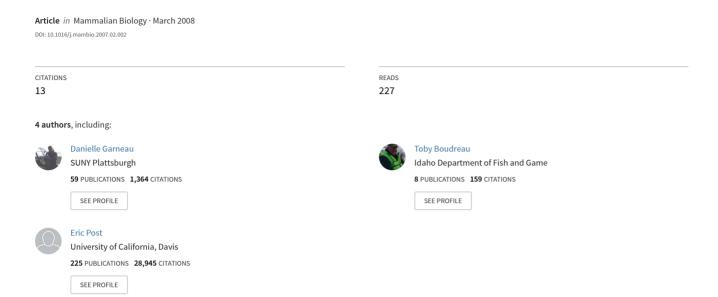
Black bear movements and habitat use during a critical period for moose calves





Mammalian Biology

Zeitschrift für Säugetierkunde



www.elsevier.de/mambio

ORIGINAL INVESTIGATION

Black bear movements and habitat use during a critical period for moose calves

Danielle E. Garneau^{a,*}, T. Boudreau^b, M. Keech^c, E. Post^d

Received 3 August 2006; accepted 3 February 2007

Abstract

In sub-Arctic and north-temperate ecosystems, opportunistic carnivores, such as black bears (*Ursus americanus*) and brown bears (*Ursus arctos*), are active on the landscape for a shorter period annually than sympatric gray wolves (*Canis lupus*). Therefore, bear movement patterns and habitat use might be expected to be more deliberate and of greater consequence, in terms of energy acquisition, than those of predators not undergoing hibernation. Habitat choices concerning feeding, bedding, and denning grounds made by black bears therefore should reflect seasonal abundance and distribution of vegetation and key prey items as these are sites where bears remain and forage for prolonged periods of time. We recorded the movement patterns of 6 GPS-collared black bears from den emergence to onset of moose (*Alces alces*) parturition in 2003. Over approximately 3 weeks prior to parturition, results from average distance calculations suggest that black bears moved closer to probable moose calving-site habitat. Additionally, the seasonal habitat use by black bears surrounding dens reflected the same trend for areas where cow moose gave birth in spring 2003, with a propensity to use needleleaf forest more than any other habitat.

© 2007 Deutsche Gesellschaft für Säugetierkunde. Published by Elsevier GmbH. All rights reserved.

Keywords: Calving grounds; Den-sites; Predation; Prey pulse; Synchrony

Introduction

Studies of American black bear (*Ursus americanus*) feeding behavior are numerous (Boileau et al. 1994; Holcroft and Herrero 1991; Welch et al. 1997). Several captive-feeding studies have been performed to assess food palatability and nutrition among bears (Bacon and Burghart 1983; Pritchard and Robbins 1990; Rode and Robbins 2000; Welch et al. 1997); fewer studies have, however, documented intra-seasonal changes in feeding

E-mail address: danielle.garneau@gmail.com (D.E. Garneau).

behavior and habitat use by wild bears in relation to seasonal food availability, including prey (Adams et al. 1995; Gende et al. 2004; Hilderbrand et al. 1999b).

In the boreal forest, predators are subject to seasonal variation in abundance of food, and have adapted to capitalize on ephemeral resources. Pulses of food items are well documented in many systems, and include oak (*Quercus* sp.) mast, berry crops, salmon (*Oncorhynchus* sp.), ants (*Formica* spp.), and neonatal ungulates (Hilderbrand et al. 1999b; Gende et al. 2004; Grosse et al. 2003; Liebhold et al. 2004; Ostfeld et al. 1996), but seasonal foraging patterns of bears have been difficult to document due to their secretive behaviors and complex

^aDepartment of Biology, Colby College, Waterville, ME 04901, USA

^bIdaho Department of Fish and Game, 1345 Barton Road, Pocatello, ID 83204, USA

^cAlaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701-1599, USA

^dDepartment of Biology, The Pennsylvania State University, Mueller Laboratory, University Park, PA 16801, USA

^{*}Corresponding author.

life-history (e.g., hibernation, omnivory) (McCutchen 1989). Moreover, the need to understand the feeding biology of black bears and brown bears in interior Alaska is amplified by the lower availability of animal protein as compared to that found near coastal streams and rivers (Hilderbrand et al. 1999b). In the absence of salmon on inland ranges, bears must fulfill their dietary demands for animal protein with small mammals, insects, and ungulates (Grosse et al. 2003; Welch et al. 1997). In lacking a cecum, bears are unable to sequester all of their required nutrients from plant matter, thus making periodic spring pulses in availability and vulnerability of animal prey critical in the annual dietary cycle of bears (Hilderbrand et al. 1999a; Welch et al. 1997; Wilton 1983).

Black bears typically do not consume animal protein immediately following den emergence, and exhibit inappetance lasting up to 2 weeks (Nelson et al. 1983; McLoughlin et al. 2002; Rogers 1976). Bears possess a simple stomach devoid of complex microbial flora, thereby limiting digestion immediately following den emergence to berries, nuts, and easily digestible animal matter (Rogers 1976). In boreal forest systems in which moose (*Alces alces*) calves may represent a substantial and highly seasonal resource for black bears, scat and stomach contents of black bears typically are comprised of horsetail (*Equisetum*) and other species of emergent aquatic vegetation (Hatler 1972; Partridge et al. 2001; Smith 1994) early in the season of moose parturition.

The dietary requirement for newly emergent and highly digestible vegetation may be a major factor influencing movements and habitat use of black bears immediately following den emergence (Hatler 1972). Several studies have suggested that black bears select lowland areas for den-sites, whereas brown bears (*Ursus arctos*) usually den in upland locations (Linnell et al. 2000). Cow moose select lowland areas near water during parturition in much the same manner as black bears select lowland den-sites (Bergerud and Page 1987; Wilton et al. 1984). Many lowland forests provide ideal foraging grounds for black bears, making moose parturition an opportune time for such predators to regain nutritional losses following denning (Hatler 1972; Wilton 1983).

In the boreal forest in late April-early May, preparturient cow moose and black bears move towards low-lying areas to feed upon newly emergent and highly digestible vegetation during an energetically demanding part of the year (Bowyer et al. 1999; Eagle and Pelton 1983; White et al. 2001). Because of sub-Arctic phenological foraging constraints at snow-melt, the only high-protein vegetation available to moose and black bears at this time are emergent aquatics, horsetail, and sedges (Johnson et al. 2002a, b; Klein 1987). At the onset of the moose calving period, black bears feed on vegetation for approximately 2–3 weeks, acclimate the

digestive tract to food intake, and begin to experience amino acid demands requiring ingestion of animal protein (Beeman and Pelton 1980; Eagle and Pelton 1983).

This study in southwestern interior Alaska compares black bear movement patterns and habitat use before and during a pulse in prey availability associated with parturition in moose. Daily locations and patterns of habitat use by GPS-collared black bears were analyzed between den departure and black bear recapture. Additionally, moose calving-site habitats were compared to habitat use by black bears to determine if both predator and prey exhibit spatial overlap. We hypothesized that as moose parturition approached, the distance from individual black bear locations to the nearest border of habitats chosen by parturient moose should decrease.

Material and methods

Twenty black bears were fitted with global positioning system (GPS)-collars (TGW-3500, Telonics, Mesa, AZ) prior to and during moose parturition in 2002 in an area encompassing the Experimental Micro-Management Area (EMMA) of Game Management Unit (GMU) 19D in southwestern interior Alaska; this area abuts Denali National Park to the west. Demographic data on GPS-collared black bears observed in this study was documented in previous work (Garneau 2005). Location fixes were attempted every 3 h during the active season (April–September) and reduced to one per day during the denning period (October-March). Black bears were darted by Alaska Department of Fish and Game (ADFG) personnel from a Robinson R-44 helicopter using a Telazol dart fired from a CO₂ pistol or rifle. Animals were processed according to (ADFG) standardized and approved procedures. Subsequent to collaring, black bears were relocated from a fixed-wing aircraft using the VHF beacon of each GPS-collar.

Over the course of the first summer 2002, three GPScollared black bears were presumed dead as a result of intra- or inter-specific predation. GPS-collars of dead black bears were retrieved, and carcasses were inspected on-site. Throughout the remainder of 2002-2003, three additional collars slipped off the necks of black bears and later were retrieved when practicable. Additionally, one large adult black bear moved off the study area following collaring in 2002. Prior to parturition in 2003, all remaining GPS-collared black bears were relocated using ADFG aerial telemetry and darted in the same manner as at capture (Institutional Care and Use Committee, University of Alaska, Fairbanks), as these bears were relocated prior to the peak of moose calving as part of an ADFG predator program. GPS-collars were removed from black bears in the study, and data were downloaded onto a computer for analysis (Garneau 2005). Six black bears, whose home ranges overlapped the radio-collared moose calving areas and were encompassed within the boundaries of the 30 m Ducks Unlimited vegetation map, were included in the analysis of daily distance of black bear locations to habitat chosen by

parturient moose. All black bear and moose calf locations falling outside the boundary of the vegetation coverage were omitted from the habitat analysis.

Concomitant with the black bear capture-recapture study, ADFG personnel deployed radio-collars on over 200 moose calves in the EMMA study site for a moose calf mortality study beginning in 2001 that ran through 2004. Dates and locations of moose calf capture-sites were used to extrapolate a 50% core calving area for parturition 2001–2003 (Boitani and Fuller 2000). The 50% core kernel utilization distribution represents the area within a home range that contains more animal locations than would be expected at random. Assumptions were made that calf capture-sites were representative of calf birth-sites since cow moose have been observed at the calving area for up to 3 weeks following parturition (Bowver et al. 1999). The boundaries of the calving area were defined as the 50% core kernel home range calculated from the locations of calf capture for each yearly (e.g., 2001-2003) parturition period using ArcView GIS (vers. 3.2) (ESRI, Redlands, CA). The 50% kernel was selected as opposed to a 95% kernel to capture the most frequently used calf habitats within the study area.

The median date of moose parturition was estimated to investigate temporal changes in average daily distance moved by black bears to moose capture-sites in relation to the onset of parturition. Median dates of moose calving were estimated for 2001–2003 separately using non-linear regression of proportion calves versus day of year and probit analysis of percent births (Caughley and Caughley 1974; Finney 1947; Skogland 1989). Birth date was extrapolated from age estimates at time of moose calf capture. We noted that habitat bias in moose calf capture locations may occur due to the logistics of heli-capture in a heterogeneous landscape (James et al. 2004). The length of the parturition season was defined as the number of days from 10-90% of recorded calves were born, and was estimated using non-linear regression, where $v = 1/[1 + e^{(-a+bx)}]$, in which y = proportion births and x = day of year (Post et al. 2003; Rutberg 1984). Finally, probit analysis was used to estimate the median date of calving, defined as the date of 50% births, for collared cow moose parturition during 2001-2003 (Finney 1947).

Daily distance from each bear location outside the den to the nearest border of the 50% core moose calving area for 2001-2003 was calculated and graphed, using the animal movement extension in ArcView GIS (vers. 3.2) (ESRI, Redlands, CA), for all bears active in spring 2003. Because similar movement patterns were observed for daily distances of black bears to the calving kernel in 2002 and 2003, daily distances moved by black bears to each unique moose calving kernel were averaged for those years combined. Average daily distances were plotted across all GPS-collared black bears versus time. Plots of individual GPS-collared black bears revealed two general patterns of movement; therefore, daily averages were calculated for black bears that denned inside or outside of the moose calving area, residents (3 adult male black bears) and non-residents (2 adult female black bears and one juvenile black bear), respectively.

Black bear and moose calf habitats were derived from a 30 m Ducks Unlimited habitat grid entitled Stony-MOA (Fehringer, D., Ducks Unlimited, Inc., Rancho Cordova, CA). The 32 habitats of the Stony-MOA habitat grid were

reclassified into 7 habitats, according to common regional habitats in McGrath. Alaska and broad habitats derived from Ducks Unlimited metadata, to facilitate analysis (1 = needleleaf forest, 2 = mixed-deciduous forest, 3 = shrub, 4 = graminoid/ sedge/ moss, 5 = aquatic, 6 = fire/ cloud cover, 7 = no data-grid coverage does not cover that extent(Garneau 2005). Habitat use is dictated by the habitat in which a moose calf or black bear location is located. Differences in proportional habitat use in 2003 were calculated from GPS-collar locations of post-denning black bears and subtracted from those same habitat proportions for moose calf capture locations to assess whether black bears used similar or different habitats as the calving areas at 4 day intervals. Proportions of habitat use are derived from the number of locations in a given habitat divided by the total number of locations for a given individual. Absolute values of differences between proportional habitat use by black bears and moose calves were taken and summed across all habitats. As in a χ^2 test, sums approximating zero were interpreted as similarity in habitat use between black bears and moose calves, whereas larger values indicated differential habitat use among predators and their prey (Siegel and Castellan 1988). Fine-scale habitat analysis was evaluated using the mean and bootstrapping procedures to calculate the 90% confidence intervals using R (vers. 2.0.1) (R Development Core Team, Vienna, Austria, 2004).

Den-sites were encompassed by a 250 m buffer (Linnell et al. 2000), and total area per habitat was calculated, using the X-tools extension of ArcView GIS (vers. 3.2)(ESRI, Redlands, CA). Similarly, calf capture locations were buffered by 250 m and total area per 7 habitats was calculated for pooled parturition data 2001–2003 and compared to den-sites of black bears to assess whether den-sites were comprised of the same habitats occurring within calving areas.

Results

The number of days between 10% and 90% moose births was 10 days in 2001 (n = 14; $r^2 = 0.79$, P = 0.001), 9 days in 2002 (n = 26; $r^2 = 0.70$, P = 0.005), and 11 days in 2003 (n = 21; $r^2 = 0.73$, P = 0.002). The median dates (± 1 S.E.) of calving were 21 May (± 3.11 days) in 2001, 20 May (± 2.72 days) in 2002, and 21 May (± 3.39 days) in 2003. These results indicate a highly consistent and predictable time of calving by moose among years in the study site (Fig. 1).

The den-sites of all three non-resident bears and two resident bears occurred in needleleaf forest habitat, whereas one resident bear denned in mixed-deciduous forest habitat. The average area surrounding black bear den-sites was comprised of 65% needleleaf forest, 30% mixed-deciduous forest, 3% shrub, and 2% graminoid/sedge/ moss habitats (Fig. 2). The average area surrounding all buffered moose calf capture-sites was comprised of 40% needleleaf forest, 14% mixed-deciduous forest, 13% shrub, 18% graminoid/sedge/moss, 10% aquatic, and 6% no data-grid coverage does not cover that extent (Fig. 2).

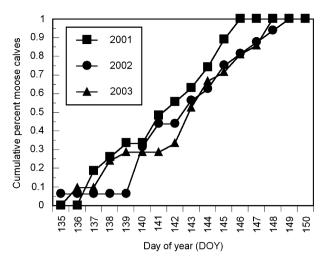


Fig. 1. Timing and progression of the moose calving season near McGrath, Alaska. Shown is the cumulative percent of collared adult female moose that had borne calves in 2001–2003, based on aerial surveys.

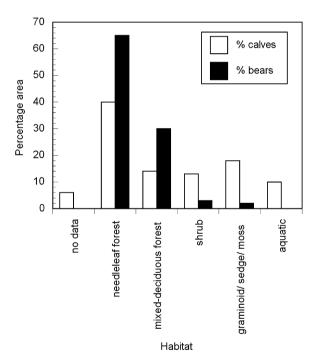


Fig. 2. Percentage area per habitat surrounding moose calf capture-sites located within the core use area (50% kernel) of the moose calving grounds 2003 and average percentage of habitat surrounding black bear den-sites (n=6) 2002 in McGrath, Alaska.

The mean date (± 1 S.E.) of den emergence in 2003 by non-resident bears was 24 April (± 1.73 days); whereas it was 19 April (± 3.21 days) for resident bears. The mean (± 1 S.E.) distance separating den-sites of non-resident black bears from the area of moose calving was $10.40 \, \mathrm{km} \pm 7.92$, whereas that separating resident

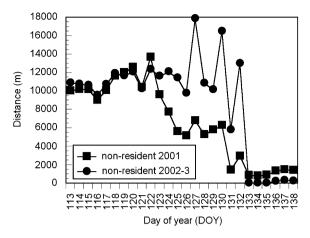


Fig. 3. Average daily distance between GPS-collar locations of non-resident black bears to the nearest boundary of the moose calving area in 2001–2003 in McGrath, Alaska. Black bear movement patterns in relation to the core moose calving area in 2002 and 2003 were similar and thus pooled. Non-resident black bears are defined as bears not denning within the moose calving area.

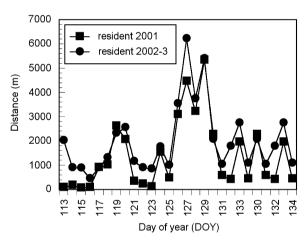


Fig. 4. Average daily distance between GPS-collar locations of resident black bears to the nearest boundary of the moose calving area in 2001–2003 in McGrath, Alaska. Black bear movement patterns in relation to the core moose calving area in 2002 and 2003 were similar and thus pooled. Resident black bears are defined as bears denning within the moose calving area.

black bears from the area of moose calving was $0.16\,\mathrm{km} + 0.13$.

At approximately 19 days post-den emergence, individual black bear distances to moose calving habitats began to decline, suggesting movement toward habitat used by moose during parturition (Figs. 3 and 4). Coincident with the onset of moose calving on 15 May (day 135), black bears entered the calving area and remained there until recapture (Figs. 3 and 4). Of the three non-resident bears (two females, one juvenile male), all made a steady progression through time

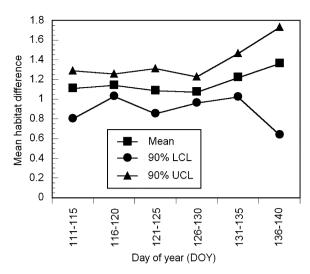


Fig. 5. The mean habitat difference between predator and prey represented by the proportion habitat of black bear locations minus proportion of moose calf capture-site habitats summed across all 7 habitats over 6 time-periods in McGrath, Alaska 2003. Values approximating 2 represent complete dissimilarity in habitat use, whereas values approximating 0 indicate complete similarity in habitat use between black bears and moose calves. Bootstrap resampling methods were used to calculate 90% confidence intervals about the mean.

towards the calving area (Fig. 3). Contrastingly, the three resident bears (adult males), which denned within the core calving area, departed the calving area as non-resident bears approached by approximately 6 May (day 126) (Figs. 3 and 4). These same resident black bears then moved back into the calving area by 12 May (day 132) (Fig. 4).

A fine-scale (4-day interval) difference calculation of habitat use between non-resident black bears and resident black bears versus habitat use by moose calves does not tend towards zero values, indicating habitat use does not appear to change significantly as moose parturition approaches (Fig. 5).

Discussion

Habitat use by carnivores and their prey varies throughout the year according to abundance and distribution of forage and conspecifics (Beeman and Pelton 1980; Eagle and Pelton 1983; MacCracken and Hansen 1984; Samson and Huot 1998). Our results suggest that during the 3 weeks following den emergence, black bears begin movement towards local moose calving areas, which is similar to brown bears in the Greater Yellowstone ecosystem using the same habitats as elk (*Cervis elaphus*) during parturition (Haroldson et al. 2002).

Haroldson et al. (2002) described female bears as remaining near their den-sites in order to forage away from larger male bears, which may explain the less variable pattern of habitat use among female black bears in this study when compared to males of the species. In McGrath, Alaska, changes in average daily distances from black bear locations to calving habitat indicate a steady, slow progression of the predator towards moose calving habitat during the first 2 weeks after den emergence, followed by several abrupt long-distance moves at the early portion of parturition that are most notable in resident black bears.

In general, the hypothesis that black bears would display closer proximity to moose calving-sites as moose parturition commenced was supported by changes in the average daily distances separating black bear locations from the moose calving area. However, habitat-use differences calculated between black bears and moose calves do not support increased similarity as parturition approaches. Numerous studies have shown that males of the species define their home range based on searching for mates and secondarily for resources, whereas females delineate use of space primarily on resource needs (Gittleman and Harvey 1982; MacDonald 1983; Sandell 1989). Similarly, the variable pattern of habitat use observed in resident black bears as compared to that of moose calves may result from the typical dispersal and foraging behavior of adult bears without cubs, such as non-reproductive females or males (Armstrup et al. 2001; Haroldson et al. 2002). Moreover, we are unable to determine whether recently emerged black bears in our study were using habitat containing the most nutritious and digestible forage plant resources (e.g., Equisetum), which is the same resource used by parturient moose, or whether they were actively searching for moose calves throughout parturition (Wilton 1983). Studies in the Great Smoky Mountains and Shenandoah National Park suggest that in systems not containing moose, black bears forage on grasses and seasonally abundant fruits (e.g., wild cherry (P. serotina), apple (Malus pumila)) during the spring season, thus suggesting that consumption of vegetation may be the primary impetus for habitat choices and secondarily animal protein (Beeman and Pelton 1980; Garner and Vaughan 1986).

In the sub-Arctic, most black bears are absent from the landscape for 7–8 months in a state of dormancy and hibernation (Schwartz et al. 1986). Therefore, selection of den-sites by black bears is of major importance because proximity to forage in late winter and early spring becomes essential for replenishing nutritional stores following den emergence (Hatler 1972; Smith 1994). Roots from forest trees and shrubs are well known ground stabilizers and are linked tightly to densite selection (Hechtel 1991; Smith 1994). Findings from this study suggest that the surroundings of black bear den-sites are primarily needleleaf forest and mixed-deciduous forest, which supports results of other Alaskan denning studies (Hechtel 1991; Smith 1994). Additionally, forest provides escape cover, whereas

graminoid/ sedge/ moss habitat near water contains emergent, highly-nutritious vegetation, following snowmelt (Hatler 1972). Numerous studies have observed black bears using aquatic sedge meadows in late winter, moose calving areas during spring, higher-elevation forests with large berry crops, and hard mast in fall (Beeman and Pelton 1980; Eagle and Pelton 1983; Powell and Seaman 1990). Black bears and cow moose in this study share similar habitat in early spring, which likely increases the probability of bear-moose encounters during the period of moose calf vulnerability immediately following parturition. This predator-prey encounter frequency is high in the southwestern interior portion of Alaska, as in 2001–2003 when 37%, 39%, and 30% of moose calves were killed as the result of black bear predation (n = 67, 81, and 51 collared moose calves, respectively) (Keech and Boudreau 2003; Garneau et al. 2007). Given that 60-70% of moose calves in this study area experience mortality as a result of predation, black bear hunting pressure plays an important regulatory role. Thus, it seems likely that cow-calf pair browsing may outweigh the cost of habitat overlap with predators. More research must be focused on the timing of predation with prey phenology in subarctic regions to better address impending plant redistribution as it relates to the distribution and abundance of the ungulate-base in multiple-predator systems.

Acknowledgments

We thank collaborators in the Alaska Department of Fish and Game, specifically P. Valkenburg, H. Reynolds, and Michelle Szepanski (now of University of Alaska Fairbanks) for assistance in capture and study design. We also thank the skilled pilots R. Swisher and T. Cambier for capture and mortality retrieval in the field. Additional thanks to current and former McGrath residents and friends: Roschelle and Jenna Boudreau, M. and Donne Fleagle, L. Egrass, T. Machacek, and Nicole Botteri for their field assistance and support. Many thanks to E. Post, D. Diefenbach, R. Yahner, and A. Taylor for manuscript advice and M. Ferrari for assistance with statistical analysis, as well as E. Long for his technical support, sound advice, and patience. Thanks to A. Mayer, Ph.D. for German translation in addition to F. Zachos and two anonymous referees for their helpful manuscript comments.

Zusammenfassung

Habitatnutzung und Bewegung von Schwarzbären während eines kritischen Zeitraumes für Elchkälber

In subarktischen und nordisch temperierten Ökosystemen sind opportunistische Fleischfresser, wie

Schwarzbären (*Ursus americanus*) und Braunbären (*Ursus arctos*), während eines kürzeren Zeitraums aktiv als die in der gleichen Landschaft lebenden Grauwölfe (*Canis lupus*).

Deshalb könnte erwartet werden, dass Bewegungsmuster und Habitatnutzung von Bären zielgerichteter und von grösseren Auswirkungen, im Bezug auf Energieaufnahme, begleitet sind, als die von Raubtieren, die keine Winterruhe halten. Die Habitatauswahl von Schwarzbären bezüglich Fressen. Ruhen und Behausung sollte deshalb die saisonale Reichhaltigkeit und Verteilung von Vegetation und Beute reflektieren, da die Bären sich an diesen Stellen für längere Zeit aufhalten und nach Nahrung suchen. Wir haben die Bewegungen von sechs, mit GPS-Halsbändern ausgestatteten, Schwarzbären vom ersten Verlassen ihrer Behausung bis zum Beginn der Elchkalbung (Alces alces) im Jahr 2003 aufgezeichnet. Die Resultate von Entfernungsberechnungen, über etwa 3 Wochen vor der Elchkalbung, weisen darauf hin, dass die Bären sich näher zu wahrscheinlichen Elchkalbungsstellen hin bewegen. Darüber hinaus reflektiert die saisonale Habitatnutzung von Schwarzbären um ihre Behausung die Wahl des Kalbungsortes von Elchkühen im Frühling 2003, mit einer Bevorzugung von Nadelwald vor jeder anderen Umgebung.

References

- Adams, L.G., Singer, F.J., Dale, B.W., 1995. Caribou calf mortality in Denali National Park, Alaska. J. Wildl. Manage. 59, 584–594.
- Armstrup, S.C., Durner, G.M., McDonald, T.L., Mulcahy, D.M., Garner, G.W., 2001. Comparing movement patterns of satellite-tagged male and female polar bears. Can. J. Zool. 79, 2147–2158.
- Bacon, E.S., Burghart, G.M., 1983. Food preference testing of captive black bears. Int. Conf. Bear Res. Manage. 5, 102–105.
- Beeman, L.E., Pelton, M.R., 1980. Seasonal foods and feeding ecology of black bears in the Smoky Mountains. Int. Conf. Bear Res. Manage. 4, 141–147.
- Bergerud, A.T., Page, R.E., 1987. Displacement and dispersion of parturient caribou at calving as antipredator tactics. Can. J. Zool. 65, 1597–1606.
- Boileau, F., Crete, M., Huot, J., 1994. Food habits of the black bear, *Ursus americanus*, and habitat use in Gaspesie Park, Eastern Quebec. Can. Field Nat. 108, 162–169.
- Boitani, L., Fuller, T.K., 2000. Research Techniques in Animal Ecology Controversies and Consequences. Columbia University Press, New York.
- Bowyer, R.T., VanVallenberghe, V., Kie, J.G., Maier, .A.K., 1999. Birth-site selection by Alaskan moose: maternal strategies for coping with a risky environment. J. Mammal. 80, 1070–1083.
- Caughley, G., Caughley, J., 1974. Estimating median date of birth. J. Wildl. Manage. 38, 552–556.

- Eagle, T.C., Pelton, M.R., 1983. Seasonal nutrition of black bears in the Great Smoky Mountains National Park. Int. Conf. Bear Res. Manage. 5, 94–101.
- Finney, D.J., 1947. Probit Analysis: A Statistical Treatment of the Sigmoidal Response Curve. Cambridge University Press, Cambridge, UK.
- Garneau, D.E. (2005). Spatio-temporal dynamics of a multiple-predator single-prey system. Ph.D. Thesis, The Pennsylvania State University, Pennsylvania, USA.
- Garneau, D.E., Post, E., Boudreau, T.A., Keech, M.A., Valkenburg, P., 2007. Spatio-temporal patterns of predation among three sympatric predators in a single-prey system. Wildl. Biol. 13, 186–194.
- Garner, J.P., Vaughan, M.R., 1986. Black bear's use of abandoned homesites in Shenandoah National Park. Int. Conf. Bear Res. Manage. 7, 151–157.
- Gende, S.M., Quinn, T.P., Hilborn, R., Hendry, A.P., Dickerson, B., 2004. Brown bears selectively kill salmon with higher energy content but only in habitats that facilitate choice. Oikos 104, 518–528.
- Gittleman, J.L., Harvey, P.H., 1982. Carnivore home range size, metabolic needs and ecology. Behav. Ecol. Sociobiol. 10, 57–63.
- Grosse, C., Kaczensky, P., Knauer, F., 2003. A food source sought by Slovenian brown bears (*Ursus arctos*)? Can. J. Zool. 81, 1996–2005.
- Haroldson, M.A., Ternent, M.A., Gunther, K.A., Schwartz, C.C., 2002. Grizzly bear denning chronology and movements in the Greater Yellowstone ecosystem. Ursus 13, 29–37.
- Hatler, D.F., 1972. Food habits of black bears in interior Alaska. Can. Field Nat. 86, 17–31.
- Hechtel, J.L., 1991. Population dynamics of black bear populations, Fort Wainwright, AK. Natural Resources Report 91-92, Alaska Department of Fish and Game. US Army Sixth Infantry Division (Light), Fort Wainwright, AK.
- Hilderbrand, G.V., Jenkins, S.G., Schwartz, C.C., Hanley, T.A., Robbins, C.T., 1999a. Effect of seasonal differences in dietary meat intake on changes in body mass and composition in wild and captive brown bears. Can. J. Zool. 77, 1623–1630.
- Hilderbrand, G.V., Schwartz, C.C., Robbins, .T., Jacoby,
 M.E., Hanley, T.A., Arthur, S.M., Servheen, C., 1999b.
 The importance of meat, particularly salmon, to body size,
 population productivity, and conservation of North American brown bears. Can. J. Zool. 77, 132–138.
- Holcroft, A.C., Herrero, S., 1991. Black bear, *Ursus americanus*, food habits in Southwestern Alberta. Can. Field Nat. 105, 335–345.
- James, A.R.C., Botin, S., Hebert, D.M., Rippin, A.B., 2004. Spatial separation of caribou from moose and its relation to predation by wolves. J. Wildl. Manage. 68, 799–808.
- Johnson, C.J., Parker, K.L., Heard, D., Gillingham, M.P., 2002a. Movement parameters of ungulates and scalespecific responses to the environment. J. Anim. Ecol. 71, 225–235.
- Johnson, C.J., Parker, K.L., Heard, D., Gillingham, M.P., 2002b. A multiscale behavioral approach to understanding

- the movements of woodland caribou. Ecol. Appl. 12, 1840–1860.
- Keech, M.A., Boudreau, T.A., 2003. Factors limiting moose at low density in Unit19D East; and response of moose to wolf control. Research Performance Report Grant W-33-1, Stud 1.58, Alaska Department of Fish and Game, Alaska.
- Klein, D., 1987. Vegetation recovery patterns following overgrazing by reindeer on St. Matthew's Island. J. Range Manage. 40, 336–338.
- Liebhold, A., Sork, V., Peltonen, M., Koenig, W., Bjornstad, O., Westfall, R., Elkinton, J., Knops, J.M.H., 2004. Within-population spatial synchrony in mast seeding of North American oaks. Oikos 104, 156–164.
- Linnell, J.D.C., Swenson, J.E., Anderson, R., Barnes, B., 2000. How vulnerable are denning bears to disturbance? Wildl. Soc. Bull. 28, 400–413.
- MacCracken, J.G., Hansen, R.M., 1984. Seasonal food habits of blacktail jackrabbits and nuttall cottontails in southeastern Idaho. J. Range Manage. 37, 256–259.
- MacDonald, D.W., 1983. The ecology of carnivore social behavior. Nature 301, 384–397.
- McCutchen, H.E., 1989. Cryptic behavior of black bears (*Ursus americanus*) in Rocky Mountain National Park, Colorado. Int. Conf. Bear Res. Manage. 8, 65–72.
- McLoughlin, P.D., Cluff, H.D., Messier, F., 2002. Denning ecology of barren-ground grizzly bears in the central Arctic. J. Mammal. 83, 188–198.
- Nelson, R., Folk, G.J., Pfeiffer, E., Craighead, J., Jonkel, C., Steiger, D., 1983. Behavior, biochemistry, and hibernation in black, grizzly, and polar bears. Int. Conf. Bear Res. Manage. 5, 284–290.
- Ostfeld, R.S., Jones, C.G., Wolff, J.O., 1996. Of mice and mast. Bioscience 46, 323–330.
- Partridge, S.T., Nolte, D.L., Ziegltrum, G.J., Robbins, C.T., 2001. Impacts of supplemental feeding on the nutritional ecology of black bears. J. Wildl. Manage. 65, 191–199.
- Post, E.S., Sporon-Boving, P., Pederson, C., MacArthur, M.A., 2003. Synchrony between caribou calving and plant phenology in depredated and non-depredated populations. Can. J. Zool. 81, 1–6.
- Powell, R.A., Seaman, D.E., 1990. Production of important black bear foods in the southern Appalachains. Int. Conf. Bear Res. Manage. 8, 183–187.
- Pritchard, G.T., Robbins, C.T., 1990. Digestive and metabolic efficiencies of grizzly and black bears. Can. J. Zool. 68, 1645–1651.
- Rode, K.D., Robbins, C.T., 2000. Why bears consume mixed diets during fruit abundance. Can. J. Zool. 78, 1640–1645.
- Rogers, L., 1976. Effects of mast and berry crop failures on survival, growth, and reproductive success of black bears. Trans. N. Am. Wildl. Conf. 41, 431–437.
- Rutberg, A.T., 1984. Birth synchrony in American Bison (*Bison bison*): response to predation or season? J. Mammal. 65, 418–423.
- Samson, C., Huot, J., 1998. Movements of female black bears in relation to landscape vegetation type in Southern Quebec. J. Wildl. Manage. 62, 718–727.

- Sandell, M., 1989. The mating tactics and spacing behavior of solitary carnivores. In: Gittleman, J.L. (Ed.), Carnivore Behavior, Ecology and Evolution. Cornell University Press, New York, pp. 164–182.
- Schwartz, C.C., Miller, S.D., Franzmann, A.W., 1986. Denning ecology of three black bear populations in Alaska. Int. Conf. Bear Res. Manage. 7, 281–291.
- Siegel, S., Castellan Jr., N.J., 1988. Nonparametric Statistics for the Behavioral Sciences, second ed. McGraw-Hill International Editions, New York, NY, USA.
- Skogland, T., 1989. Comparative social organization of wild reindeer in relation to food, mates, and predator avoidance. Adv. Ethol. 29, 1–74.

- Smith, M.E., 1994. Black bear denning ecology and habitat selection in interior Alaska. M.S. University of Alaska, Fairbanks, Fairbanks, AK.
- Welch, C.A., Keay, J., Kendall, K.C., Robbins, C.T., 1997. Constraints on frugivory by bears. Ecology 78, 1105–1119.
- White, K.S., Testa, J.W., Berger, J., 2001. Antipredator strategies of Alaskan moose: are maternal trade-offs influenced by offspring activity? Can. J. Zool. 79, 2055–2062.
- Wilton, M.L., 1983. Black bear predation on young cervids a summary. Alces 19, 136–148.
- Wilton, M.L., Carlson, D.M., McCall, C.I., 1984. Occurrence of neonatal cervids in the spring diet of black bear in south central Ontario. Alces 20, 95–105.

Available online at www.sciencedirect.com

