Wolf homesite attendance patterns

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Abstract: Adult gray wolves, *Canis lupus* L., 1758, frequent den and rendezvous sites (homesites) during summer to bring food to pups and to ensure security of the pups. We monitored homesite attendance of several adult wolves from a single pack in Isle Royale National Park, Michigan, for 6 years. Pack size, number of pups, and prey density varied during the period of monitoring. Given the effect of prey density on wolf behavior, we predicted that wolf homesite attendance patterns would vary with prey density. We also examined the effects of varying pack size, social status, and number of pups on homesite attendance. Contrary to our expectations, prey density did not appear to be a significant predictor of homesite attendance statistics such as hours per day at the homesite or length of absence from the homesite. Furthermore, when prey density and social status remained the same, homesite attendance (hours/day) of individual wolves monitored for multiple years varied substantially. Our results show homesite attendance to be highly variable and not well predicted by prey density.

Résumé : Les loups, *Canis lupus* L., 1758, adultes fréquentent leur tanière ainsi que des points de rendez-vous au cours de l'été pour apporter de la nourriture aux louveteaux et pour en assurer la sécurité. Nous avons étudié le patron d'utilisation de ces sites par plusieurs loups d'une même meute au parc national de l'Isle Royale, le Michigan, pendant 6 années. La taille de la meute, le nombre de louveteaux et la densité des proies ont varié au cours de notre étude. Étant donné l'effet connu de la densité des proies sur le comportement des loups, nous avons posé l'hypothèse selon laquelle la présence des loups à leur tanière et aux points de rendez-vous varie avec la densité des proies. Nous avons aussi étudié les effets de la taille des meutes, du statut social et du nombre de louveteaux sur la fréquentation de la tanière et des points de rendez-vous. Contrairement à notre prédiction, la densité des proies ne permet pas de prédire avec précision des statistiques telles que le nombre d'heures de présence par jour ou la durée de l'absence à la tanière et aux points de rendez-vous. De plus, même si les densités de proies et les statuts sociaux demeurent les mêmes, le patron de fréquentation de la tanière et des points de rendez-vous varie considérablement chez les individus suivis pendant plusieurs années. Nos résultats montrent que la présence des loups à leur tanière et aux points de rendez-vous est très variable et ne peut être facilement prédite à partir de la densité des proies.

[Traduit par la Rédaction]

Introduction

Reproductive success of gray wolves, *Canis lupus* (L., 1758), is partly determined by survival rates of pups, which can vary greatly during the first 6 months of life (0.48–0.89, Ballard et al. 1987; Fuller 1989). Factors that contribute to pup survival include availability of food and protection from other large predators, both of which are provided by parents and other pack members at homesites in spring and summer. Homesites include the initial den plus a series of rendezvous sites where the pups are left while older wolves forage (Joslin 1967). Although both breeding and nonbreeding adults deter potential predators at homesites (Murie 1944; Theberge and Pimlott 1969; Peterson et al. 1984; Veitch et al. 1993), the effectiveness of threat deterrence by nonbreeders has been questioned (Harrington and Mech 1982; Harrington et al. 1983). In addition, inexperienced hunters, such as year-

lings, may attend homesites to acquire food for themselves from other foraging wolves (Harrington et al. 1983).

As breeding status varies, homesite attendance is also thought to vary. Yearling and breeding males attend homesites less frequently, whereas yearling and breeding females attend homesites more frequently (Harrington and Mech 1982; Ballard et al. 1991) and travel the least (Jędrzejewski et al. 2001). Breeding females had the highest attendance rates in large packs (Ballard et al. 1991). Harrington and Mech (1982) believed that wolves with low attendance rates were foraging, while wolves with high attendance rates benefited from food delivered by foraging wolves or knowledge of foraging opportunities such as locations of prey carcasses.

The relationship between adult attendance and pup survival is uncertain, as most previous studies of homesite attendance were based on irregular periods of monitoring, visual observation, and (or) small sample sizes gathered during a single year of monitoring (e.g., Theberge and Pimlott 1969; Harrington and Mech 1982; Ballard et al. 1987). One extensive study found large wolf packs to have higher pup survival, provided that prey were abundant (Harrington et al. 1983). However, because these findings were not based on direct homesite monitoring, the contribution of individual wolves to pup survival is uncertain.

We monitored homesite attendance of wolves in the same pack during two periods of differing prey density. Because wolves travel more when prey abundance is low (Jędrzejewski

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Table 1. Wolf (*Canis lupus*) and moose (*Alces alces*) population dynamics and wolf homesite attendance patterns in Isle Royale National Park (ISRO), Michigan.

Wolf ID, summer of monitoring	Moose density (moose/km^2)		East pack size in Feb.		No. of pups observed during summer	No. of pups that survived to 9 months	Daily attendance rate (h/day)	Median duration of absence (h)
	ISRO	East pack territory	Total	Pups				
F1, 1991	2.96	2.50	4	0	2 or 3	2	9	24.8
M1, 1991	2.96	2.50	4	0	2 or 3	2	11.5	11.5
F1, 1992	3.48	2.16	5	2	N/A	2	2	12.3
M1, 1992	3.48	2.16	5	2	N/A	2	2.3	8.5
F1, 1993	3.28	2.80	7	2	N/A	4	4	7
M2, 1993	3.28	2.80	7	2	N/A	4	6.6	4.3
M2, 1997	1.30	1.60	6	2	5	2	8.5	8.5
F2, 1998	1.39	N/A	5	2	6	6	12	5.3
M3, 1998	1.39	N/A	5	2	6	6	3	12
F2, 1999	1.57	N/A	10	6	3	2	6	16.5

Note: Moose density estimates are from the winter following homesite monitoring in order to include the number of calves available during summer. Pack size and number of pups (9 months of age) were determined 3 months prior to summer homesite monitoring. N/A, data not available.

et al. 2001), we expected attendance to fluctuate with varying prey density. We anticipated that variation in homesite attendance would affect the number of pups surviving to 9 months of age. Finally, we assessed how homesite attendance varied with respect to pack size, time of day, and Julian day (i.e., age of pups).

Materials and methods

Study area

Isle Royale National Park (ISRO), Michigan, is an island in the northwest portion of Lake Superior (47°55′N, 89°W) with an area of 544 km^2. The island is characterized by a series of bedrock ridges running the length of the island. The northeast portion of the island, site of this study, supports spruce (*Picea glauca* (Moench) Voss and *Picea mariana* (P. Mill.) B.S.P.), white birch (*Betula papyrifera* Marsh.), aspen (*Populus tremuloides* Michx. and *Populus grandidentata* Michx.), and balsam fir (*Abies balsamea* (L.) P. Mill.). From May until August, sunrise occurs between 0600 and 0700 and sunset occurs between 2100 and 2200. The study area and population are further described by Peterson (1977) and Peterson et al. (1998).

During summer, wolf diet on ISRO comprises primarily moose (*Alces alces* (L., 1758)) (85%) and smaller amounts of beaver (*Castor canadensis* Kuhl, 1820) (14%) and snowshoe hare (*Lepus americanus* Erxleben, 1777) (Thurber and Peterson 1993). Humans are not permitted to hunt wildlife on ISRO. Given the lack of other large predators or prey, the wolves and moose of ISRO represent, essentially, a single-predator, single-prey system. During our observation periods, moose density ranged from 3.0 to 3.3 moose/km^2 between 1991 and 1993 and from 1.3 to 1.6 moose/km^2 between 1997 and 1999 (Peterson and Vucetich 2001). Also, between winter 1992 and winter 2000, beaver density declined steadily from 24.3 colonies/100 km^2 to less than 4 colonies/100 km^2 (Peterson and Vucetich 2001).

East pack demography

We monitored summer homesite attendance of the east pack of ISRO. During the two periods of observation, 1991–

1993 and 1997–1999, the east pack was one of three territorial packs occupying the northeast third of ISRO. As part of an ongoing study of predator–prey relationships, wolves (including the east pack) and moose on ISRO have been extensively monitored during winter (Peterson et al. 1998). Relevant findings of previous research (Peterson et al. 1998; Peterson and Vucetich 2001) are presented below and in Table 1.

The size of the east pack varied between 4 and 10 wolves. Pack size minus young of the year varied from 3 to 5 and was similar during each sampling period (1991–1993, mean = 4; 1997–1999, mean = 3.7). Annual estimates of pack size and reproductive status were based on aerial surveys conducted 4 months prior to our annual homesite observations. Reproductive status of adult radio-collared wolves was assigned based on observation of vaginal bleeding during estrous, courtship behavior, and dominance behavior directed toward other pack members.

The number of pups surviving to 9 months of age was not highly variable. In most years of this study (four of six), two pups survived to 9 months. Four pups survived to 9 months in 1993, and six pups survived to 9 months in 1998. When pups could be counted at the summer homesite, they numbered between three and six. Within each summer, the east pack remained at the same homesite for 8–12 weeks.

The size of the east pack territory in winter averaged 245 km^2 between 1991 and 1993 and 221 km^2 between 1997 and 1999. These estimates include areas of frozen inland lakes and bays of Lake Superior. Within the east pack territory, moose density varied between 1.6 (winter 1997) and 2.8 moose/km^2 (winter 1993).

Field methods

Wolves were captured and fitted with radio collars using techniques described by Thurber and Peterson (1993) and approved by the Michigan Technological University Institutional Animal Care and Use Committee. Radio-collared wolves were monitored at homesites between May and August using an automatic monitoring station comprising a radio receiver (models TR-1 and TDP-2, Telonics Inc., Mesa,

Arizona), directional antenna, power source (solar panel or 12-V battery), and paper chart recorder (Gulton Industries Inc., Manchester, New Hampshire). Individual wolf frequencies were monitored for periods of 15 min, two times per hour, separated by a reference transmitter.

An east pack homesite was found by aerial telemetry in the spring of 1991 and a monitoring station was placed on a high ridge 2 km away. At this homesite, three members of the east pack were monitored in three summers between 1991 and 1993. Between 1997 and 1999, we monitored four members of the east pack from a recording station 200 m from a different homesite. One or two wolves were monitored each summer and in most years we were not able to determine whether the wolves used the homesite as an initial den site or a rendezvous site.

To complement the telemetry data, we monitored wolf activity at the homesite during the summers of 1997–1999 from a distance of 200 m using binoculars and spotting scopes. In each of the three summers, observations were made on 8–28 days for 3–16 h each day. From these observations, distributed throughout the summer, we noted the numbers of pups and adults, social interactions between the wolves, and presence of radio-collared wolves.
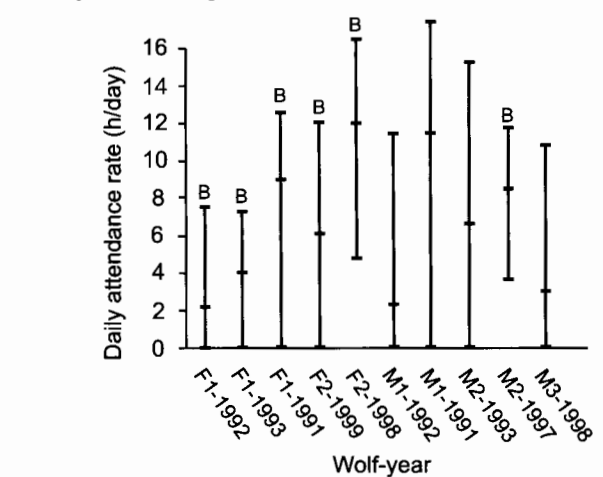
Analytical methods

We organized our data by first determining the presence or absence of radio-collared wolves for each 30-min interval of the day. Next, we calculated daily and monthly attendance rates by dividing the number of 30-min periods wolves were present by the total number of 30-min periods monitored. On two occasions (in May 1993 and July 1993), atmospheric interference and temporary receiver failure resulted in the loss of monitoring data for portions of consecutive days. Our analysis excludes these periods. For analyses involving multiple hypothesis tests, we used the Dunn–Šidák method for calculating experiment-wise error rates using a nominal error rate of 0.05 (Sokal and Rohlf 1995).

Daily patterns of homesite attendance

To test the hypothesis that daily attendance rate depends on reproductive status and sex, we considered a sampling unit to be one summer of monitoring of one wolf (hereafter, wolf-summer). We used the Mann–Whitney and Kruskal–Wallis tests to evaluate null hypotheses of equality of median attendance rates among wolf-summers with various reproductive status and sex (Sokal and Rohlf 1995). We also tested whether median daily attendance of wolf-summers was significantly correlated with pack size, prey density, or number of pups surviving to 9 months of age. Conversely, we tested whether duration of absence was correlated with pack size, prey density, or number of pups surviving to 9 months of age. Duration of absence differentiates between attendance patterns characterized by many short absences and those characterized by a few long absences and may reflect hunting effort (Harrington and Mech 1982).

To assess the hypothesis that homesite attendance varies according to time of day, we first determined the 4-h periods of maximum and minimum attendance. We then used the G test (Sokal and Rohlf 1995) to assess whether attendance during the maximum and minimum periods differed significantly. We also assessed whether daily attendance rates were

Fig. 1. Daily rates of attendance at the homesite for individual wolves (*Canis lupus*) monitored in summer at Isle Royale National Park, Michigan. For each individual, the median is represented, enclosed by the 25th and 75th percentiles of the distribution of daily attendance rates for the period 18 June to 22 July. B, breeding wolf.

significantly correlated with Julian day (which is directly related to age of the pups).

Correlation of attendance

We hypothesized that simultaneously monitored wolves would attend the homesite individually, rather than in groups, to maximize the time that any adult wolf is in attendance. To assess this hypothesis of negatively correlated attendance, we observed the proportions of 30-min periods with (*i*) both wolves *A* and *B* present, (*ii*) only wolf *A* present, (*iii*) only wolf *B* present, and (*iv*) neither wolf *A* nor wolf *B* present. We tested for significant differences among these proportions using the χ^2 test of independence (Sokal and Rohlf 1995).

Results

We monitored five wolves for a total of 93 weeks. These wolves included a breeding female monitored for three summers (F1), a breeding female (F2) and a nonbreeding male (M1) each monitored for two summers, and a nonbreeding male (M3) monitored for one summer. We also monitored another male (M2) that bred in one year but not in another. In total, we observed 10 wolf-summers of homesite attendance (Table 1). We compared daily attendance rate among wolf-summers over the period 18 June – 22 July, as this was the longest time during which 8 of 10 wolf-summers were represented.

Daily patterns of homesite attendance

The median daily attendance rate varied substantially among wolves (Fig. 1). For example, median daily attendance rates ranged from 2.0 (wolf F1 in 1992) to 12.0 h/day (wolf F2 in 1998). Attendance rates also varied substantially among years for each wolf monitored for more than one year. For example, the daily attendance rate of nonbreeding wolf M1 differed significantly between the two years in which he was monitored ($U = 724.5$, $P = 0.037$). The me-

Fig. 2. Diurnal attendance of radio-collared wolves at homesites in Isle Royale National Park for the period 18 June to 22 July. Each representation of attendance is labeled according to the wolf (F, female; M, male) and the year of observation. Shaded areas represent darkness between sunset and sunrise.
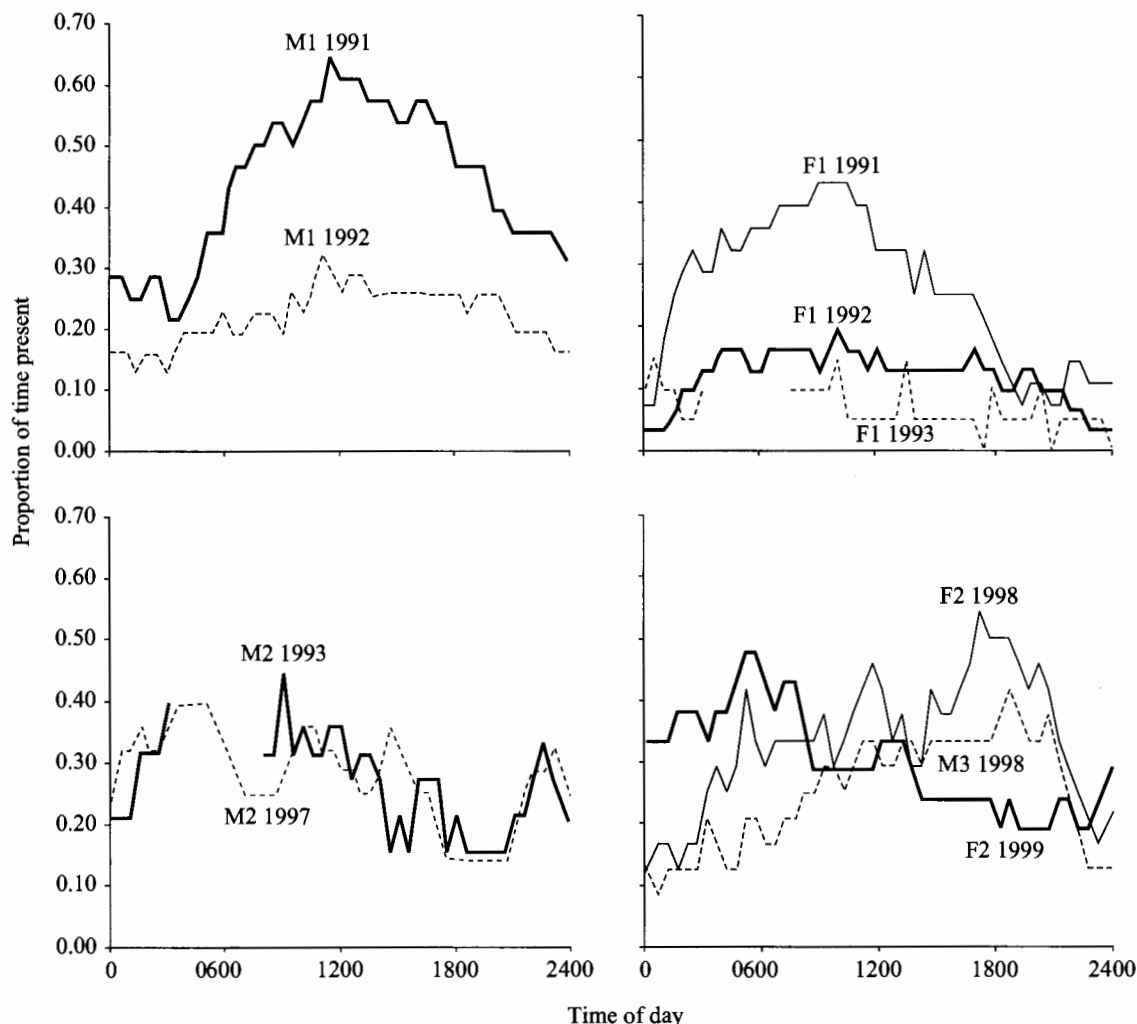
dian attendance rate of breeding female F1 was similar in 1992 (2 h/day) and 1993 (4 h/day), but much higher in 1991 (9 h/day). However, these attendance rates were highly variable within each of the three wolf-summers (18 June – 22 July), and the difference in median rates was not significant ($H = 2.71$, $P = 0.258$).

Median duration of absence for all monitored wolves was not correlated with the number of pups that survived to 9 months ($\rho = 0.45$, $P = 0.10$), pack size ($\rho = -0.11$, $P = 0.49$), or prey density ($\rho = 0.00$, $P = 0.93$). Moreover, significant associations with these variables were not detected when breeders and nonbreeders were considered separately. Despite our inability to detect significant associations, median durations of absence varied substantially among wolves. For example, the median duration of absence was 5.3 h for breeding female F2 in 1998 and 24.8 h for breeding female F1 in 1991 (Table 1).

Attendance rates did not appear to depend on reproductive status. For example, nonbreeding wolves had the two highest daily attendance rates as well as some of the lowest rates (Fig. 1). Low daily attendance characterized nonbreeding wolves (i.e., wolves M1 and M3) that dispersed from the

east pack shortly after these periods of monitoring. Another example of the potential dissociation between attendance rate and breeding status is male M2, whose change from a nonbreeder in 1993 to a breeder in 1997 was not associated with a change in attendance rate ($U = 303$, $P = 0.984$). Aside from these examples, rigorous quantification of the association between reproductive status and attendance rate was prevented by small sample sizes and variation in uncontrolled variables (e.g., sex).

The proportion of time a wolf was present during the 4-h period of highest attendance was significantly greater than that during the 4-h period of lowest attendance for all wolves except one ($P < 0.001$). The period of highest attendance tended to be during daylight hours for 8 of the 10 wolf-summers (Fig. 2), and the period of lowest attendance was at night for 7 of 10 wolf-summers (Fig. 2). However, the specific times of highest and lowest attendance varied among wolves (Fig. 2). For example, the attendance of breeding female F2 peaked at approximately 1800 in 1998, but the attendance of breeding female F1 peaked at approximately 1000 in 1991.

Daily attendance declined throughout the summer season

for 6 of 10 wolf-summers ($P < 0.01$; Fig. 3). Of these 6 wolf-summers, 4 represented breeding wolves and 2 represented nonbreeding wolves. Additionally, for the three wolves (M1, M2, F2) that were each monitored in two different summers, attendance declined throughout the season in one year but not the other. However, wolf F1's daily attendance declined throughout all three seasons during which she was monitored.

Correlation of attendance

Simultaneously monitored wolves displayed positively correlated homesite attendance ($P < 0.03$) for all pairwise comparisons. This pattern was distinct and occurred for all pairs and for all months tested. These results are consistent with visual observations at the homesite. In 443 h of observation (over 46 days during the summers of 1997–1999), all four observed departures of radio-collared wolves from the homesite involved two or three uncollared wolves.

Discussion

We observed three significant patterns within the highly variable homesite attendance. First, for most monitored wolves, likelihood of presence peaked during daylight. Secondly, daily attendance rate declined through most wolf-summers according to age of pups or Julian day. Finally, for all simultaneously monitored wolves, attendance was positively correlated.

In general, the lowest homesite attendance occurred during the night (Fig. 2) and the highest attendance occurred during daylight (Fig. 2), allowing wolves to forage during periods of prey activity. Moose are active primarily during the crepuscular hours, while beaver are nocturnal (Dyck and MacArthur 1992). In Poland, wolf activity peaked at dawn and dusk, when wolves killed most prey (Theuerkauf et al. 2003). Similarly, visual observation of wolves on Ellesmere Island revealed wolves departing to hunt in the evening (Mech and Merrill 1998). In addition, during nightly absences from the homesite, a breeding female monitored in Ontario traveled near waterways, presumably hunting beaver (Kolenosky and Johnston 1967).

For most wolves, especially breeding females, daily attendance rate declined according to Julian day (Fig. 3). In early summer, breeding females were characterized by high daily attendance rates (18–20 h/day) equivalent to those reported elsewhere for breeding females (17–24 h/day) with similarly sized packs but lower prey densities (Harrington and Mech 1982; Ballard et al. 1991). Daily attendance rate declined through the summer to less than 8.4 h/day for the period 18 June – 22 July. The decline in attendance, also observed elsewhere (Harrington and Mech 1982; Ballard et al. 1991; Theuerkauf et al. 2003), occurs as dietary requirements of the growing pups increase and distance travelled by breeding females increases (Jędrzejewski et al. 2001), perhaps a result of greater foraging effort. These attendance patterns, in addition to observations of multiple regurgitations to the pups, seem to indicate that breeding females take an active role in providing food to the pups.

At homesites, pups are thought to benefit from adult wolves deterring potential threats (Murie 1944; Theberge and Pimlott 1969; Peterson et al. 1984; Veitch et al. 1993).

Fig. 3. Seasonal decline in daily attendance rates of radio-collared wolves at homesites in Isle Royale National Park. Within each graph, multiple years for the same wolf and (or) multiple wolves are represented. F, female; M, male.
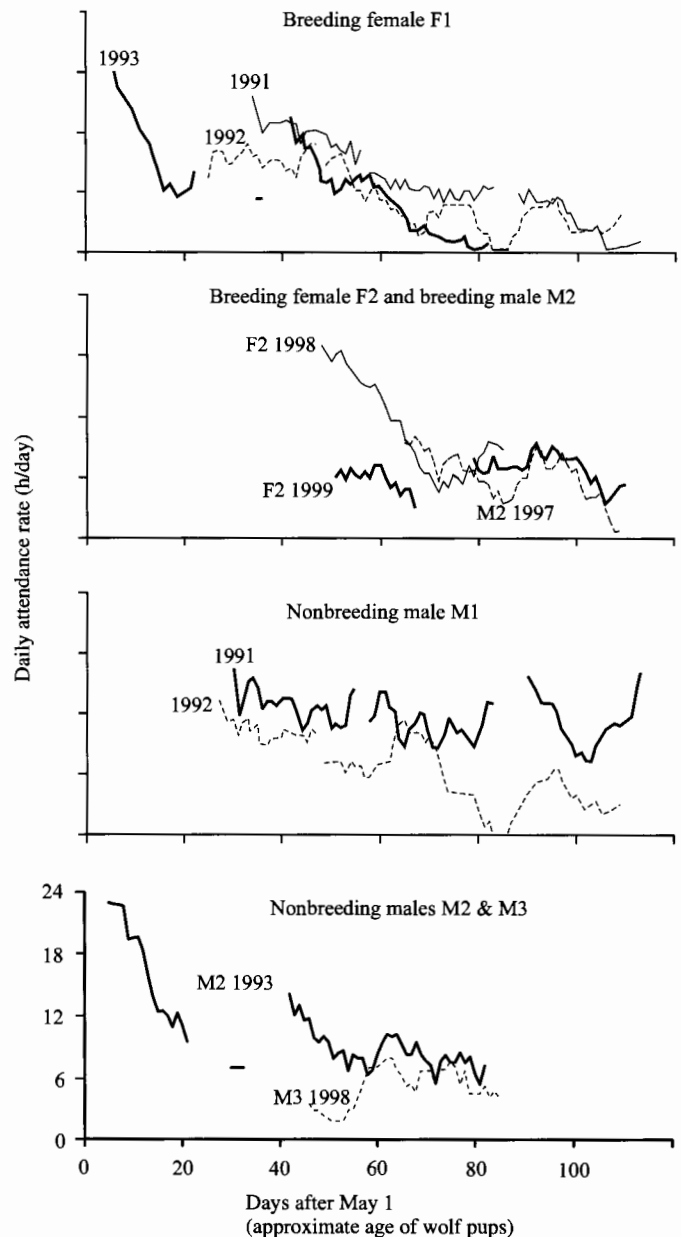
Consequently, we expected adult wolves to attend the homesite as often as possible. However, we observed highly correlated attendance among all simultaneously monitored wolves. Probably the result of hunting for nocturnal and crepuscular prey species such as beaver and moose, this pattern of attendance results in groups of wolves attending the homesite for short periods rather than single wolves attending for long periods, and has been reported elsewhere (Chapman 1977; Harrington and Mech 1982). Black bears, *Ursus americanus* Pallas, 1780, are absent at ISRO but are a threat to pups where wolves and bears coexist (Rutter and Pimlott 1968). While correlation of attendance reduces the total time that adult wolves are at the homesite, the atten-

dance is diurnal and thus concentrated at the homesite when black bear activity is greatest (Debruyn 1997).

Previous research has documented variation in homesite attendance of nonbreeding wolves, especially yearlings (Harrington and Mech 1982; Hertel 1984; Ballard et al. 1991). Indeed, we observed variable homesite attendance patterns among wolves of the same social status and sex, and even for individual wolves monitored in multiple years. However, the variable homesite attendance occurred among summers of relatively constant prey density and pack size. In addition, when prey density and pack size varied, homesite attendance remained relatively constant. For example, between the summers of 1993 and 1997, wolf M3 changed social status from a nonbreeding male to a breeding male, prey density decreased by over 60%, and 4 years passed, but the wolf's homesite attendance did not change significantly.

We expected to find a positive relationship between moose density and homesite attendance, but daily attendance rate and duration of absence were unrelated to moose density (Table 1). The low moose density in this study (0.9 moose/km^2) was higher than levels at which wolf reproductive success may decline $(0.2 \text{ moose/km}^2;$ Messier 1987), suggesting that moose density may not have been low enough to affect homesite attendance. Even so, east pack homesite attendance and absence were similar to those in other areas of much lower prey density. For instance, breeding females at ISRO during periods of high prey density exhibited midsummer daily attendance rates (2–7 h/day) similar to that of a breeding female experiencing severe prey shortage in Minnesota (6.6 h/day; Harrington and Mech 1982). In addition, a breeding male also monitored during low prey density in Minnesota exhibited a duration of absence (20 h; Harrington and Mech 1982) similar to that observed for a breeding male at ISRO (18.7 h). However, the absence of a corresponding increase in attendance and decrease in duration of absence during periods of high prey density is inexplicable, especially given relationships between wolf activity and prey density reported elsewhere (Jędrzejewski et al. 2001).

Harrington et al. (1983) hypothesized that yearlings and perhaps other nonbreeding wolves attend the homesite primarily to receive food from foraging wolves. Although it is difficult to measure actual food exchange, we observed varying attendance patterns in a nonbreeding wolf, suggesting changing reliance on the pack. In 1991, nonbreeding male M1 (age unknown) exhibited a high daily attendance rate typical of that observed for yearlings (Harrington and Mech 1982; Ballard et al. 1991). However, in 1992 the same wolf exhibited a much lower attendance rate, similar to that of breeding female F1 monitored during the same period (Fig. 1). The drop in attendance occurred during relatively stable environmental conditions but perhaps resulted from a maturation of hunting skills and decreased reliance on the pack for food. Indeed, M1 permanently left the east pack the following winter. Although this wolf was characterized by a low attendance rate in the second summer, his contribution of food to pups remains uncertain.

The success of rearing pups was not affected by variation in daily attendance rates or duration of absence (Table 1). In Minnesota, pack size affected the number of pups surviving to 9 months of age, depending on prey density (Harrington

and Mech 1983). However, we did not find this relationship in either the high or the low prey density periods. The lack of a relationship in our results tends to diminish the importance of the homesite in terms of pup protection. Although black bears are absent from ISRO, other potential threats to young pups exist, such as red fox (*Vulpes vulpes* (L., 1758)), moose, or other wolves.

We conclude that wolf homesite attendance patterns vary according to time of year, time of day, and the presence of other wolves. We believe that other variables such as individual health, proximity of prey carcasses, loss of key pack members, or hunting skill of the individual may contribute to variation in attendance and may obscure the effects of prey density, social status, or pack size on daily attendance rate and duration of absence. Our results provide no evidence for a protective effect of homesite attendance on the number of wolf pups surviving to 9 months of age at ISRO. To determine how homesite attendance affects reproductive success of wolf populations, future studies might be improved by focusing on food exchange between pack members. Although we documented some food exchange between wolves, the distance between our observation area and the homesite was too great (200 m) to observe each exchange. With knowledge of which wolves are providing and receiving food at the homesite, we can better understand the factors that determine the reproductive success of wolf populations.

Acknowledgements

References

Ballard, W.B., Whitman, J.S., and Gardner, C.L. 1987. Ecology of an exploited wolf population in south-central Alaska. Wildl. Monogr. **98**: 1–54.

Ballard, W.B., Ayres, L.A., Gardner, C.L., and Foster, J.W. 1991. Den site activity patterns of gray wolves, *Canis lupus*, in south central Alaska. Can. Field-Nat. **105**: 497–504.

Chapman, R.C. 1977. The effects of human disturbance on wolves (*Canis lupus* L.). M.Sc. thesis, University of Alaska, Fairbanks, Alaska.

Debruyn, T.D. 1997. Habitat use, food habits and population characteristics of female black bears in the central Upper Peninsula of Michigan : a geographic information system approach. Ph.D. thesis, Michigan Technological University, Houghton, Mich.

Dyck, A.P., and MacArthur, R.A. 1992. Seasonal patterns of body temperature and activity in free-ranging beaver (*Castor canadensis*). Can. J. Zool. **70**: 1668–1672.

Fuller, T.K. 1989. Population dynamics of wolves in northcentral Minnesota. Wildl. Monogr. **105**: 1–41.

Harrington, F.H., and Mech, L.D. 1982. Patterns of homesite attendance in two Minnesota wolf packs. *In* Wolves of the world: perspectives of behavior, ecology, and conservation. *Edited by* F.H. Harrington and P.C. Paquet. Noyes, Park Ridge, N.J. pp. 81–105.

Harrington, F.H., Mech, L.D., and Fritts, S.H. 1983. Pack size and wolf pup survival: their relationship under varying ecological conditions. Behav. Ecol. Sociobiol. **13**: 19–26.

Hertel, H.H. 1984. The role of social niche in juvenile wolves: puppyhood to independence. M.Sc. thesis, University of Minnesota, Duluth, Minn.

Jędrzejewski, W., Schmidt, K., Theuerkauf, J., Jedrzejewska, B., and Okarma, H. 2001. Daily movements and territory use by radiocollared wolves (*Canis lupus*) in Bialowieza Primeval Forest in Poland. Can. J. Zool. **79**: 1993–2004.

Joslin, P.W.B. 1967. Movements and home sites of timber wolves in Algonquin Park. Am. Zool. **7**: 279–288.

Kolenosky, G.B., and Johnston, D.H. 1967. Radio-tracking wolves in Ontario. Am. Zool. **7**: 289–303.

Mech, L.D., and Merrill, S.B. 1998. Daily departure and return patterns of wolves, *Canis lupus*, from a den at 80°N latitude. Can. Field-Nat. **112**: 515–517.

Messier, F. 1987. Physical condition and blood physiology of wolves in relation to moose density. Can. J. Zool. **65**: 91–95.

Murie, A. 1944. The wolves of Mount McKinley. U.S. Natl. Park Serv. Fauna Natl. Parks U.S. Fauna Ser. **5**.

Peterson, R.O. 1977. Wolf ecology and prey relationships on Isle Royale. U.S. Natl. Park Serv. Sci. Monogr. Ser. **11**.

Peterson, R.O., and Vucetich, J.A. 2001. Ecological studies of wolves on Isle Royale. Annual report. Isle Royale Natural History Association, Houghton, Mich.

Peterson, R.O., Bailey, T.N., and Woolington, J.D. 1984. Wolves of the Kenai Peninsula, Alaska. Wildl. Monogr. **88**: 1–52.

Peterson, R.O., Thomas, N.J., Thurber, J.M., Vucetich, J.A., and Waite, T.A. 1998. Population limitation and the wolves of Isle Royale. J. Mammal. **79**: 829–841.

Rutter, R.J., and Pimlott, D.H. 1968. The world of the wolf. J.B. Lippincott, Philadelphia and New York.

Sokal, R.R., and Rohlf, F.J. 1995. Biometry: the principles and practice of statistics in biological research. W.H. Freeman and Company, New York.

Theberge, J.B., and Pimlott, D.H. 1969. Observations of wolves at a rendezvous site in Algonquin Park. Can. Field-Nat. **83**: 122–128.

Theuerkauf, J., Jędrzejewski, W., Schmidt, K., Okarma, H., Ruczyński, I., Śnieżko, S., and Gula, R. 2003. Daily patterns and duration of wolf activity in the Bialowieza Forest, Poland. J. Mammal. **84**: 243–253.

Thurber, J.M., and Peterson, R.O. 1993. Effects of population density and pack size on the foraging behavior of gray wolves. J. Mammal. **74**: 879–889.

Veitch, A.M., Clark, W.E., and Harrington, F.H. 1993. Observations of an interaction between a barren-ground black bear, *Ursus americanus*, and a wolf, *Canis lupus*, at a wolf den in northern Labrador. Can. Field-Nat. **107**: 95–97.

dance is diurnal and thus concentrated at the homesite when black bear activity is greatest (Debruyn 1997).

Previous research has documented variation in homesite attendance of nonbreeding wolves, especially yearlings (Harrington and Mech 1982; Hertel 1984; Ballard et al. 1991). Indeed, we observed variable homesite attendance patterns among wolves of the same social status and sex, and even for individual wolves monitored in multiple years. However, the variable homesite attendance occurred among summers of relatively constant prey density and pack size. In addition, when prey density and pack size varied, homesite attendance remained relatively constant. For example, between the summers of 1993 and 1997, wolf M3 changed social status from a nonbreeding male to a breeding male, prey density decreased by over 60%, and 4 years passed, but the wolf's homesite attendance did not change significantly.

We expected to find a positive relationship between moose density and homesite attendance, but daily attendance rate and duration of absence were unrelated to moose density (Table 1). The low moose density in this study (0.9 moose/km^2) was higher than levels at which wolf reproductive success may decline (0.2 moose/km^2; Messier 1987), suggesting that moose density may not have been low enough to affect homesite attendance. Even so, east pack homesite attendance and absence were similar to those in other areas of much lower prey density. For instance, breeding females at ISRO during periods of high prey density exhibited midsummer daily attendance rates (2–7 h/day) similar to that of a breeding female experiencing severe prey shortage in Minnesota (6.6 h/day; Harrington and Mech 1982). In addition, a breeding male also monitored during low prey density in Minnesota exhibited a duration of absence (20 h; Harrington and Mech 1982) similar to that observed for a breeding male at ISRO (18.7 h). However, the absence of a corresponding increase in attendance and decrease in duration of absence during periods of high prey density is inexplicable, especially given relationships between wolf activity and prey density reported elsewhere (Jędrzejewski et al. 2001).

Harrington et al. (1983) hypothesized that yearlings and perhaps other nonbreeding wolves attend the homesite primarily to receive food from foraging wolves. Although it is difficult to measure actual food exchange, we observed varying attendance patterns in a nonbreeding wolf, suggesting changing reliance on the pack. In 1991, nonbreeding male M1 (age unknown) exhibited a high daily attendance rate typical of that observed for yearlings (Harrington and Mech 1982; Ballard et al. 1991). However, in 1992 the same wolf exhibited a much lower attendance rate, similar to that of breeding female F1 monitored during the same period (Fig. 1). The drop in attendance occurred during relatively stable environmental conditions but perhaps resulted from a maturation of hunting skills and decreased reliance on the pack for food. Indeed, M1 permanently left the east pack the following winter. Although this wolf was characterized by a low attendance rate in the second summer, his contribution of food to pups remains uncertain.

The success of rearing pups was not affected by variation in daily attendance rates or duration of absence (Table 1). In Minnesota, pack size affected the number of pups surviving to 9 months of age, depending on prey density (Harrington

and Mech 1983). However, we did not find this relationship in either the high or the low prey density periods. The lack of a relationship in our results tends to diminish the importance of the homesite in terms of pup protection. Although black bears are absent from ISRO, other potential threats to young pups exist, such as red fox (*Vulpes vulpes* (L., 1758)), moose, or other wolves.

We conclude that wolf homesite attendance patterns vary according to time of year, time of day, and the presence of other wolves. We believe that other variables such as individual health, proximity of prey carcasses, loss of key pack members, or hunting skill of the individual may contribute to variation in attendance and may obscure the effects of prey density, social status, or pack size on daily attendance rate and duration of absence. Our results provide no evidence for a protective effect of homesite attendance on the number of wolf pups surviving to 9 months of age at ISRO. To determine how homesite attendance affects reproductive success of wolf populations, future studies might be improved by focusing on food exchange between pack members. Although we documented some food exchange between wolves, the distance between our observation area and the homesite was too great (200 m) to observe each exchange. With knowledge of which wolves are providing and receiving food at the homesite, we can better understand the factors that determine the reproductive success of wolf populations.

Acknowledgements

References

Ballard, W.B., Whitman, J.S., and Gardner, C.L. 1987. Ecology of an exploited wolf population in south-central Alaska. Wildl. Monogr. **98**: 1–54.

Ballard, W.B., Ayres, L.A., Gardner, C.L., and Foster, J.W. 1991. Den site activity patterns of gray wolves, *Canis lupus*, in south central Alaska. Can. Field-Nat. **105**: 497–504.

Chapman, R.C. 1977. The effects of human disturbance on wolves (*Canis lupus* L.). M.Sc. thesis, University of Alaska, Fairbanks, Alaska.

Debruyn, T.D. 1997. Habitat use, food habits and population characteristics of female black bears in the central Upper Peninsula of Michigan : a geographic information system approach. Ph.D. thesis, Michigan Technological University, Houghton, Mich.

Dyck, A.P., and MacArthur, R.A. 1992. Seasonal patterns of body temperature and activity in free-ranging beaver (*Castor canadensis*). Can. J. Zool. **70**: 1668–1672.

Fuller, T.K. 1989. Population dynamics of wolves in northcentral Minnesota. Wildl. Monogr. **105**: 1–41.

Harrington, F.H., and Mech, L.D. 1982. Patterns of homesite attendance in two Minnesota wolf packs. *In* Wolves of the world: perspectives of behavior, ecology, and conservation. *Edited by* F.H. Harrington and P.C. Paquet. Noyes, Park Ridge, N.J. pp. 81–105.

Harrington, F.H., Mech, L.D., and Fritts, S.H. 1983. Pack size and wolf pup survival: their relationship under varying ecological conditions. Behav. Ecol. Sociobiol. **13**: 19–26.

Hertel, H.H. 1984. The role of social niche in juvenile wolves: puppyhood to independence. M.Sc. thesis, University of Minnesota, Duluth, Minn.

Jędrzejewski, W., Schmidt, K., Theuerkauf, J., Jedrzejewska, B., and Okarma, H. 2001. Daily movements and territory use by radiocollared wolves (*Canis lupus*) in Bialowieza Primeval Forest in Poland. Can. J. Zool. **79**: 1993–2004.

Joslin, P.W.B. 1967. Movements and home sites of timber wolves in Algonquin Park. Am. Zool. **7**: 279–288.

Kolenosky, G.B., and Johnston, D.H. 1967. Radio-tracking wolves in Ontario. Am. Zool. **7**: 289–303.

Mech, L.D., and Merrill, S.B. 1998. Daily departure and return patterns of wolves, *Canis lupus*, from a den at 80°N latitude. Can. Field-Nat. **112**: 515–517.

Messier, F. 1987. Physical condition and blood physiology of wolves in relation to moose density. Can. J. Zool. **65**: 91–95.

Murie, A. 1944. The wolves of Mount McKinley. U.S. Natl. Park Serv. Fauna Natl. Parks U.S. Fauna Ser. **5**.

Peterson, R.O. 1977. Wolf ecology and prey relationships on Isle Royale. U.S. Natl. Park Serv. Sci. Monogr. Ser. **11**.

Peterson, R.O., and Vucetich, J.A. 2001. Ecological studies of wolves on Isle Royale. Annual report. Isle Royale Natural History Association, Houghton, Mich.

Peterson, R.O., Bailey, T.N., and Woolington, J.D. 1984. Wolves of the Kenai Peninsula, Alaska. Wildl. Monogr. **88**: 1–52.

Peterson, R.O., Thomas, N.J., Thurber, J.M., Vucetich, J.A., and Waite, T.A. 1998. Population limitation and the wolves of Isle Royale. J. Mammal. **79**: 829–841.

Rutter, R.J., and Pimlott, D.H. 1968. The world of the wolf. J.B. Lippincott, Philadelphia and New York.

Sokal, R.R., and Rohlf, F.J. 1995. Biometry: the principles and practice of statistics in biological research. W.H. Freeman and Company, New York.

Theberge, J.B., and Pimlott, D.H. 1969. Observations of wolves at a rendezvous site in Algonquin Park. Can. Field-Nat. **83**: 122–128.

Theuerkauf, J., Jędrzejewski, W., Schmidt, K., Okarma, H., Ruczyński, I., Śnieżko, S., and Gula, R. 2003. Daily patterns and duration of wolf activity in the Bialowieza Forest, Poland. J. Mammal. **84**: 243–253.

Thurber, J.M., and Peterson, R.O. 1993. Effects of population density and pack size on the foraging behavior of gray wolves. J. Mammal. **74**: 879–889.

Veitch, A.M., Clark, W.E., and Harrington, F.H. 1993. Observations of an interaction between a barren-ground black bear, *Ursus americanus*, and a wolf, *Canis lupus*, at a wolf den in northern Labrador. Can. Field-Nat. **107**: 95–97.