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Source: Wildlife Biology, 13(2) : 186-194

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/0909-6396(2007)13[186:SPOPAT]2.0.CO;2

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Garneau, D.E., Post, E., Boudreau, T., Keech, M. & Valkenburg, P. 2007: Spatio-temporal patterns of predation among three sympatric predators in a single-prey system. - Wildl. Biol. 13: 186-194.

The manner in which species partition space and time to minimize competition for shared, limited resources has been a major focus of theoretical and empirical ecology. Although numerous examples exist of intra-guild dietary separation among coexisting species, studies of spatio-temporal partitioning among species sharing a single food type are rare. We investigated spatio-temporal patterns of multi-species predation on individually-marked moose *Alces alces* calves in an Alaskan boreal forest community where moose are the only large herbivore, and constitute the primary prey of coexisting black bears *Ursus americanus*, brown bears *U. arctos* and gray wolves *Canis lupus*. The two most closely related predators, black bears and brown bears, overlapped temporally and spatially in their consumption of moose calves, as indicated by univariate analyses. Moreover, both bear species segregated spatially from wolves when killing moose calves. Hence, our study appears to support key predictions of predator coexistence on a shared resource: namely, that bears and wolves differentiate spatially or temporally in their use of a pulsed prey, presumably to minimize competition.

Key words: black bears, brown bears, gray wolves, moose calves, space, time

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Received 26 July 2005, accepted 12 March 2006

Associate Editor: Mads C. Forchhammer

MacArthur's (1958) warbler study played a fundamental role in defining niche theory on the basis of his observations of spatial and behavioural partitioning of shared resources by coexisting sympatric predators. Although temporal and spatial niche partitioning has been offered as an explanation for coexistence of sympatric species (McPeek 1998, Schmitz 1998, Schmitz & Blake-Suttle 2001), most studies of coexisting species foraging at the same trophic level have focused on documenting differences in food habits as a means of explaining coexistence. For instance, there are many documented examples of coexistence of multiple predators with divergent prey requirements or foraging strategies in aquatic systems (Soluk & Collins 1988, Soluk 1993, McIntosh & Townshend 1994, 1996, Soluk & Richardson 1997, Peckarsky & McIntosh 1998). McIntosh & Townshend (1996), for example, documented that native Galaxias *Galaxias vulgaris* and introduced brown trout *Salmo trutta* actively feed during different times of the day, whereas Woodward & Hildrew (2002) documented a clear relationship between body size of coexisting invertebrate stream predators and size of prey consumed.

Studies of niche separation in terrestrial systems have provided ample evidence of dietary divergence among coexisting species with numerous prey (Neale & Sacks 2001, Caravalho & Gomes 2004, Jacomo et al. 2004), but studies of niche separation among coexisting species with common food requirements are apparently rare. Schmitz & Sokol-Hessner (2002), and numerous related studies (Schmitz & Blake-Suttle 2001, Sokol-Hessner & Schmitz 2002), however, have reported on the basis of studies in old-field invertebrate communities that coexistence among members of the predator guild is facilitated by differences in foraging behaviour and locations. The relevance of the results of old-field arthropod studies to unmanipulated natural systems has been challenged (Oksanen et al. 1981, Menge & Sutherland 1987) and defended (McPeek 1998, Schmitz 1998, Persson 1999), but evidence from additional terrestrial systems would bolster the conclusions of experimental studies.

At our study site in subarctic Alaska, there exists a guild of large carnivores consisting of two species of omnivorous ursids, black bears *Ursus americanus* and brown bears *U. arctos*, and a carnivorous canid, gray wolves *Canis lupus*, but only a single species of ungulate prey, moose *Alces alces*. Other studies in North American systems where these predators coexist on ungulate prey have documented the importance of moose in their diets (Osborne et al. 1991, Ballard & van Ballenberghe 1997, Green et al. 1997, Young & McCabe 1997, Mech et al. 1998). However, our study is, to our knowledge, the first to document patterns of predation by bears and wolves where moose are the only ungulate prey.

Methods

The study site lies within a 31,080 km^2 area of southwestern Alaska, adjacent to the Kuskokwim River. Differences in regional topography are evident in a mosaic of mixed conifer (e.g. white spruce *Picea glauca*, black spruce *Picea mariana*), paper birch *Betula papyrifera* forest and black spruce muskeg. Understory vegetation is mainly ericaceous shrubs (e.g. blueberry *Vaccinium* sp., crowberry *Empetrum nigrum*, Labrador tea *Ledum groenlandicum*) and moss *Sphagnum* sp.

In spring and summer 2001, the Alaska Department of Fish and Game (ADFG) deployed radio-collars (Telonics, Mesa, AZ) on 50 adult female moose for subsequent monitoring of condition, reproduction and movement. All monitored animals were collared within a 25-km^2 circular area around the village of McGrath, following approved wildlife capture protocols (Institutional Animal Care & Use Committee, University of Alaska, Fairbanks). Beginning in May 2001 and 2002, 66 and 81 moose calves, respectively, were radio-collared (Telonics, Mesa, AZ), and their survival was monitored daily throughout the critical 6-8 week period following birth (Ballard et al. 1981, Gasaway et al. 1992). The majority of the calves collared were born to collared cow moose; however, if an uncollared cow moose was sighted with a neonate during the collaring procedure, that calf was also collared. All collars were equipped with mortality sensors, and when mortalities were detected, they were located aerially from a fixed-wing aircraft. Location fixes were recorded with the on-board GPS unit of the radio-tracking aircraft, and subsequently visited on the ground for collar retrieval, carcass inspection, site description and cause of death.

The majority of moose calf mortalities during the critical period were investigated within 24-48 hours of detection of the mortality signal to minimize the risk of scavenging. Calf mortalities were ascribed to predation if signs of hair, scat or carcass disposition could be linked to a specific predator species. Numerous studies of bear predation on ungulates, for example, have documented cooling pits and scrapings in the vicinity of the carcass (Elgmork 1982, Vander Wall 1990). Additionally, bear scat in spring usually comprises vegetable and animal matter, indicative of an omnivorous predator (Hatler 1972). Predation, attributable to bears characteristically results in the eversion of the pelt as it is more difficult to digest (Wilton 1983). Gray wolves typically consume a larger proportion of the neonate carcass, including pelt and hoof caps. Wolf scat will usually contain a larger proportion of animal material and fur than that of other predators (Wilton 1983). We assumed independence of moose calf mortality sites based on the understanding that black bears, brown bears and gray wolf packs consume an ungulate approximately every 5.7, 6.1, and 1.2 days, respectively (Burkholder 1959, Ballard et al. 1981, Ballard et al. 1990). Additionally, other studies conducted in Alaska have documented densities of 90 black bears, 28 brown bears and 2.8 gray wolves per 1,000 km^2, suggesting that there are numerous predators in the area, thus reducing the likelihood that one predator killed all moose calves in this region (Ballard et al. 1990).

Aerial monitoring of calf survival continued on a bi-weekly basis through early July, when most calves were large and had gained enough experience to effectively avoid predators (Boudreau 2001). Distributional counts of moose calf mortalities in space and time were examined in histograms according to predator, with pooling applied to the time scale.

To assess if pooling of data on spatial and temporal calf mortality from 2001 and 2002 was justifiable, non-parametric Mann-Whitney tests were performed; pooling of data maximized sample size for a subsequent non-parametric ANOVA by ranks (Kruskal-Wallis; Siegel & Castellan Jr. 1988). Differences in timing (dates) and locations (habitat) of calf mortalities among the three predators were analyzed using Kruskal-Wallis tests. However, the Kruskal-Wallis tests allowed only for gross assessment of differences among predators, and did not permit evaluation of dependence or independence in spatial and temporal patterns of predation by individual species in relation to spatial and temporal patterns of other species. Hence, we also analyzed partitioning of space and time among predators using multivariate generalized linear (GLM) and additive (GAM) models (Hastie & Tibsharani 1990, Venables & Ripley 1999). In the GLM for each predator, we denoted either spatial locations or dates of calf mortalities by the focal predator as the dependent variable, with locations and dates of calf mortalities by the other predators as potential predictor variables. If GLM results indicated no linear relationships between predictor and dependent variables, we re-ran the analyses using spline functions for each predictor variable (GAMs). We noted that GAMs indicated only the significance of non-linearity of individual predictors as opposed to the statistical significance of the relationship among dependent and predictor variables. Therefore, the terms identified as significantly non-linear in the GAMs were tested for model significance in the GLMs, where they were entered as non-linear quadratic terms. Significant and positive t-values from GLM outputs were interpreted as evidence of spatial or temporal overlap, whereas significant and negative t-values were indicative of spatial or temporal segregation. Non-significant t-values were interpreted as evidence of spatial or temporal independence among predators.

For the spatial analyses, habitats in which moose calf mortalities occurred were assigned based on the 30-m grid cell in which they were located, using ArcView GIS (vers. 3.2; ESRI, Redlands, CA). The vegetation was derived from the 30-m Ducks Unlimited Stony-MOA vegetation grid, where 32 habitats were reclassified into seven habitats to facilitate analyses (D. Fehringer, Ducks Unlimited, Inc., Rancho Cordova, CA). Pooling of habitats was based on the appearance of predominant microhabitats encountered over the duration of the 3-year study and in accordance with primary habitats listed in Ducks Unlimited metadata. Habitats were considered either: 1) needleleaf forest, 2) mixed-deciduous forest, 3) shrub, 4) graminoid/sedge/moss, 5) aquatic, 6) fire/cloud cover, or 7) no data/not covered within grid extent.

Results

In 2001 and 2002, black bears foraged for moose calves mainly in mixed-deciduous forest and needleleaf forests (Fig. 1A). During 2001, brown bears killed moose calves in needleleaf forest, shrub and graminoid habitats more than in any other habitat (Fig. 1B). In 2002, four moose calf mortalities attributed to brown bears fell outside the extent of the Ducks Unlimited vegetation coverage, potentially

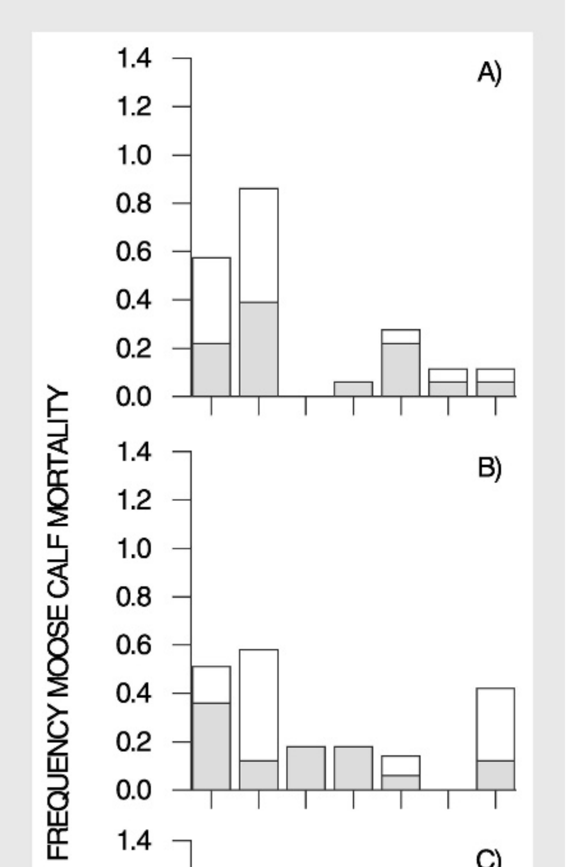

Figure 1. Distribution of habitats in which black bears (A; N = 18), brown bears (B; N = 17) and gray wolves (C; N = 11) killed moose calves in McGrath, Alaska. Bars in white and gray represent data for 2001 and 2002, respectively.

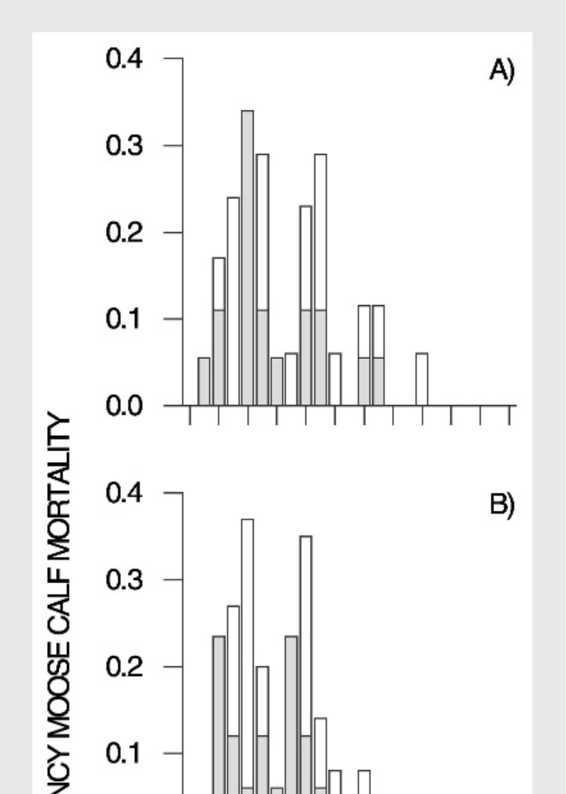

Figure 2. Distribution of days on which black bears (A; N = 18), brown bears (B; N = 17) and gray wolves (C; N = 11) killed moose calves in McGrath, Alaska. All data were pooled by 4-day intervals for display in the histogram. Bars in white and gray represent data for 2001 and 2002, respectively.

Table 1. Results of Kruskal-Wallis non-parametric ANOVA by ranks of moose calf mortality (caused by black bear (1), brown bear (2) and gray wolf (3)) dates and locations in McGrath, Alaska, during 2001-2002.

Grouping variables	Black bear Brown bear Gray wolf	Black bear Brown bear	Black bear Gray wolf	Brown bear Gray wolf
Sample size	$N_1 = 34$	$N_1 = 34$	$N_1 = 34$	$N_2 = 30$
	$N_2 = 30$	$N_2 = 30$	$N_3 = 28$	$N_3 = 28$
	$N_3 = 28$			
Space	$R_1 = 48.75$	$R_1 = 30.84$	$R_1 = 35.41$	$N_2 = 34.08$
	$R_2 = 52.97$	$R_2 = 34.38$	$R_3 = 26.75$	$N_3 = 24.59$
	$R_3 = 36.84$			
Time	$R_1 = 44.47$	$R_1 = 33.87$	$R_1 = 28.10$	$N_2 = 25.10$
	$R_2 = 40.55$	$R_2 = 30.95$	$R_3 = 35.63$	$N_3 = 34.21$
	$R_3 = 55.34$			

concealing use patterns (see Fig. 1B). Based on the remaining 2002 data, brown bears killed moose calves primarily in mixed-deciduous forests (see Fig. 1B). Gray wolves killed moose calves primarily in needleleaf forest in both years (Fig. 1C).

No differences existed between years in spatial and temporal patterns of predation by black bears ($U = 113.5$, $P = 0.297$), brown bears ($U = 69.5$, $P = 0.086$) or gray wolves ($U = 78.0$, $P = 0.487$) on moose calves, based on pairwise Mann-Whitney tests; therefore, data were pooled for subsequent analyses.

Spatial patterns of predation on moose calves differed among the three predators ($\chi^2 = 6.2$, df = 2; $P = 0.046$) as indicated by Kruskal-Wallis tests (Table 1). Pairwise spatial comparisons revealed lack of spatial segregation between black bears and brown bears ($\chi^2 = 0.6$, df = 1, $P = 0.431$), but segregation between gray wolves and brown bears ($\chi^2 = 5.0$, df = 1, $P = 0.025$), and between black bears and gray wolves ($\chi^2 = 4.0$, df = 1, $P = 0.047$). Multivariate tests of space use by black bears, however, indicated independence from brown bears ($t = 0.0$, df = 24, $P > 0.500$) and gray wolves ($t = 0.9$, df = 24, $P > 0.200$) in GLM analysis. Similarly, brown bear space use revealed no relationship with patterns of space use by black bears ($t = 0.0$, df = 24, $P > 0.500$) or gray wolves ($t = -0.4$, df = 24, $P > 0.500$) in GLM analysis. Finally, space use by gray wolves was independent of those of black bears ($t = 0.5$, df = 24, $P > 0.500$) and brown bears ($t = -0.5$, df = 24, $P > 0.500$).

Black bears killed moose calves during early parturition, with black bear predation peaking within days 150-160 and persisting through day 200 (Fig. 2A). Timing of predation by brown bears on moose calves overlapped that by black bears, but began later, peaked earlier and ended sooner (Fig. 2B). Timing of predation on moose calves by gray wolves overlapped that of both bear species, but persisted later in the season (Fig. 2C).

Furthermore, black bears killed moose calves earlier than other predators, beginning on day 143 (see Fig. 2A). The histograms suggest a transition from black bear to brown bear-induced moose calf mortalities during the middle of the season within days 150-180 (see Fig. 2B). In contrast, predation on moose calves by gray wolves in 2002 occurred later and persisted longer than predation by the other two predator species (see Fig. 2C)

Lack of temporal segregation among the three predator species ($\chi^2 = 4.8$, df = 2, $P = 0.093$) resulted from Kruskal-Wallis tests of pooled data (see Table 1). Temporal overlap between black bears and brown bears ($\chi^2 = 0.4$, df = 1, $P = 0.531$), overlap between black bears and gray wolves ($\chi^2 = 2.7$, df = 1, $P = 0.102$), but segregation between brown bears and gray wolves ($\chi^2 = 4.2$, df = 1, $P = 0.040$) was evidenced in pairwise Kruskal-Wallis tests.

Overlap with brown bears ($t = 4.1$, df = 26, $P < 0.050$), but independence from gray wolves ($t = -1.2$, df = 26, $P > 0.200$) resulted from a GLM of temporal patterns of black bear predation. Likewise, temporal overlap with black bears ($t = 3.6$, df = 26, $P < 0.050$) and independence from gray wolves ($t = 1.3$, df = 26, $P > 0.200$) was evidenced by a GLM of temporal patterns of brown bears. Finally, the GLM of gray wolf predation indicated no relation to predation by black bears (t = -0.5, df = 24, P > 0.500) or brown bears (t = 0.6, df = 24, P > 0.500).

Discussion

Niche theory predicts that when sympatric species overlap in use of a shared resource along one dimension, they must differ along another to coexist (Hutchinson 1957, MacArthur 1958). In accordance with this concept of niche complementarity, coexisting species often display different food needs or feeding habits (Cody 1968, Schoener 1974, Emmons 1980, Pyke 1982, McKenzie & Rolfe 1986). Typically, intra-guild differences in body size are reflected in differential preferences for food size; for instance, larger and smaller predators may select for larger and smaller prey, respectively (Brown & Davidson 1977, Davidson 1978). Evolution of body- and prey size differences among sympatric predators reflects selection for reduced interspecific competition (Rosenzweig 1966).

However, in communities lacking multiple prey species, such as in this study system, sympatric predators must differentiate in other ways to minimize competition. Indirect evidence of spatial segregation among sympatric carnivores in the Eurosiberian region has been documented in the form of divergent spatial distributions of the primary prey of each predator (Caravalho & Gomes 2004). Although our Kruskal-Wallis test of the pooled data failed to detect any relationship among the three predators in spatial patterns of predation on moose calves, the pairwise comparisons supported the hypothesis of spatial segregation among predator species inhabiting the study site.

Although our analyses indicate independent space use by black bears, brown bears and gray wolves at the spatial scale we investigated, there remains a possibility that these predators also partition space within finer-scale habitat classes that we were unable to identify. Experiments in old-field arthropod systems indicate, for example, fine-scale habitat partitioning among three sympatric spiders (e.g. salticid *Phidippus rimator*, pisaurid *Pisaurina mira* and lycosid *Hogna rabida*) within different portions of the herbaceous canopy (Schmitz & Blake-Suttle 2001, Sokol-Hessner & Schmitz 2002). Observations of spider predation in old-field communities indicate, for example, not only a size-specific predator preference for grasshopper prey, but also a time-specific period of foraging activity (Schmitz & Blake-Suttle 2001, Ovadia & Schmitz 2002). Moreover, bobcats *Lynx rufus* and coyotes *Canis latrans* coexisting in California do not show spatial segregation at the landscape scale, but they do display differential habitat use at the home-range scale, suggesting avoidance (Neale & Sacks 2001).

Similarly, although our analyses indicate a lack of temporal segregation between black bears and brown bears, they might actually segregate behaviourally or at a temporal scale not studied here. For example, gray wolves prey upon moose calves during a longer period throughout the summer season and are probably capable of subduing larger, more mobile moose more regularly than are bears. Ambush-style black bears and brown bears may experience greater temporal constraints when preying on moose calves because their efficacy diminishes as moose calves grow in size and mature in age (White et al. 2001). Additionally, it is possible that bears and wolves in our study separate at a finer temporal scale than investigated. In remote locations in Canada, research indicates that black bears are primarily diurnal foragers, relying on daylight to seek prey items (Lariviere et al. 1994). Recent publications support the diurnal and nocturnal foraging efficiency of brown bears (Klinka & Reimchen 2002) which may explain the coexistence of the two bear species in our system. Similarly, a study of gray wolves in Poland maintains that they time their activity to the crepuscular hours when hunting efficiency is high, which would enhance temporal separation of the three predator species where they coexist (Theuerkauf et al. 2003).

Studies suggesting differential foraging habitat selection between coursing and ambush predators have been observed in a large-scale system involving sympatric wolves and mountain lions *Felis concolor* (Husseman et al. 2003). Husseman et al. (2003) suggested that coursing predators often kill prey in unpreferred habitat, resulting at the termination of a chase. Conversely, the same work proposes ambush predators most often kill prey in their preferred microhabitats (e.g. dense cover), suggesting that kill-sites by ambush predators are more suitable descriptions of preferential hunting habitat than those of their coursing counterparts. Thus, one must be cautious when interpreting mortality site habitats of moose calves attributed to gray wolves, as they may also represent the location where prey were consumed or cached as opposed to the exact predation site. Notably, however, in numerous instances during our investigation, we were able to trace the path of the predator from the initial point of contact to the site of the carcass using sign such as blood trails, matted vegetation, broken branches, bone fragments and prey hair, so we are fairly confident that our locations reflect kill sites. Moreover, evidence from other studies suggests that gray wolves may consume prey at the kill site until satiated, and hence may be more likely to remain at the kill site in defense of the prey item as opposed to caching (Vander Wall 1990). It is unlikely that bears cached their prey at a site away from the actual kill site because few studies have documented bear caching behaviour (Elgmork 1982). Furthermore, the likelihood of caching behaviour in both bears and wolves is slight as moose calves are small during the 6-week period during which we collected data each year, and hence probably were consumed in entirety.

Finally, the different hunting styles of wolves and bears may also contribute to the spatial separation between them as documented here. The coursing style of hunting by gray wolves may force moose calves into refuge habitats, specifically forest cover. Contrastingly, ambush-style predators, such as the two bear species included in our study, may stalk their prey in more diverse habitats, as the results from our study suggest. While dietary segregation appears to be a common strategy among coexisting species occupying the same trophic level (Neale & Sacks 2001, Woodward & Hildrew 2002, Caravalho & Gomes 2004, Jacomo et al. 2004), such a strategy is not an option where the number of food choices is limited. Our results appear to provide evidence in support of the hypothesis that predator species with overlapping distributions and food requirements must partition time or space in order to make use of a shared resource.

Acknowledgements - we would like to thank collaborators in the Alaska Department of Fish and Game, specifically M. Szepanski and H. Reynolds for assistance with capture and study design. We also thank the skilled helicopter and fixed-wing pilots R. Swisher and T. Cambier for capture and mortality retrieval in the field. Many thanks to McGrath residents and friends: R. & J. Boudreau, M. & D. Fleagle, L. Egrass, T. Machacek and N. Botteri for their field assistance and support. Additional thanks to D. Diefenbach, A. Taylor, R. Yahner and two anonymous referees for constructive comments. This research was supported in part by a grant to E. Post from the U.S. National Science Foundation.

References

Ballard, W.B., Miller, S.D. & Whitman, J.S. 1990: Brown and black bear predation on moose in southcentral Alaska. - Alces 26: 1-8.

Ballard, W.B., Spraker, T.H. & Taylor, K.P. 1981: Causes of neonatal moose calf mortality in south central Alaska. - Journal of Wildlife Management 45: 335-342.

Ballard, W.B. & van Ballenberghe, V. 1997: Predator/prey relationship. - In: Franzmann, A.W. & Schwartz, C.C. (Eds.); Ecology and management of the North American moose. Smithsonian Institution Press, Washington, D.C., USA, pp. 247-274.

Boudreau, T. 2001: Wildlife Research Study (1.58) Plan: Factors limiting moose at low density in Unit 19D east, and response of moose to wolf control and increased harvest of bears. - Alaska Department of Fish and Game, Juneau, AK, USA, 9 pp.

Brown, J.K. & Davidson, D.W. 1977: Competition between seed-eating rodents and ants in desert ecosystems. - Science 196: 880-882.

Burkholder, B.L. 1959: Movements and behavior of a wolf pack in Alaska. - Journal of Wildlife Management 23: 1-11.

Caravalho, J.C. & Gomes, P. 2004: Feeding resource partitioning among four sympatric carnivores in the Peneda-Geres National Park (Portugal). - Journal of Zoology 263: 275-283.

Cody, M.L. 1968: On the methods of resource division in grassland bird communities. - American Naturalist 102: 107-148.

Davidson, D.W. 1978: Size variability in the worker caste of a social insect (Veromessor pergandei Mayr) as a function of the competitive environment. - American Naturalist 112: 523-532.

Elgmork, K. 1982: Caching behavior of brown bears (Ursus arctos). - Journal of Mammalogy 63: 607-612.

Emmons, L.H. 1980: Ecology and resource partitioning among nine species of African rain forest squirrels. - Ecological Monographs 50: 31-54.

Gasaway, W.C., Boertje, R.D., Grangaard, D.V., Kelleyhouse, D.G., Stephenson, S.O. & Larsen, D.G. 1992: The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. - Wildlife Monographs 120: 1-59.

Green, G.I., Mattson, D.J. & Peek, J.M. 1997: Spring feeding on ungulate carcasses by grizzly bears in Yellowstone National Park. - Journal of Wildlife Management 61: 1040-1055.

Hastie, T.J. & Tibsharani, R.J. 1990: Generalized additive models. - Chapman & Hall, New York, 352 pp.

Hatler, D.F. 1972: Food habits of black bears in interior Alaska. - The Canadian Field Naturalist 86: 17-31.

Husseman, J.S., Murray, D.L., Power, G., Mack, C., Wenger, C.R. & Quigley, H. 2003: Assessing differential prey selection patterns between two sympatric large carnivores. - Oikos 101: 591-601.

Hutchinson, G.E. 1957: Concluding remarks. - Cold Springs Harbor Symposia on Quantatitive Biology 22: 415-427.

Jacomo, A.T.D.A., Silveira, L. & Diniz-Filho, J.A.F. 2004: Niche separation between the maned wolf (Chrysocyon brachyurus), the crab-eating fox (Dusicyon thous) and the hoary fox (Dusicyon vetulus) in central Brazil. - Journal of Zoology 262: 99-106.

Klinka, D.R. & Reimchen, T.E. 2002: Nocturnal and diurnal foraging behaviour of brown bears (Ursus arctos) on a salmon stream in coastal British Columbia. - Canadian Journal of Zoology 80: 1317-1322.

Lariviere, S., Huot, J. & Samson, C. 1994: Daily activity patterns of female black bears in a northern mixed-forest environment. - Journal of Mammalogy 75: 613-620.

MacArthur, R. 1958: Population ecology of some warblers of Northeastern coniferous forests. - Ecology 39: 599-619.

McIntosh, A.R. & Townshend, C.R. 1994: Interpopulation variation in mayfly antipredator tactics: Differential effects of contrasting predatory fish. - Ecology 75: 2078-2090.

McIntosh, A.R. & Townshend, C.R. 1996: Interactions between fish, grazing invertebrates and algae in a New Zealand stream: A trophic cascade mediated by fish-induced changes to grazer behaviour? - Oecologia 108: 174-181.

McKenzie, N.L. & Rolfe, J.K. 1986: Structure of bat guilds in the Kimberley Mangroves, Australia. - Journal of Animal Ecology 55: 401-420.

McPeek, M.A. 1998: The consequences of changing the top predator in a food web: A comparative experimental approach. - Ecological Monographs 68: 1-23.

Mech, L.D., Adams, L.G., Meier, T.J., Burch, J.W. & Dale, B.W. 1998: The wolves of Denali. - University of Minnesota Press, Minneapolis, 227 pp.

Menge, B.A. & Sutherland, J.P. 1987: Community regulation: variation in disturbance, competition, and predation in relation to gradients of environmental stress and recruitment. - American Naturalist 130: 730-757.

Neale, J.C.C. & Sacks, B.N. 2001: Resource utilization and interspecific relations of sympatric bobcats and coyotes. - Oikos 94: 236-249.

Oksanen, L., Fretwell, S.D., Arruda, J. & Niemela, P. 1981: Exploitation ecosystems in gradients of productivity. - American Naturalist 118: 240-262.

Osborne, T.E., Paragi, T.F., Bodkin, J.L., Loranger, A.J. & Johnson, W.N. 1991: Extent, cause, and timing of moose calf mortality in western interior Alaska. - Alces 27: 24-30.

Ovadia, O. & Schmitz, O.J. 2002: Linking individuals with ecosystems: Experimentally identifying the relevant organizational scale for predicting trophic abundances. - Proceedings of the National Academy of Science 99: 12927-12931.

Peckarsky, B.L. & McIntosh, A.R. 1998: Fitness and community consequences of avoiding multiple predators. - Oecologia 113: 565-576.

Persson, L. 1999: Trophic cascades: Abiding heterogeneity and the trophic level concept at the end of the road. - Oikos 85: 385-397.

Pyke, G.H. 1982: Local geographic distributions of bumblebees near Crested Butte, Colorado: Competition and community structure. - Ecology 63: 555-573.

Rosenzweig, M.L. 1966: Community structure in sympatric Carnivora. - Journal of Mammalogy 47: 602-612.

Schmitz, O.J. 1998: Direct and indirect effects of predation and predation risk in old field interaction webs. - American Naturalist 151: 327-342.

Schmitz, O.J. & Blake-Suttle, K. 2001: Effects of top predator species on direct and indirect interactions in a food web. - Ecology 82: 2072-2081.

Schmitz, O.J. & Sokol-Hessner, L. 2002: Linearity in the aggregate effects of multiple predators in a food web. - Ecology Letters 5: 168-172.

Schoener, T.W. 1974: Resource partitioning in ecological communities. - Science 185: 27-39.

Siegel, S. & Castellan, N.J. Jr. 1988: Nonparametric statistics for the behavioral sciences, 2nd edition. - McGraw-Hill International editions, New York, NY, USA, 399 pp.

Sokol-Hessner, L. & Schmitz, O.J. 2002: Aggregate effects of multiple predator species on a shared prey. - Ecology 83: 2367-2372.

Soluk, D.A. 1993: Multiple predator-effects: Predicting combined functional response of stream fish and invertebrate predators. - Ecology 74: 219-225.

Soluk, D.A. & Collins, N.C. 1988: Balancing risks? Responses and non-responses of mayfly larvae to fish and stonefly predators. - Oecologia 77: 370-374.

Soluk, D.A. & Richardson, J.S. 1997: The role of stoneflies in enhancing growth of trout: A test of the importance of predator-predator facilitation within a stream community. - Oikos 80: 214-219.

Theuerkauf, J., Jedrzejewski, W., Schmidt, K., Okarma, H., Ruczynski, I., Sniezko, S. & Gila, R. 2003: Daily patterns and duration of wolf activity in the Bialowieza forest, Poland. - Journal of Mammalogy 84: 243-253.

Vander Wall, S.B. 1990: Food hoarding in animals. - University of Chicago Press, Chicago, IL, USA, 445 pp.

Venables, W.N. & Ripley, B.D. 1999: Modern applied statistics with S-PLUS. - Springer-Verlag, New York, 520 pp.

White, K.S., Testa, J.W. & Berger, J. 2001: Behavioral and ecological effects of differential predation pressure on moose in Alaska. - Journal of Mammalogy 82: 422-429.

Wilton, M.L. 1983: Black bear predation on young cervids: A summary. - Alces 19: 136-148.

Woodward, G. & Hildrew, A.G. 2002: Body-size determinants of niche overlap and intraguild predation within a complex food web. - Journal of Animal Ecology 71: 1063-1074.

Young, D.D. Jr. & McCabe, T.R. 1997: Grizzly bear predation rates on caribou calves in Northeastern Alaska. - Journal of Wildlife Management 61: 1056-1066.