Wolf-avoidance strategies of moose

Philip W. Stephens and Rolf O. Peterson

Two possible anti-predator strategies of prey were suggested by the distribution of
moose at Isle Royale, a 544 km² island with numerous offshore islets. Aerial surveys
in winter indicated that moose density on small islets (<1.5 km²) averaged 415%
greater than on the main island, with about 11% of the calf population existing on the
small islets which comprise less than 2% of the total land area. On small islets and
shorelines, protection from wolves (in the form of escape terrain) is provided by
nearby water in summer and coniferous cover in winter. Calves on islands appear to
have a higher survival rate. In summer, cow moose with calves were seen more
commonly in camps with human activity (and no wolves) than away from camps,
suggesting that people provided a refuge from wolf predation for this unhunted
moose population. These subtle patterns of habitat selection by moose are attributed
to the intensive natural selection pressure of wolf predation.

P. W. Stephens and R. O. Peterson (correspondence), Dept of Biological Sciences,
Michigan Technological University, Houghton, MI 49931, USA.

1. Introduction

Coevolution of predators and prey has produced an
impressive array of morphological and behavioral
characteristics that enhance survival and reproductive
success (Bertram 1978, Harvey and Greenwood 1978,
Pianka 1978, Gosling and Petrie 1981). Coloration,
specialized anatomy, social organization, patterns of
habitat selection, and defensive behaviors of large
mammalian prey have thus been shaped to a considera-
ble degree by natural selection in the form of predation
by large carnivores (e.g. Geist 1971, Bergerud 1974,
Jarman 1974, Jarman and Jarman 1979, Sinclair and
Griffiths 1979). However, behavioral adaptations of
prey are "often very subtle and exceedingly complex"
(Eisenberg 1981: 420), and our ability to sort out such
complexity has been limited by lack of detailed knowl-
edge of prey life history and behavior, the low fre-
quency at which predation is actually observed, and, in
the case of large carnivores, reduction or elimination of
key species even in remnant natural habitats. Thus,
while the white-tailed deer *Odocoileus virginianus*
Zimm. has recieved an enormous amount of scientific

attention in North America, possible anti-predator
strategies associated with patterns of social organization
and habitat selection have only recently been postulated
(Hirth 1977, Mech 1977, Nelson and Mech 1981).

In Isle Royale National Park, Michigan, unhunted
wolf *Canis lupus* L. and moose *Alces alces* L. popula-
tions have co-existed since the late 1940's (Mech 1966).
During continuing studies of these species at Isle Royale
in the 1970's, two anti-predator strategies were sug-
gested by the distribution of moose, especially cows
with calves, relative to small offshore islets and human
camps.

2. Study area

Lying in Lake Superior, 24 km south of the Canadian
mainland, Isle Royale (48°N, 89°W) consists of a 544
km², 72 km long island plus several islets which range up
to 1.4 km² in size. While 27 islets measure at least 10 ha,
all islets comprise less than two percent of Isle Royale's
area. Two upland vegetation types exist on the main
island: a boreal forest of white spruce *Picea glauca* –
balsam fir *Abies balsamea* around the perifery, and a

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hardwood forest of sugar maple *Acer saccharum* – yellow birch *Betula alleghaniensis* in the southwestern central uplands (Linn 1957). Islets and Lake Superior shorelines comprise the boreal type.

Peterson (1977) described general winter conditions on the island. Midwinter snow depth is normally 60 cm in open areas, about 17 cm more than under heavy conifer (Peterson and Allen 1974). Extremes occurred during surveys in 1972 (Peterson 1977) and 1979, when maximum snow depths exceeded 100 cm, and in 1981, when snowcover was relatively thin (maximum: 59 cm) and patchy. Snow especially impedes moose movement if greater than 70 cm deep (Coady 1974). Substantial ice typically exists between islets and the main island from late December until late February.

The main island has no roads but humans have access to all parts of the island via an extensive 278-km trail system. People are virtually absent from November through April, while from June through August human activity is concentrated at 32 camps that have at least one permanent building. Three of the largest (Rock Harbor, Mott Island, and Windigo) accomodate up to several hundred people; few of the others have more than 15–30 at a time.

3. Methods

In January and February of 1972, 1974, 1979–81, stratified samples of plots were counted from light aircraft to estimate moose numbers on the main island, while complete counts were made of moose on major surrounding islets (Stephens and Peterson, in preparation). After leaf-fall in late October, 1972–1981, sex and age composition counts were conducted from light aircraft (Peterson 1977).

Annual counts of relative summer moose abundance utilized the number of moose observed per distance

hiked by researchers as they searched for wolf packs and moose carcasses from 1970 to 1980. From early June through late August research teams hiked an average of 960 km yr^{-1}, of which a third was off-trail. Routes were well-distributed throughout the island, traversing all major habitats, including swamps, bogs, ridges, forests, stream and pond banks, lake shores, and human camps.

Only land-based observations of moose initially seen from outside of buildings were included in the summer ground count. Each observation was classed as an unlikely, possible or probable repeat of moose previously counted, based on its location, sex, age, and other distinguishing characteristics, such as bell shape and size, hock sores, and abnormal growths. Probable repeats were excluded from the count.

Sex, age, time, and general location were noted for all moose observations; hiking routes were drawn on 1:62500 topographic maps. During 1976–1980, observation locations were also plotted on similar maps, and relative visibility (poor, moderate, or good) and observation duration were recorded with other variables on a prepared form.

4. Results

Two to eight percent of the total winter moose population was on islets (Tab. 1). Winter moose densities on islets averaged 7.1 moose km^{-2}, 415% greater (range 162–700%) than on the main island (Paired t-test, t = 4.04, P < 0.01). Densities on islets tended to be greater than in localized heavy-use areas within 2 km of shorelines (7 vs. 5 moose km^{-2}; Paired t-test, t = 1.46, P = 0.22). In addition, the population on islets possessed a greater proportion of calves than did the sample from the main island (20 vs. 11%; Paired t-test, t = 4.06, P < 0.05). In 1981, when most of the islet areas were examined, 8.3% of the total estimated moose population was found on islets. Similarly, during the October 1979

Tab. 1. Comparisons between winter moose populations on the main island, in stratum 3 (i.e., areas of greatest moose concentrations on the main island), and on islets. All populations figures were derived from quadrat counts and corrected for sightability. Islets comprised less than 2% of the area of the archipelago.

Parameter	Year					Overall
	1972	1974	1979	1980	1981	
Moose km^{-2}						
Main island	1.6	1.5	1.6	1.0	0.8	1.3
Stratum 3	4.6	5.5	6.2	5.5	3.3	5.0
Islets[a]	5.9	12.3	4.2	7.9	5.1	7.1
% calves						
Main island	[b]	11.6	7.8	12.2	14.4	11.3
(N of moose).............		(69)	(115)	(98)	(97)	(379)
Stratum 3	[b]	18.6	10.7	7.5	25.0	13.3
(N of moose).............		(51)	(56)	(67)	(36)	(210)
Islets[a]	[b]	20.4	14.3	25.9	17.6	20.2
(N of moose).............		(44)	(14)	(27)	(34)	(119)

a. The proportion of islet area counted was 48% in 1972, 1974, 1977 and 1980 and 87% in 1981.
b. Calves were not distinguishd from other.

Tab. 2. Proportions of calf and adult moose populations located on islets in midwinter, based on winter quadrat counts, autumn aerial composition counts, and wolf-kill data.

Parameter	Year			Overall
	1979	1980	1981	
Total winter population[a]	888	585	481	–
Proportion of calves from previous autumn count ..	0.09	0.11	0.07	–
Wolf-kills/day[b]	0.7	0.6	0.4	–
Winter calf population				
Total	64	52	24	140
On islets....................................	2	7	6	15
(%)	(3)	(14)	(25)	(11)
Winter adult population				
Total	824	533	457	1814
On islets....................................	12	20	28	60
(%)	(2)	(4)	(6)	(3)

a. In 1981, for example, if a midwinter population of 481 is assumed (based on the quadrant count), and a total of 36 moose killed by wolves from 1 Nov–31 Jan (if 0.4 moose/day were killed during that time: from Peterson, unpubl. data) an autumn population of 517 can be calculated. Furthermore, 7% of these moose were calves (based on the autumn aerial survey) and 12 calves were killed by wolves (if 34% of the moose killed were calves: from Peterson 1977: 151) during November–January, then the midwinter moose population would have consisted of 24 calves and 457 adults.
b. Kill period assumed to be 90 days between the autumn composition counts and the winter quadrat counts.

aerial count (the only year when islets were extensively sampled in autumn), the proportion of cows observed with calves was greater on islets than on the main island (62 vs. 21%, $\chi^2 = 4.75$; P < 0.05).

Distribution of moose twins in winter indicates further the significance of islets and shoreline habitats for calves. During aerial surveys in October (1959–1973) only 11% of cow moose with calves had twins (Peterson 1977). In winter, twin calves are exceedingly rare – only 8 sets were recorded among 3800 aerial moose observations at Isle Royale during 1973–82. Four sets of twins were observed on islets, and 3 of the remaining 4 sets were less than 100 m from the shoreline on the main island.

To asses the demographic significance of islets as a refuge from wolf predation, data on cow density on islets at the time for birth is desirable. Available data are only from winter, but these can be used to estimate the proportion of calves present on islets at least at this time of year; it is likely that cow/calf density on islets would be much greater near the time of birth.

The proportions of midwinter adult and calf populations which inhabited islets can be estimated for the years 1979–1981 if several assumptions are made (Tab. 2). We estimated that 11% and 3% of the calf and adult populations, respectively, existed on islets in winter during this three year period, though islets comprise less than 2% of the area of the archipelago.

Moose on islets were exposed to predation pressure in winter when ice bridges typically formed to all islets. We have examined remains of 98 moose that died on islets, primarily killed by wolves in winter. This sample comprised 44% calves, 27% adult (yearling and older) males, and 29% adult females. Moose dying on the main island (N = 1270) comprised 32% calves, 35%

adult males, and 33% adult females ($\chi^2 = 7.03$, P = 0.03).

During summers, we found that cows and calves were likewise not distributed randomly with respect to human camps; cows and calves appeared there more often than bulls. Cows comprised 84% (N = 100) of the yearling and adult moose in camps, and only 45% (N = 183) of the population located further than 1 km from these areas ($\chi^2 = 39.36$, P < 0.01; Fig. 1). Moreover, cows in camps were seen more commonly with calves than those more than 1 km away from camps (34 vs 23%; Wilcoxon paired T-test, T = 0.00, P = 0.05; Fig. 2). The proportion of moose observed within 1 km of human camps was essentially the same during 1976–1980 ($\chi^2 = 1.03$, P > 0.90).

The above differences were not due to observational bias. Relative visibility values assigned to calves were no different for those in camps than for those in the back-country ($\chi^2 = 0.01$, P > 0.90). Furthermore, we did not watch cows in camps much longer than those in the backcountry (median: 5.0 vs. 2.5 min.; Mann-Whitney; U = 5987.0, P = 0.05), nor did we observe those with calves for a longer time than those without calves (Mann-whitney, U = 8320.5, P = 0.35).

5. Discussion

5.1. Distribution relative to islets

We propose that the preference shown by Isle Royale moose for islets is largely attributable to the survival advantage that accrues for very young calves. We suggest further that the well known preference of moose for conifer in winter may reflect anti-predator behavior, not simply moose selection of habitats with a moderate
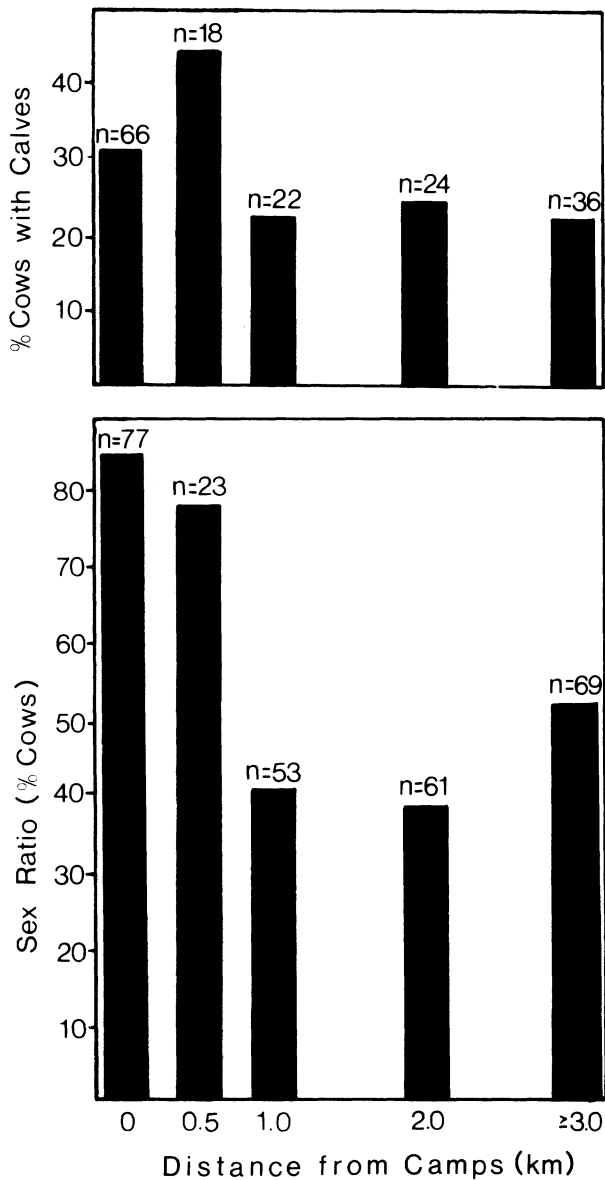
Fig. 1. Distribution of cows relative to bulls, and of cows with calves to cows without calves, as a function of distance from human camps.

winter microclimate and less snow, as commonly suggested (Van Ballenberghe and Peek 1971, Phillips et al. 1973, Coady 1974, Peterson and Allen 1974, Peek et al. 1976, Peterson 1977). Peterson (1977) suggested that conifers may be preferred by cows with calves because of the protection provided from wolf attack. It is clear from Mech's (1966: 174–189) observations that moose commonly seek conifer cover and windfalls during encounters with wolves. One of us (ROP) has often seen moose use structural features of the habitat to reduce exposure to wolf attack. Winter microclimate appears similar on both islets and the adjacent shoreline

of the main island. Therefore microclimate differences do not adequately explain the heavier use of islets by moose.

Moose have coevolved with capable predators; wolves prey on moose year-round (Mech 1966, Peterson 1977) and bears (*Ursus arctos* and *Ursus americanus*) kill primarily calf moose less than 2 months old (Franzmann et al. 1980, Ballard et al. 1981). Mortality rates for calves are highest early in life and predators may claim the majority of calves at this time (Franzmann et al. 1980, Ballard et al. 1981). Strong selection pressure thus exists for behavior that reduces the frequency of predator encounters for young calves. Moose inhabiting small islands probably experience reduced contacts with predators and also are able to escape into nearby water during actual encounters. Water provides a highly effective defense for moose that is widely used during moose-wolf encounters (Peterson, unpubl. data).

Peterson (1955: 63–64) and Edwards (1978: 50) have commented on the tendency of cows to seek islands and insular areas immediately prior to birthing. The disproportionately great number of cows with calves on islets during our 1979 October aerial count, as well as during the winter, suggests an abnormally high year-round usage of islets.

Island occupancy is most advantageous early in the life of a calf (first summer), when there ar no ice bridges to the mainland that facilitate wolf travel, and when calves participate only minimally in their own defense. It is not clear that island occupancy is similarly advantageous in winter, at least at Isle Royale. Islets there are distributed around the periphery of the main island, along primary wolf travel routes, and many islets harboring moose are repeatedly visited by wolves in the course of a single winter. The high proportion of calves among moose dying of wolf predation on small islands in winter is evidence of the abundance and vulnerability of calves on islets during that season. The proportion of both calf and adult moose on islets increased as wolf predation declined (Tab. 2), suggesting that predation pressure influenced the proportion of moose using islets, particularly cows with calves.

Why then, do some cows with calves remain on islets for much of the year? First, it may be quite advantageous for moose to be thoroughly familiar with local escape terrain (Pulliainen 1974), especially if spatial orientation of cow and calf relative to protective cover is critical to survival. Secondly, the moose we observed on islets in winter are probably only a remnant of the cow/calf pairs present at the time of birth. Calf concentrations on islets in winter may result from strong selection for islet occupancy in summer and continued preference in winter for familiar sites that provide maximal protection against wolves whenever they appear.

Calves comprise a high proportion of the kills made by wolves on small islets, and the sex ratio of the other moose killed there was about equal. This suggests that

calves are indeed vulnerable in these sites in winter and that cows do not select islets in winter to the point where males are excluded. These data, together with the inverse relationship between predation pressure and islet occupancy in winter, suggest that the winter preponderance of calf moose on islets results from a higher calf survival rate there in summer and fall.

How significant are the islets to the Isle Royale moose population as a whole? We estimated that 11% (Tab. 2) of the midwinter calf population was found on islets, and presented data which suggested that survival of calves on islets was higher than on the main island. Very likely the calves found on islets in winter were also born there, since the selective advantage of inhabiting islets would be greatest for very young calves. It is also likely that many calves born on islets are moved back to the mainland before winter; the islets on which Edwards (1978) found cows and calves in summer are usually not used by moose in winter. We conclude that the proportion of calves born on islands is greater than 11% and is probably of demographic significance.

5.2. Distribution relative to human settlements

On Isle Royale, cows with calves comprise a larger proportion of the population around human camps than bulls or cows without calves. Wolves rarely traveled within 1 km of these settlements during the summer months. We propose that human camps provided a refuge from wolf predation for cows with calves. Geist (1980) has suggested that deer (*Odocoileus hemionus*) also find refuge from predators around human settlements. Other authors have suggested that, in some circumstances, moose that are hunted tend to avoid areas of human concentration (Hancock 1976, Rolley and Keith 1980).

The disproportionate number of observations of cows with calves in camps is attributed to an actual difference in moose distribution by sex and age, rather than observational bias. A reasonable explanation is that the use of camp areas by cows benefited calves. Since visibility values for calves in camps were no different from those in the backcountry it appears that any habituation to humans which they or their mothers might have acquired in camps did not affect their visibility. Furthermore, the slight difference in median observation times for camp and backcountry cows seemed too small to substantially increase the probability of sighting calves that might have been present.

5.3. Conclusion

We found that Isle Royale moose occurred at higher density on offshore islets and a higher proportion of calves existed both on islets and near camps. Peterson (1977) earlier found evidence that calves may be more common along the shoreline of Isle Royale. While a more favorable winter microclimate may exist on islets

and along shorelines, this would not explain the preponderance of cows and calves relative to camps in summer, nor the winter concentrations of moose on islets. We suggest that predator avoidance is the primary factor responsible for the observed distribution patterns relative to both islets and camps. Cow moose may deliberately choose islands and camps as relatively predator-free birth sites, but calf abundance on islets in winter seems to result largely from higher early survival of calves. In any case, coevolution of wolves and moose has apparently resulted in subtle patterns of habitat selection which confer a survival advantage that seems especially clear for moose calves, the age group most vulnerable to wolves.

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