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Authors: Laundré, John W., and Hernández, Lucina

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John W. Laundré & Lucina Hernández

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Pumas *Puma concolor* are stalking predators of large ungulates that usually cache their prey. We hypothesize that they require specific habitats to successfully stalk their prey and that they select cache sites based on some set of criteria. We tested these predictions during a study of predation by pumas on mule deer *Odocoileus hemionus* in south-central Idaho and northwestern Utah, USA. We found cache points of puma-killed deer in winter by locating radio-collared pumas. We then located where pumas had killed deer (kill points) by tracks in the snow. We classified these kill points relative to the dominant forest type and association with open, edge or forested areas. At a subset of the kill points and associated cache points, we also estimated tree and shrub density, tree diameter at breast height (dbh), shrub height and slope. Pumas killed deer more often than expected ($P < 0.001$) in juniper-pinyon habitat and in edge areas. Tree densities and dbh at cache points were significantly greater ($P < 0.001$) than at kill points or surrounding areas. We concluded that pumas relied on specific habitat characteristics to kill mule deer, and selected cache sites with older, larger trees.

Key words: hunting habitat, Idaho, kill-sites, mule deer, pumas, Utah

John W. Laundré, Instituto de Ecología, A.C. Durango Regional Center, Km 5 carr. a Mazatlán, 34000, Durango, Durango, México, and Idaho State University, Pocatello, ID 83209, USA - e-mail: launjohn@prodigy.net.mx
Lucina Hernández, Instituto de Ecologia, A.C., Durango Regional Center, Km 5 Carr. a Mazatlán, 34000, Durango, Durango, México - e-mail: lucina@fauna.edu.mx

Corresponding author: John W. Laundré

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The diet of pumas *Puma concolor* in North America consists primarily of large ungulates (Anderson 1983) that they stalk to kill (Koford 1946, Hornocker 1970, Seidensticker, Hornocker, Wiles & Messick 1973, Wilson 1984). Researchers have observed that large stalking felids usually need to approach to within 15-20 m of their prey for a successful attack (Elliot, Cowan & Holling 1977, Van Orsdol 1984). To approach potential prey, stalking predators require sufficient 'hunting cover' (Elliott et al. 1977 , Van Orsdol 1984, Sunquist & Sunquist 1989).

Pumas therefore should have rather specific habitat requirements for successful hunting (Hornocker 1970, Laing 1988, Sunquist & Sunquist 1989), and some field evidence supports this prediction. Logan & Irwin (1985) found higher use by pumas and more cache sites in mixed conifer and mountain mahogany *Cercocarpus ledifolius* habitat in steep or rugged terrain. They 'inferred'

that animals were using these areas to approach their prey. Laing (1988) found kill/cache sites more often than expected in pinyon-juniper/lava rock habitat and attributed that to cover and topographic features which provided good stalking cover. Koehler & Hornocker (1991) also found that pumas preferred specific forest types and terrain, again ascribing this to stalking cover. Jalkotzy, Ross & Wierzchowski (2000), in a regional scale analysis, found more kills in areas with greater terrain ruggedness. However, apart from these general considerations and larger scale analyses, few studies have measured specific habitat characteristics of actual sites where pumas have captured their prey. Most of the data are actually from cache sites which can be up to 200 m from kill sites (J.W. Laundré, unpubl. data) and may not represent actual kill habitat. Thus, the prediction that pumas require specific habitat characteristics to successfully hunt remains untested.

Pumas hunt singly and typically kill prey larger than themselves. Consequently they often have to cache it for later use. Caching behaviour is common among the large solitary felids (Schaller & Vasconselos 1978, Sunquist 1981) and is a method to conserve food and to protect it from scavengers and competitors, including conspecifics (Sunquist & Sunquist 1989). Pumas cache their prey by placing it under a tree or bush and covering it with soil, leaves, sticks (Shaw 1989) and snow. Apart from this observation, there has been little quantification of cache site characteristics for pumas. They can drag their prey up to 200 m from the kill site, often passing up seemingly adequate cache sites (J.W. Laundré, pers. obs.). This would indicate that some site selection is occurring. Thus, we predict that pumas are not caching their prey under the first available tree, but are instead selecting some factor or factors that make one site better than another.

Our objective was to test the predictions that habitat characteristics of sites where pumas killed mule deer *Odocoileus hemionus* in winter and subsequently cached them, are unique subsets of the various habitats available. The results of testing these predictions could help increase our understanding of what constitutes successful winter hunting and caching habitat for pumas and potentially, how habitat can affect the impact of pumas on their prey.

Study area

Our study was performed in the counties of Cassia (south-central Idaho) and Box Elder (northwestern Utah), USA. The site spanned about 2,500 km^2 and contained five small, isolated mountain ranges with elevations of 1,830-3,151 m a.s.l. Mountain ranges were fragmented into open and forested habitat patches that varied in size, complexity and isolation from nearby patches. Climate was characterized by hot, dry summers (20-35°C) and cold, windy winters (-25 to 4°C). Humidity rarely exceeded 40%, and precipitation was sporadic with an annual mean of 30 cm.

Forested patches were divided into four major types: 1) Douglas fir, a forest type dominated by Douglas fir *Pseudotsuga menziensii* but with occasional subalpine fir *Abies lasiocarpa*, 2) quaking aspen *Populus tremuloides*, 3) juniper-pinyon, a woodland mix of juniper *Juniperus osteosperma* and *J. scopulorum* and pinyon pine *Pinus edulis*, and 4) curl-leaf mountain mahogany *Cercocarpus ledifolius*. Dominant shrubs in open areas included big sagebrush *Artemisia tridentata*, gray rabbitbrush *Chrysothamnus nauseosus*, bitterbrush *Purshia tridentata*, and buffaloberry *Shepherdia rotundifolia*.

Methods

In the winters of 1985-2001, we located sites where pumas cached mule deer carcasses (cache sites) by either walking into the area of a radio-collared animal or following tracks found crossing roads. At each cache site, we marked the actual location of the carcass (cache point) with flagging. When possible, we located the area (kill site) and actual location (kill point) where the pumas killed the deer by following tracks in the snow. Thus, some sites located consisted only of cache sites/points whereas for others we were able to identify cache and kill sites/points.

At identified kill points, we classified the surrounding site relative to macro structure in the categories open, edge or forest. Our criteria for the open, edge or forest designations were based on the distance from a forest patch and/or density of trees. Sites were classified as open if they were more than 20 m outside the edge of a forest. Edge sites were those from 20 m outside a forest patch to 15 m into the forest patch (Altendorf, Laundré, López-Gonzáles & Brown 2001, Holmes 2000). We also designated 'edge like' areas where the distance among trees permitted seeing a minimum of 20 m. The 20-m limit was based on data reported for other stalking felids as the typical distance from its prey a predator needs to approach undetected for a successful attack (Sunquist & Sunquist 1989). Kill sites within a forest patch and >15 m from an opening were considered forest sites. For kill sites located at edges and in forests, we classified the forest type based on the pre-

dominant tree species (Juniper-pinyon, Douglas fir, aspen and mountain mahogany) as described above. We also classified the forest types at cache-only sites when there were no other forest types within 200 m (maximum drag distance; J.W. Laundré, unpubl. data).

We revisited most sites the following summers and measured tree density, tree diameter at breast height (dbh), shrub density, shrub height and slope. Shrub measurements were limited to shrubs 50 cm high or more. We rationalized that in the winter when snow was often >50 cm deep, shrubs <50 cm would likely not function as cover for a puma. We used the point quarter method in measuring these characteristics (Brower, Zar & von Ende 1990) at cache and kill points. We also established a grid of 16 points, 10 m apart and centered on the cache or kill points (Fig. 1) and took the same measurements. We used the averages of the measurements from these 16 points as estimates for cache and kill sites and compared them to the data from the cache and kill points.

To determine if kill points were equally distributed in the three macro structural types (open, edge and forest) we used a G-test design (Zar 1999). As pumas usually drag their prey into forested areas (J.W. Laundré, pers. obs.), we did not perform this test on cache sites. We also used a G-test design to test for equal selection of forest type. This test included kill sites and cache sites where we were able to identify the forest type. The expected number of sites per structure and forest type were calculated based on the percentage of each type in the study area. As accurate vegetation maps were not available for the area, we estimated the percentage of each category by centering a transparent grid (1,000 grid cells) over U.S. Bureau of Land Management and Forest Service colour aerial photographs of the mountains in the study area (Marcum & Loftsgaarden 1980). We limited the estimation to the mountains because pumas rarely used the valleys. Each photo covered an area of approximately 10 km^2. We selected only those photos that covered elevations ≥2,000 m a.s.l., because pumas in our study rarely used areas at lower elevation (J.W. Laundré, unpubl. data). In each photo, we randomly selected 50 of the grid cell intersections and classified where they fell on the photo relative to open, edge or forest and to Douglas fir, juniper/pinyon, mountain mahogany or aspen forest type. We then used the number of intersections in each

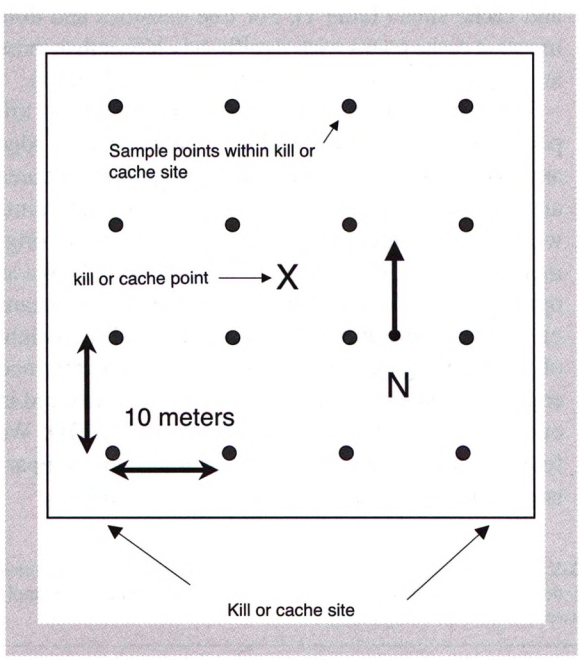

Figure 1. Experimental design to measure tree density, tree diameter at breast height (dbh), shrub density, shrub height, and slope at kill and cache sites. Kill and cache points (x) were the center sample points of the grid. Kill and cache sites were defined as a 50 × 50 m area surrounding kill and cache points. All grids were oriented magnetic north-south for uniformity.

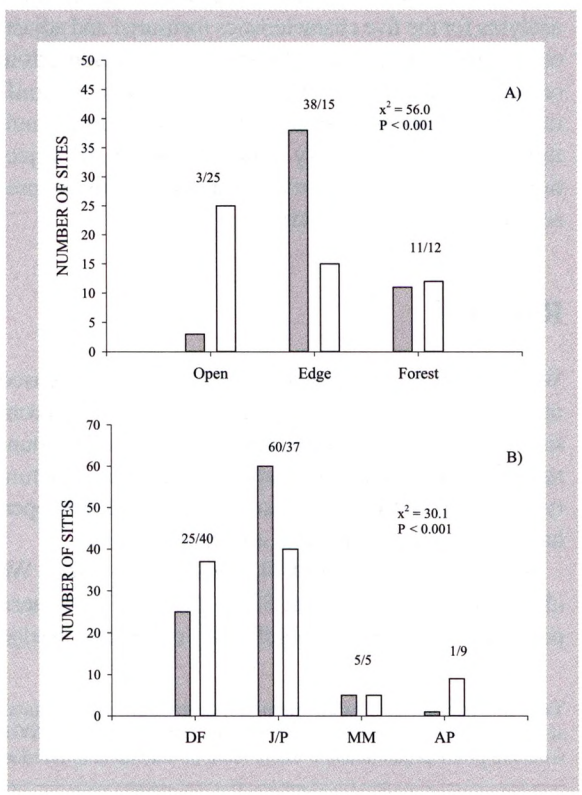

Figure 2. Observed (■) and expected (□) number of kill points found in the three structural classifications (open, edge and forest; A) and four forest types (Douglas fir (DF), juniper-pinyon (J/P), mountain mahogany (MM) and aspen (AP); B). The figures above the columns gives the number of observed and expected sites in each of the three structural classes and each of the four forest types.

Table 1. Means (± SE) of micro structure measurements at 38 kill points, kill sites (area immediately around the kill point), cache points and cache sites (area immediately around cache point). The results of the main treatment effects (sites) from the two-way analysis of variance comparisons are presented. Where there is a significant difference among sites, the mean that was found different by multiple range testing is indicated with an asterisk (*).

	Kill point	Kill site	Cache point	Cache site	F	P
Tree density (#/100 m^2)	5.2 ± 1.4	3.2 ± 0.48	9.2 ± 1.3*	4.1 ± 0.5	7.4	<0.001
Tree dbh (cm)	12.7 ± 1.4	11.0 ± 0.9	17.7 ± 1.2*	12.9 ± 0.7	8.1	<0.001
Shrub density (#/100 m^2)	24.0 ± 5.1	15.8 ± 3.4	13.6 ± 2.9	13.4 ± 2.4	2.1	0.10
Shrub height (cm)	76.4 ± 3.2	77.4 ± 2.8	83.4 ± 3.4	82.6 ± 2.4	2.1	0.10
Slope (%)	13.3 ± 1.3	15.8 ± 1.3	14.9 ± 1.4	15.1 ± 0.9	0.7	0.56

category to estimate the percentage covered by each structure type.

For the micro structural analysis, we used a two-way analysis of variance to test the null hypothesis that cache or kill points did not differ in structure from the surrounding cache and kill sites, nor between each other. The first treatment (points/sites) was to test for differences among kill points, cache points, kill sites and cache sites. The second treatment was among the different kills that we found. We used this design to partition out the inter-site variability and to better test the main hypothesis of no differences among kill points, cache points, kill sites and cache sites. We did these analyses for the five characteristics measured and adjusted the probabilities for multiple tests with a Bonferroni correction factor (Neu, Byers & Peek 1974). If significant differences were found among sites, we used a multiple range test to identify those differences. All rejection levels were set at $P < 0.05$, and all means are presented with ± standard errors.

Results

We sampled 71 aerial photos (3,550 points) and based on this analysis, forest composition in our study area consisted of 44.0% Douglas fir, 40.9% juniper, 5.3% mountain mahogany, and 9.8% aspen. Relative to structure types, 48.2% of the study area ≥2,000 m a.s.l. was open habitat, 28.5% edge habitat, and 23.3% forest.

We located cache sites of 94 deer killed by pumas. We identified the kill points at 52 of these sites. Of these points, pumas killed deer significantly more often in edge and less often in open habitats (Fig. 2A). For 91 sites, we were able to classify the forest type associated or most likely associated with the kill sites. The remaining three sites were classified as open and, thus, did not have a forest type associated with them. Based on our analysis, pumas killed significantly more deer in the juniper-pinyon forest type and significantly fewer in the Douglas fir forest type (Fig. 2B).

We took measurements of microhabitat structure at 76 areas. Of these, 38 had both kill and accompanying cache points. There were five with kill points only because pumas killed but did not drag the deer and 33 cache-only sites (we could not reliably determine the kill point). We used only the 38 sites with data from both kill and cache sites in our statistical comparison. For these areas, we found no differences in shrub density, shrub height, or slope among kill points, cache points, kill sites and cache sites (Table 1). For tree densities and dbh, means at cache points were significantly higher than those at kill points, kill sites and cache sites (see Table 1).

Relative to our analysis of macro structure at kill points, our field designation of these points as open, edge and forest was based on our visual perception of the area and was subject to possible bias. For the 43 kill points where we took micro structural measurements, we originally classified 31 as edges, nine as forest and three as open. To test for possible bias, we compared the means of tree densities, dbh, shrub density, and shrub height of these three groups to corresponding predetermined edge, forest and open areas we previously measured in our study area (Table 2; Altendorf et al. 2001). We found no significant differences in any of the comparisons, which indicates that this bias was minimal.

Table 2. Comparison of mean micro habitat structure measurements at kill points (KP) designated as open, edge and forest to the same measurements made at predetermined sites (PS) (Altendorf et al. 2001). By definition, there were no tree measurements in open areas. Sample sizes are given in parentheses. There were no statistical differences between any of the comparisons.

	Edge		Forest		Open	
	KP	PS	KP	PS	KP	PS
Tree density (#/100 m^2)	2.9 ± 0.6 (31)	3.5 ± 0.9 (14)	14.0 ± 3.8 (9)	10.0 ± 2.8 (14)		
Tree dbh (cm)	10.9 ± 2.1 (31)	10.9 ± 4.0 (14)	11.6 ± 2.1 (9)	15.9 ± 2.1 (14)		
Shrub density (#/100 m^2)	15.8 ± 4.2 (31)	14.3 ± 3.8 (14)	10.8 ± 3.1 (9)	11.8 ± 4.0 (14)	40.0 ± 16.6 (4)	22.9 ± 8.1 (14)
Shrub height (cm)	73.8 ± 3.7 (31)	73.3 ± 1.9 (14)	94.8 ± 8.4 (9)	78.9 ± 3.6 (14)	65.7 ± 4.3 (4)	60.1 ± 4.3 (14)

Discussion

Other studies (Hornocker 1970, Logan & Irwin 1985, Laing1988, Koehler & Hornocker 1991, Williams, McCarthy & Picton1995, Jalkotzy et al. 2000) have also documented that pumas use specific forest/terrain types and, based primarily on cache site data, catch more prey in these areas. Our data from actual kill points support the findings of these previous studies in that we also found pumas killing more deer than expected in one forest type and less in another (see Fig. 2). However, in our area at least, these differences were possibly more related to winter habitat selection by deer. Juniper-pinyon areas are usually at lower elevations and on south-southwest facing slopes, which are used frequently by deer in the winter (J.W. Laundré, pers. obs.). Less-used Douglas fir areas are at higher elevations and are used by deer early in the winter but are abandoned as snow depths increase (J.W. Laundré, pers. obs.). Thus, it may be more than just a forest type effect on catchability of deer. Indeed, previous authors (Hornocker 1970, Logan & Irwin 1985, Laing1988, Koehler & Hornocker 1991) have interpreted their results in terms of preferred forest/terrain types providing the right conditions for pumas to successfully stalk their prey, i.e. stalking habitat. Additionally, Laing (1988) found overstory cover and horizontal visibility to differ from areas of high and low puma use, indicating the possible importance of structural characteristics. However, it had yet to be tested if these results can be extrapolated to where pumas actually kill deer. In our study area we were able to identify kill points at 52 sites. Signs in the snow indicated that pumas usually made contact with the deer within 10 m of the initiation of pursuit, and that deer rarely travelled more than 10-15 m after the puma made contact. So we considered these points to be representative of the entire attack sequence. Data from the macro and micro structure analyses at these identified kill points clearly indicate that structural characteristics are important factors, at least in the winter, and that these characteristics are found in edge and edge-like areas. Thus, it is not the forest type that a puma is in, but where it is within that forest type that is important to its winter hunting success.

Studies of other stalking felids demonstrate that these are more successful if they approach their prey to within 10-20 m before attacking (Sunquist & Sunquist 1989). Although we found no reported data, we assumed that pumas need to approach to similar distances. Sunquist & Sunquist (1989) also stressed the importance of stalking cover to enable a predator to approach undetected to within these distances. For example, grass heights of 0.3-0.8 m increased capture success of African lions *Panthera leo* (Elliott et al. 1977, Van Orsdol 1984).

This need for stalking predators to approach undetected explains the selective use of edge areas found in our study. We would expect a low number of kills in the open areas where the high visibility puts the puma at a disadvantage (Laing 1988). The low number of kills found in the forest is likely a result of a combination of factors. Tree densities possibly are too high and obscure the puma's view (Laing 1988); the average density of trees at forest kill points (see Table 2) equates to an approximate tree-to-tree distance of 7 m (Brower et al. 1999). Additionally, deer generally use the forest area for resting (Collins 1983). At these times deer are stationary and usually vigilant (J.W. Laundré, pers. obs.) and have a greater chance of seeing an approaching puma and escaping before its arrival. Forest edges or edge-like areas, on the other hand, are areas where deer are most likely to be moving, e.g. from feeding in open areas to forest bed sites. Additionally, mean tree-to-tree distances are approximately 17 m which may provide adequate visibility to detect moving deer but still sufficient cover to approach undetected to within attacking distance. We propose that it is these elements of edge and edge-like areas that enhance a puma's ability to detect and approach close enough to attack deer, making these areas successful winter hunting habitat for pumas in our area. It was difficult to ascertain actual kill points in the summer. Thus, we do not have comparable data for this season to test if puma hunting patterns change in this season. Others (Seidensticker et al. 1973, Williams et al. 1995) have reported that pumas rely more on small mammals in summer than in winter and thus, their hunting strategies may differ at these times.

For large, solitary predators like pumas, attacking a prey larger than themselves represents a major energy expenditure (Ackerman, Lindzey & Hemker 1986) and, if successful, a major energy gain for that investment. In the framework of optimal foraging theory, meat stolen by other animals can represent a major loss of the benefits (energy gain) relative to the costs (energy expended) and becomes a relevant aspect of the acquisition of prey. In energetic terms, then, an important consideration for a predator beyond what to kill and where to kill it is how to save that energy for its use. As the loss of meat to other animals, including conspecifics, can be extensive (Wright 1960, Packer 1986, Sunquist & Sunquist1989, Murphy, Felzien, Hornocker & Ruth 1998), caching should be a highly developed adaptation. Most accounts of caching behaviour in felids are quite general, e.g. placing their kills in dense cover (Schaller &

Vasconselos 1978, Sunquist 1981, Sunquist & Sunquist 1989), or in the case of leopards *Panthera pardus*, placing their kills in trees (Houston 1979). For pumas, the general observation of caching their prey under trees (Shaw 1989) was supported by our data. Because the cache point is at the base of one or more trees, the average distance measurement of the four quadrants at this point would be extremely small, resulting in our higher tree density estimates relative to the surrounding area (cache site). However, what we did not predict was the significantly larger dbh estimates at the cache points. Pumas did not randomly place their kills under the most convenient tree but selected trees with significantly larger dbh (= older, taller trees). This suggests that cache site selection, at least for pumas, may be both important and complex. Why tree size would be a selection factor can only be speculated at this time. Based on observation of tracks around kill sites, we believe that pumas often rest up to 100 m from the cache site (J.W. Laundré, unpubl. data). Reports by others of dead coyotes *Canis latrans* at kill sites (Boyd & O'Gara 1985, Koehler & Hornocker 1991, Murphy et al. 1998) indicate that pumas actively defend their cached prey at times. Perhaps the taller tree at the cache site enables pumas to maintain visual contact with the cache site and thus, to better defend it from scavengers. Obviously, further, more detailed analyses of cache site characteristics than made here are needed to define the role of this and other possible factors in the selection of cache sites by pumas. Other factors that could be important include height of lowest branches or basal circumference.

In conclusion, the results of our study suggest that pumas hunt more successfully in the winter at the edges of forest patches and select cache sites at the base of larger, older trees. Thus, the effectiveness of puma predation in the winter is limited by habitat structure (Logan & Irwin 1985) and both pumas and mule deer in our study area are aware of these limits (Holmes 2000, Altendorf et al. 2001). Additionally, Koloski & Lindzey (2000), in a comparison between two forested areas with different edge densities, found that within home ranges of pumas from both areas, edge densities were equal. Therefore, pumas may not only be selecting successful hunting habitat, forest edges, on a localized daily scale but also on a larger home range scale; i.e. a minimal amount of edge in the home range may be needed to catch sufficient prey. Based on these observations, we predict that the use of an area by pumas in the winter, and puma impact on prey populations during that season will be related to the proportion of successful hunting habitat available.

Successful caching of prey by pumas can reduce their kill frequency and, thus, reduce their potential impact on prey populations. Inadequate caching habitat might lead to higher losses of kills, and hence a higher kill frequency (Hornocker 1970, Murphy et al. 1998). Based on this, we predict that prey populations in areas with good hunting but poor caching habitat would experience higher levels of predation.

The implications of these predictions are that the effects of puma predation might be managed by manipulating characteristics of successful hunting and caching habitat. Such management of predation effects via habitat manipulation could potentially help reduce some current human conflicts related to predator-prey relationships.

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References

Ackerman, B.B., Lindzey, F.G. & Hemker, T.P. 1986: Predictive energetics model for cougars. - In: Miller, S.D. & Everett, D.D. (Eds.); Cats of the World: Biology, conservation, and management. National Wildlife Federation, Washington, D.C., pp. 333-352.

Altendorf, K.B., Laundré, J.W., López-González, C.A. & Brown, J.S. 2001: Assessing effects of predation risk on foraging behavior of mule deer. - Journal of Mammalogy 82: 430-439.

Anderson, A.E. 1983: A critical review of literature on puma (Felis concolor). - Special Report n° 54, Denver, Colorado Division of Wildlife, Denver, Colorado, 91 pp.

Boyd, D. & O'Gara, B.W. 1985: Cougar predation on coyotes. - Murrelet 66: 17.

Brower, J.E., Zar, J.H. & von Ende, C.N. 1990: Field and laboratory methods for general ecology. 3rd edition. - Wm. C. Brown Publishers, 237 pp.

Collins, W.B. 1983: Feeding behavior and habitat selection of mule deer and elk on northern Utah summer range. - Journal of Wildlife Management 47: 646-663.

Elliot , J.P., Cowan, I.M. & Holling, C.S. 1977: Prey capture in the African lion. - Canadian Journal of Zoology 55: 1811-1828.

Holmes, B.R. 2000: The mountain lion in Southeastern Idaho: Population characteristics and a test of optimal foraging theory. - M.Sc. thesis, Idaho State University, 96 pp.

Hornocker, M.G. 1970: An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. - Wildlife Monographs 21: 1-29.

Houston, D.C. 1979: The adaptions of scavengers. - In: Sinclair, A.R.E. & Norton-Griffiths, M. (Eds.); Serengeti: Dynamics of an Ecosystem. University of Chicago Press, pp. 263-286.

Jalkotzy, M.G., Ross, P.I. & Wierzchowski, J. 2000: Regional scale cougar habitat modeling in Southwestern Alberta, Canada. - Abstract Sixth Mountain Lion workshop, San Antonio, Texas, p. 19.

Koehler, G.M. & Hornocker, M.G. 1991: Seasonal resource use among mountain lions, bobcats, and coyotes. - Journal of Mammalogy 72: 391-396.

Koford, C.B. 1946: A California mountain lion observed stalking. - Journal of Mammalogy 27: 274-275.

Koloski, J.H. & Lindzey, F.G. 2000: Mountain lion home range use in a fragmented landscape.- Abstract of the Sixth Mountain Lion workshop, San Antonio, Texas, p. 21.

Laing, S.P. 1988: Cougar habitat selection and spatial use patterns in southern Utah. - M.Sc. thesis, University of Wyoming, 68 pp.

Logan, K.A. & Irwin, L.L. 1985: Mountain lion habitats in the Big Horn Mountains, Wyoming. - Wildlife Society Bulletin 13: 257-262.

Marcum, C.L. & Loftgaarden, D.O. 1980: A nonmapping technique for studying habitat preferences.- Journal of Wildlife Management 44: 963-968.

Murphy, K.M., Felzien, G.S., Hornocker, M.G. & Ruth, T.K. 1998: Encounter competition between bears and cougars: some ecological implications. - Ursus 10: 55-60.

Neu, C., Byers, C.R. & Peek, J.M. 1974: A technique for analysis of utilization-availability data. - Journal of Wildlife Management 38: 541-545.

Packer, C. 1986: The ecology of sociality in felids. - In: Rubenstein, D.I. & Wrangham, R.W. (Eds.); Ecological Aspects of social evolution. Princeton University Press, pp. 429-451.

Schaller. G.B. & Vasconselos, J.M.C. 1978: Jaguar predation on capybara. - Zeitschrift für Säugetierkunde 43: 296-301.

Seidensticker, J.C., IV, Hornocker, M.G., Wiles, W.V. & Messick, J.P. 1973: Mountain lion social organization in the Idaho Primitive Area. - Wildlife Monograph 35: 1-60.

Shaw, H. 1989: Soul among lions. - Johnson Books, 140 pp.

Sunquist, M.E. 1981: The social organization of tigers (Panthera tigris tigris) in Royal Chitawan National Park, Nepal. - PhD thesis, University of Minnesota, 98 pp.

Sunquist, M.E. & Sunquist, F.C. 1989: Ecological constraints on predation by large felids. - In: Gittleman, J.L. (Ed.); Carnivore behavior, ecology and evolution. Cornell University Press, pp. 283-301.

Van Orsdol, K.G. 1984: Foraging behaviour and hunting success of lions in Queen Elizabeth National Park, Uganda. - African Journal of Ecology 22: 79-99.

Williams, J.S., McCarthy, J.J. & Picton, H.D. 1995: Cougar habitat use and food habits on the Montana Rocky Mountain front.- Intermountain Journal of Science 1: 16-28.

Wilson, P. 1984: Puma predation on guanacos in Torres del Paine National Park, Chile. - Mammalia 48: 515-522.

Wright, B.S. 1960: Predation on big game in East Africa. - Journal of Wildlife Management 24: 1-15.

Zar, J.H. 1999: Biostatistical Analysis, 4th edition. - Prentice Hall, 929 pp.