0.72	0.43	0.21	0.10
WalkerS	0.02	0.09	0.55	0.61	0.43	0.30
WalkerN	0.26	0.66	0.46	0.28	0.28	0.06
IndianS	0.02	0.46	0.39	0.40	0.60	0.13
KnoxN	0.81	0.29	0.14	0.41	0.05	0.30
KnoxS	0.07	0.13	0.43	0.42	0.50	0.46

$\chi^2 = 582.2$, df = 46, $P < 0.001$

				Bonferroni CI	
Habitat	RSF_{RAW}	RSF_{STD}	SE	Lower	Upper
Open	0.4	0.1	0.1	0.2	0.7
Edge	1.1	0.4	0.1	0.9	1.3
Forest	1.6	0.5	0.3	0.9	2.2

Table 2. Proportions of open, edge and forest habitat used and available for 12 pumas in the southeastern Idaho and south-central Idaho/northern Utah study areas during 1997-1999, and corresponding rankings for each habitat category. Rankings are 0-2 with 0 being the habitat least used. For pair-wise comparisons, + equals used more than and - equals used less than; a triple sign equals a significant difference at the $\alpha = 0.05$ level.

	Open		Edge		Forest	
Lion ID	Used	Available	Used	Available	Used	Available
LAC	0.05	0.22	0.43	0.27	0.52	0.51
HAZ	0.08	0.35	0.49	0.42	0.43	0.23
PEE	0.07	0.31	0.55	0.35	0.38	0.35
WHI	0.12	0.30	0.38	0.26	0.50	0.45
ROX	0.13	0.50	0.27	0.35	0.60	0.15
CHL	0.15	0.36	0.22	0.40	0.63	0.25
TIN	0.40	0.36	0.60	0.40	0.00	0.25
CEC	0.06	0.47	0.72	0.43	0.21	0.10
MIS	0.08	0.41	0.34	0.43	0.59	0.16
RER	0.23	0.18	0.49	0.41	0.29	0.41
WA1	0.04	0.48	0.58	0.39	0.38	0.14
KS1	0.05	0.13	0.26	0.42	0.69	0.46

$\chi^2 = 48.3$, df = 2, $P < 0.0001$

Habitat	Open	Edge	Forest	Rank
Open		- - -	- - -	(0)
Forest	+ + +	-		(1)
Edge	+ + +		+	(2)

Table 1). For the data from the 13 drainage sides, the standardized resource-selection functions for each habitat category indicated that if equally available, pumas would be four times more likely to choose edge over open and approximately five times more likely to choose forest over open (see Table 1). Based on the Bonferroni confidence intervals, pumas used open areas significantly less than available (upper limit < 1) and significantly less than edge or forest areas (see Table 1). The probability of using forest areas is greater than that for edge, but the difference is not significant because there is considerable overlap between the respective confidence intervals (see Table 1). Additionally, because the confidence intervals for edge and forest area both include 1.0, the use of either of these two resource types is not significantly different from available.

Compositional analysis

We used 30 sets of tracks (≈ 30 km total length) from 12 different pumas (nine females, three males) for the compositional analysis. Of the 30 track sets, 26 were from 10 radio-collared pumas (nine females, one male), and four were from two different male pumas (based on track measurements) of unknown identity. Based on results of the compositional analysis, pumas used open areas significantly less than edge or forest areas (Table 2). Edge was ranked as being used more often than forest, but the difference was not significant.

Discussion

Foraging optimality for a predator such as the puma should be a balance between prey availability and catchability. Deer used open more than edge areas (availability; Altendorf et al. 2001) however, pumas killed more deer in the edge areas (catchability; Laundré & Hernández 2003). Based on these results, if pumas were foraging optimally while hunting, we predicted they would use edge areas more than open areas. The results of the resource-selection function analysis and the composition analysis support this prediction. Regarding our results of the composition analysis, Bingham & Brennan (2004) recently demonstrated that there could be a high probability of Type I error if the analysis included habitat types with < 6% availability and 0% usage by an animal. In our analysis, none of the three habitat types ever had < 10% availability and only one of our animals (TIN) had 0% usage of a habitat with 25% availability (see Table 2). Thus, we assumed that the probability of a Type I error in our analysis was acceptable and that the results of the analysis were not affected by inflated Type

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I error rates. Consequently, we concluded that the results of the composition analysis also supported our prediction.

Pumas stalk their ungulate prey to approach undetected to within a striking distance of approximately 20 m (Young 1946, Robinette et al. 1959, Wilson 1984, Beier et al. 1995). To accomplish this, some cover is necessary (Logan & Irwin 1985, Laing 1988) and open areas do not provide enough cover. This avoidance of open areas with relatively more prey but less catchability, and use of edge areas with relatively less prey but with higher catchability suggests optimality in the foraging strategies of pumas. Moreover, this result is most likely not just a simple avoidance of open habitat by pumas because they readily attack and kill porcupines in the open (Sweitzer 1996), although admittedly, a prey that requires less stealth to hunt than a mule deer.

Regarding forest vs edge areas, deer used edge and forest areas almost equally (Altendorf et al. 2001), but pumas killed more deer in the edge habitat (Laundré & Hernández 2003). Because we did not find any difference in use of these areas by pumas, these results do not support our prediction that pumas are foraging optimally. We can offer three possible explanations for this. The first explanation is related to our experimental design. The edge width we defined for this study (40 m) may not be biologically significant to pumas. We chose an edge width based on the need for pumas to approach their prey within 25 m before attacking and on assumptions of reduced visibility from > 15 m into the forest. If either of these assumptions were in error, e.g. a puma may need to be closer to the forest edge to easily detect deer in open areas, then the edge width for a puma would be narrower than defined here. Reductions or increases in edge width distances could result in differences in use between these two resources.

A second explanation why pumas in our study did not use forest areas significantly different from edge areas is that the forest interior may offer alternate benefits to pumas. Brown et al. (1999) suggest one possible benefit: in a μ-driven (fear) model of predator-prey interactions, a puma depletes a food patch by frightening prey rather than killing it. This is supported by various field observations where the presence of pumas caused deer or elk to move away from an area (Hornocker 1970, Seidensticker et al. 1973, Ashman et al. 1983). Thus, for a puma, detection of its presence by prey will reduce catchability. This form of resource depression (Charnov et al. 1976) suggests that pumas moving through edge areas may increase their chance of being detected by their prey (presumably out in the open) and reduce their chances of a successful hunt. An adaptive strategy consistent with optimal foraging theory would be to use the forest to approach the edge in an effort to locate prey, but then retreat again to the forest to travel to the next area of edge. Although pumas in this case may be using the forest as a travel corridor, the fact that they have killed deer in the forest indicates that even during these times they are actively hunting and will take prey if the opportunity presents itself.

Forest cover could also provide safety benefits to pumas, especially to females with kittens. Instances of male pumas killing females or their kittens have been documented (Robinette et al. 1961, Hornocker 1970, Spreadbury et al. 1996, Murphy 1998; J.W. Laundré, pers. obs.). Females with kittens may travel more in the forest to better protect themselves and their young in an effort to avoid male conspecifics. Moreover, females tend to leave their kittens in the vegetatively dense forest interior (J.W. Laundré, pers. obs.), possibly for protection before they go off hunting. This suggests that females with kittens may be incorporating more of an element of predation risk, again consistent with optimal foraging theory, in their activities than other social classes of pumas.

A third possible explanation for no significant difference in the use of edge vs forest areas as predicted may be that the proportion of tracks in an area is not the best measurement of the amount of use. According to Beier et al. (1995), pumas on their study area in California hunted by alternating periods of movement and stasis. They documented that a puma remained fairly stationary (presumably stalking or lying in wait) for an average of 0.7 hours, then apparently 'gave up' and slowly traveled an average distance of 1.4 km in 1.2 hours to another area. They found that this pattern was repeated about six times on nights when no prey was killed. If this behaviour is similar for the pumas in our study, then they could show intensive use of a habitat type in time rather than distance, and track data would not reflect this use. However, our winter snow-tracking data did not indicate that pumas were often sitting or lying in wait. For six tracking sessions (out of 30), we documented only five times where a puma lay down, possibly in ambush, and three times where impressions in the snow indicated a puma was sitting. No prey items were found during these six tracking sessions, and the mean tracking distance of the sessions was 1,780 m (SD = 793 m; range: 1,240-3,120 m). Beier et al. (1995) also performed post-monitoring tracking year-round, while we relied exclusively on tracks in snow. Thus, assuming that puma behaviour is relatively similar between the two studies, there may be differences in puma hunting strategies based on environmental conditions (e.g. temperature). In winter,

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pumas may have less tendency to remain stationary for as long or as often as when hunting in warmer conditions. Consequently, we concluded that for our study, the use of the proportion of tracks that we found in each habitat was a valid measure of their relative use.

In summary, based on the distribution of kill sites found in our study area (Laundré & Hernández 2003), we predicted from optimal foraging theory that pumas should use the edge resource type significantly more often than forest and open types. As predicted, pumas did use open resource types significantly less than would be expected by chance, and significantly less than edge or forest areas. This result, especially considering that deer in our study area were found to selectively use the open resource type (Altendorf et al. 2001), supports the prediction that pumas may be foraging optimally. The high use of forest areas, despite the lower number of kills found, most likely indicates alternate benefits related to hunting success and at least for females with kittens, protection from male conspecifics. Thus, the lack of difference found between the use of forest and edge areas may not necessarily reflect a failure of optimal foraging theory to explain the movements of pumas, as it does our inability to fully understand all the elements that play a part in the foraging decisions made by pumas when moving about in their home range.

Acknowledgements - funding for this project was provided by grants from Safari Club International (Idaho Chapter), Earthwatch Institute, and the United States Bureau of Land Management. Additional funding was provided by the ALSAM Foundation and Grant No. S97-11 from the Graduate Student Research and Scholarship Committee of Idaho State University, Pocatello, Idaho. The Idaho Department of Fish and Game provided logistical and material support. The project was approved by the Idaho State University Animal Welfare Committee, Animal Protocol Review No. 11-96-287. We thank B.J. Mincher of Safari Club International, C. Anderson, D. Meints, M. Demick, M. Hurley and B. Compton of the Idaho Department of Fish and Game, and D.P. Streubel, J. Loxterman, L. Heady, K. Altendorf, S. Blum, G. Pratt, T. Peterson, M. Sanford, D. Nelson, H. Geiger and J. Lee from Idaho State University. We also thank the numerous Earthwatch Institute volunteers for their assistance in the data collection and analysis. We appreciate the inputs of H. Shaw and F. Lindzey in reviewing this manuscript, and we especially thank K. Jafek, K. Allred, K. Hall, J. Meyers, S. Sherick and K. Perry for the use of their trained dogs.

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