

Den Site Activity Patterns of Gray Wolves, *Canis lupus*, in Southcentral Alaska

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Den site attendance and activity patterns of Gray Wolves within two wolf packs in southcentral Alaska were studied in 1980 and 1981 using a combination of activity radio transmitters and direct observations from blinds and fixed-wing aircraft. One wolf pack was electronically monitored for 17 continuous days in 1980 and another for 43 continuous days in 1981. They were observed for 277 and 369 hours, respectively. Alpha females spent more time at dens than other pack members. The alpha female of a pack of four adult wolves spent less time at the den than did the alpha female from a pack of eight adult wolves suggesting that in smaller packs, alpha females may have a more active role in providing food for pups. Den attendance by other pack members was highly variable. Yearling males tended to avoid dens until after parturition. Yearling females from the large pack tended to spend more time at the den than those from a smaller pack. When pups were from 2–7 weeks of age, they were left unattended from 5–15% of the time. There was a high probability that groups of wolves would be present at the den during mid-day. Wolves tended to depart from the den between 2100 and 2400 h and arrive between 2100 and 0400 h.

Key Words: Gray Wolf, *Canis lupus*, summer, activity, attendance, den site, homesites, Alaska

Gray Wolf (*Canis lupus*) summer activities are centered around den and rendezvous sites for the raising of pups. Adult and yearling wolves share in providing nourishment for pups by hunting and returning to homesites to regurgitate food to pups, but the amount of food contributed varies by sex, age, hunting experience, social status, and other factors (Mech 1970). The contribution of individual wolves to pup survival may be particularly important in populations that experience high mortality. If hunting, trapping, and other mortality remove key individuals which contribute food to pups, pup survival or health could be influenced. Several studies conducted in areas of little to no human exploitation have described behavior patterns of wolves at homesites (Murie 1944; Joslin 1966; Harrington and Mech 1982). However, only Harrington and Mech (1982) provide quantitative data concerning attendance and behavior by individual wolves by sex and age class.

The purpose of this study was to quantify and compare den attendance and level of activity of adult and yearling wolves for two packs in southcentral Alaska. At the onset of denning, the Susitna pack in 1980 numbered four wolves (two adults and two yearlings), while the Watana pack in 1981 numbered eight wolves (three adults and five yearlings). Both packs had abundant prey. We hypothesized that the Susitna alpha female would spend more time away from the den to hunt because she would lack adequate food contributions from the three remaining pack members. At the Watana den, we expected the alpha female and yearlings to spend significantly

more time at the den due to the pack's relatively large size. We expected yearlings from the Watana pack to meet their own food needs, provide more food to the pups, and spend more time at the den than yearlings from the Susitna Pack (Harrington et al. 1983).

Study Area

The study occurred in the upper Susitna Basin of southcentral Alaska located approximately 325 km northeast of Anchorage. Topography, elevation, climate, vegetation, and fauna of the area have been described (Skoog 1968; Bishop and Rausch 1974; Ballard 1982; Ballard et al. 1987). Briefly, vegetation along the Susitna River and its major tributaries was dominated by spruce (*Picea glauca* and *P. mariana*) and birch (*Betula papyrifera*). Generally, above 800 m vegetation was dominated by willow (*Salix* spp.) and Dwarf Birch (*Betula glandulosa*) giving way to mat and cushion and shrub tundra at elevations > 950 m. The Susitna pack, studied in 1980, denned along the Susitna River, south of the mouth of Tyone Creek. The Watana Pack, studied in 1981, denned north of the Susitna River near the mouth of Watana Creek. Both pack territories intersected portions of the range of the Nelchina Caribou (*Rangifer tarandus*) herd which numbered 18 000 to 20 000 during the study (Bergerud and Ballard 1988). Moose (*Alces alces*) densities were about 600/1000 km² (Ballard et al. 1987, 1991). Locations and spatial relationships of wolf pack territories were provided by Ballard et al. (1987).

Methods

During May and June, the pattern of activity at dens of the Susitna Pack (1980) and the Watana Pack (1981) were investigated. Both packs were studied as part of a 10-year study of predator-prey relationships (Ballard et al. 1981a, 1987).

Wolves were captured to attach activity transmitters using methods described by Ballard et al. (1982b). Ages of captured wolves were determined by tooth replacement and wear and previous known history (Ballard et al. 1987). Alpha individuals were identified based upon a combination of known pack histories, known sex and age composition, and behavioral characteristics described by Mech (1970). Individual wolves were identified by the abbreviated pack name (S = Susitna Pack and W = Watana Pack) and the last three digits of their assigned permanent accession number.

Activity transmitters contained a mercury tip switch that caused the signal amplitude and pulse width to vary depending on position of the head and neck of the animal. If the animal's head was immobile, the pulse width of the radio signal decreased. Conversely, when the animal was moving, the pulse rate increased. The transmitters were similar to those described by Beier and McCullough (1988) used on White-tailed Deer (*Odocoileus virginianus*). The radio-transmitter collars were color coded with canvas tape to aid identification of individual wolves.

Within 0.4 km of each den, a 3-m tall monopole antenna was erected and connected to a portable digital data processor which fed into a programmable scanning receiver (Telonics Inc., Mesa, Arizona). The pulse interval (activity) and amplitude (signal strength) of radio signals from individual activity transmitters were recorded on a strip-chart recorder (Gulton Inc., Manchester, New Hampshire) which advanced at a rate of 20.3 cm per hour. The instruments were powered by a 12-volt battery and all were housed in a plastic container for weather protection. Individual collared wolves were monitored once every 3 minutes in 1980 and once every 11 minutes in 1981. A reference transmitter was placed nearby to calibrate activity and attendance of wolf transmitters. Each occasion we arrived and departed from the blind, we marked the date and time on the paper spools so activity data could be calibrated to specific dates and times.

The presence and absence of radio-equipped wolves were grouped into six 4-hour periods. Patterns of arrival and departure were tested by Chi-square analysis (Snedecor and Cochran 1973). Expected values were generated by assuming equal probability of arrival and departure over each period. Total hours each wolf was present at the den was determined by electronic monitoring or ground observation. During periods when the strip-chart

recorder was out of paper (Susitna – one period of 56 hours, Watana – four periods totaling 14 hours) ground observations substituted for electronic monitoring. Daily ground observations were made from 8 May – 8 June 1980 and 7 May – 22 June 1981 for the Susitna and Watana wolves, respectively. Time spent away from dens was determined by the number of hours individual wolves were undetected through electronic or ground monitoring. Dates and times wolves were observed away from the den from fixed-wing aircraft were compared with periods wolves were electronically recorded or visually observed at dens.

Behavior of individual wolves electronically monitored was classified each hour as either "active" or "inactive" based on the change in amplitude and period of the recorded radio signal. Gillingham and Bunnell (1985) determined that specific behaviors could not be reliably detected with mercury tip switches. However, Bier and McCullough (1988) reported that highly reliable data on bedded versus active behavior could be attained if sampling interval was adjusted for species and environment. We also could not identify specific behaviors by electronic monitoring but, based on comparisons of visual observations with telemetric data, we believed we could detect periods of inactivity from active periods. For this study, we defined "active" as all physical movements other than those associated with lying or standing. An index to overall activity of the den was obtained by dividing the total number of hours a wolf was active by the total hours the individual was at the den.

Each den was observed by one individual from a blind placed so that den entrances could be accurately monitored without disrupting wolf behavior. Blinds were located 150 m and 280 m from the Susitna and Watana den entrances, respectively. Observation periods ranged from 5-12 hours daily and covered a 32-day period at the Susitna den in 1980 and a 47-day period at the Watana den in 1981. During ground observations, den attendance of radio-collared wolves was determined by manually scanning signals every 30 minutes with a receiver attached to a hand-held 2-element antenna (Telonics). Individual wolves were identified by collar color, radio frequency, and pelage color and pattern. Specific notes on behavior of individual wolves and interactions among wolves were recorded (Foster and Ballard 1985).

Activity away from the den was determined by radio-tracking and visually observing collared wolves from fixed-wing aircraft using methods described by Mech (1974) and Ballard and Whitman (1988). Radio signals were received with a programmable scanning receiver (Telonics). Each radioed wolf was observed about twice per week at irregular hours.

Pack Histories

Susitna Pack: At parturition on 1 May, the pack was composed of alpha female S-295, new alpha male S-305, yearling female S-302, and yearling male S-306. The alpha male and female were equipped with activity transmitters and were monitored continuously by strip-chart recorder. Wolves S-302 and S-306 wore conventional radio collars and were monitored by ground observation, electronic scanning with hand-held antennas, and from fixed-wing aircraft. Based on the parturition date, pups produced this season were not sired by S-305. Six pups were successfully raised during 1980.

Watana Pack: During pup rearing, the Watana Pack numbered eight wolves. Five had activity transmitters: alpha female W-308, yearling female W-324, yearling male W-325, yearling male W-345, and yearling female W-346. One yearling female W-323 had a conventional radio collar, one adult male carried a nonfunctional radio collar, and one adult male was uncollared. On 8 May, W-308 entered the den. Between 1 May and 10 May Watana pack members adult male W-310, yearling male W-344, and one other dispersed. W-323 and W-346 also appeared to have dispersed, traveling 83 km from the den, but they returned to the den on 12 May and remained with the Watana pack for the duration of the study. A total of six pups were successfully raised in 1981.

Results and Discussion

Two Susitna pack members were electronically monitored for 17 days in 1980, while five Watana pack members were continuously monitored for 43 days in 1981 (Table 1). Electronic monitoring commenced at the Susitna den on 20 May 1980 and the Watana den on 8 May 1981 and continued through 10 June and 22 June, respectively. Wolves were observed from blinds near dens for 646 hours: 277 hours at the Susitna den site in 1980 and 369 hours at the Watana den in 1981. Parturition occurred on 1 May 1980 at the Susitna den and between 10-11 May 1981 at the Watana den.

The Watana alpha female (W-308) remained continuously (98%) at the den until 5 June and the pups were 25-26 days old (Table 1). After 5 June, she was absent from the den 2-18 hours daily. Similarly, the Susitna alpha female (S-295) was absent on a daily basis for periods of 2-12 hours after 27 May, when the pups were believed to be 26 days old. However, S-295 was not electronically monitored before 20 May, and the total time spent away from the den before pup weaning could not be determined. Between 9 and 19 May, S-295 was present at the den for 74.5 (83.7%) of 89 total hours of ground observation time. Her longest known absence from the den during that period was seven hours.

Adequate nutrition for pups may be one factor determining when and how long maternal females

TABLE 1. Activity and den site attendance of wolves equipped with activity radio transmitters in two wolf packs located in southcentral Alaska during late May and June in 1980 and 1981.

Pack ID no. ^a	Pre-weaning ^c							Post-weaning						
	Sex	Age	No. days monitored	H at den	H active	$\bar{X}$ h/day at den	% obs. at den	% obs. active	No. days monitored	H at den	H active	$\bar{X}$ h/day at den	% obs. at den	% obs. active
S-295	F	Ad	5	83	12	16.6	69.2	14.5	11	198	49	18.0	75.0	24.7
S-305	M	Ad	5	27	7	5.4	22.5	25.9	12	76	22	6.3	26.4	28.9
W-308	F	Ad	29	685	259	23.6	98.4	37.8	14	263	129	18.8	78.2	49.0
W-324	F	Yrl	25	233	125	9.3	38.8	53.6	13	113	61	8.7	36.2	54.0
W-325	M	Yrl	26	124	62	4.8	19.9	41.9	14	63	35	4.5	18.8	55.6
W-345	M	Yrl	29	31	19	1.1	4.5	61.3	14	41	26	2.9	12.2	63.4
W-346	F	Yrl	29	308	160	10.6	44.3	51.9	14	100	43	7.1	29.8	43.0

^a Pre-weaning period was 1 May - 27 May 1980 and 10 May - 5 June in 1981.

^b S = Susitna pack and W = Watana pack; yearling male S-302, yearling female S-306, yearling female W-323, one collared W-adult with a nonfunctioning transmitter, and one W-uncollared adult male were monitored from blinds, fixed-wing aircraft, and electronic monitoring by scanning from blind with hand-held antenna (see text).

will leave the dens. Harrington and Mech (1982) reported that their alpha female was absent from the den 12 to 20% of the time for periods as long as 17 hours between prenatal and weaning. After weaning and for the next two months, the Minnesota female spent only one-third of her time near the den site. Den attendance of their female prior to weaning was similar to that of the Susitna female in this study but much lower than that of the Watana female. Wolves in the Minnesota pack were food stressed due to low densities of White-tailed Deer (38.5/1000 km²) (Harrington and Mech 1982). Wolves in our study were not food stressed in terms of Moose, i.e., Moose densities $\geq$ 600/1000 km² (Ballard et al. 1990), and appeared to have access to abundant small prey based upon scat analyses (Ballard et al. 1987, and unpublished data). The Susitna female and pups may still have been food stressed if lack of experienced pack members or lack of a committed alpha male caused insufficient food being brought to the den. The Susitna alpha female participated more in hunting than did the Watana alpha female during the pre-weaning period but not during the post-weaning period. Both females, however, spent more time at homesites than did other pack members.

When the alpha females left the dens, it was for brief periods compared to other pack members (Table 2). All excursions for Watana female W-308 lasting 10-18 hours occurred after 16 June, and all were associated with prey carcasses. Upon her return to the den, she was frequently observed regurgitating to her pups. Similarly for other adults and yearlings, all excursions involving freshly killed ungulate carcasses exceeded 12 hours.

There were differences between the alpha females on dates and duration of excursions. Susitna female S-295 was away from the den for > 10-hour periods after 19 May (pups 19 days old) but none of the excursions exceeded 12 hours. In contrast, the Watana female did not leave for > 10 hours until after 17 June (pups 36 days old), and none exceeded 18 hours but all involved kill sites.

Based upon time away from the den and observations of the alpha female regurgitating food to pups, the Susitna female appeared to be a more active participant than the Watana female in obtaining food for pups. We speculate that this was a function of pack size, experience, and structure (Harrington et al. 1983; Ballard et al. 1987: 23). If the Susitna female had been monitored daily from fixed-wing aircraft like the Watana pack, we suspect her longer duration excursions would have been related to fresh ungulate kills.

Attendance near dens by subordinate pack members was highly variable. Overall, yearling males spent less time at the den and were absent longer than yearling females ($t = -4.748, P < 0.001$). Two female yearlings, W-324 and W-346, spent 40% of their time at the den. Both wolves were timid, submitting to all members of the pack. They also tried to nurse and beg food from other wolves returning to the den. Sixty-seven percent of W-346's absences were less than nine hours, and she was the only wolf other than the alpha female whose absences from the den never exceeded 31 hours. Wolves W-324 and W-346 averaged 9.1 and 9.5 hours per day near the den, respectively (Table 1), but W-346 was present daily while wolf W-324 was away from the den site on at least five occasions for >24 hour periods (Table 2). Long absences from the den typically were associated with activity at prey carcasses.

Although yearling females W-324 and W-346 spent nearly equal amounts of time at the den (Table 1), when only one yearling was present it was W-324 78% of the time. We suggest that the greater amount of den attendance by W-324 and W-346 was primarily selfish and contributed little to pup survival. These smaller, less aggressive wolves may have been spending proportionately more time at the den because they were obtaining food from other pack members by begging (Harrington et al. 1983). Den attendance by the other yearlings was highly variable and their roles concerning pup survival are not fully understood.

TABLE 2. Frequency of duration of absences by individual wolves from two den sites during May and June 1980 and 1981 in southcentral Alaska as determined by electronic monitoring of radio signals.

Pack name	ID no.	Age - sex	Duration of excursion (h)			
			1-2	3-9	10-30	31+
Susitna	295	Adult-female	5	10	4	-
	305	Adult-male	2	3	-	7
Watana	308	Adult-female	10	9	3	-
	324	Yrlg-female	4	10	15	6
	325	Yrlg-male	7	7	16	6
	345	Yrlg-male	5	5	7	4
	346	Yrlg-female	16	24	12	0

• All three excursions occurred after 16 June 1981.

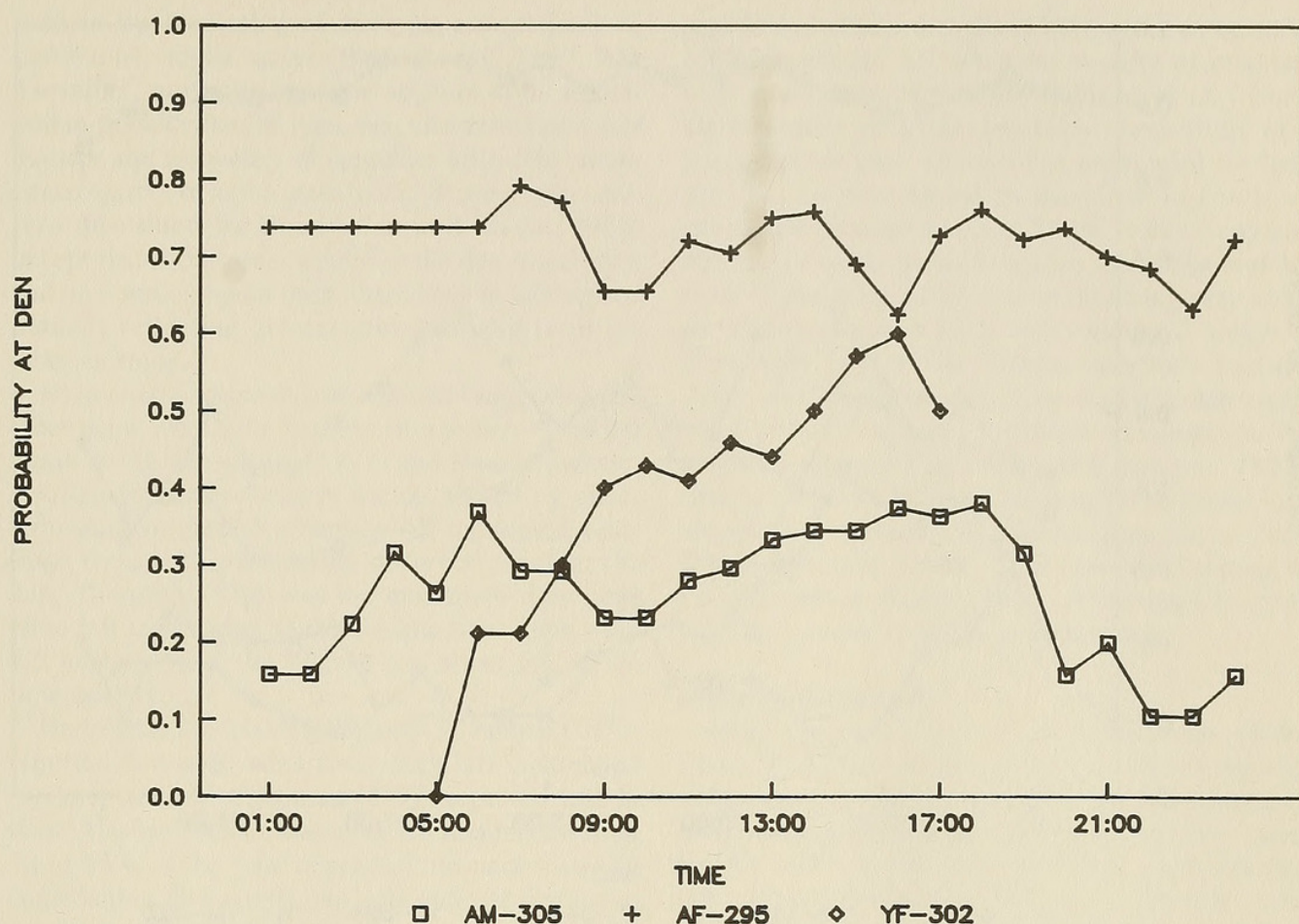


FIGURE 1. Probability of finding individual radio-collared wolves on an hourly basis at the Susitna wolf den as determined from continuous monitoring of radio signals from 20 May through 7 June 1980 in southcentral Alaska (AM = adult male, YM = yearling male, and AF = adult female).

There were 63 possible combinations of association for the six radio-collared wolves at the Watana den site but only 41 were observed. Absences from the den site usually involved male yearlings W-345 and W-325 (Table 2).

Harrington and Mech (1982) reported that den-site attendance by yearlings differed from other pack members. Their yearling males tended to stay away from homesites until after parturition. One of our yearling males (W-345) exhibited the pattern of attendance they described. This wolf left the pack area with two other wolves prior to parturition and returned to the den three weeks after parturition in early June. In comparison, yearling male W-325 spent more time near the den prior to and for one week following parturition. W-325 was submissive to all other males in the pack and most of his absences from the den were of short duration in the accompaniment of W-324.

There were no significant differences ($P > 0.05$) in arrival and departure times for alpha female S-295, but the frequency of such activity appeared more numerous in afternoon and early evening hours (50% of 40 observations between 1300 and 2000 hours). Alpha male S-305 exhibited a tendency to leave the

den site between 1700-2000 hours (50% of 14 observations) and return between 0500-1200 (73% of 11 observations). After departure from the den, he usually remained away for 30-36 hours. There were no distinct patterns of arrival or departure times for individual Watana pack members. When individuals were pooled, however, there was a tendency for departure between 2100 and 2400 hours (27% of 191 observations) and arrival between 2100 and 0400 hours (51% of 174 observations). Arrival and departure times observed in this study were comparable to those reported by Kolenosky and Johnston (1967) in Ontario. In our study, wolves were most active at the den between 0600 and 0800 and 2100 and 2300 hours. Arrivals and departures occurred least frequently during 1300-2000 hours.

Because of the larger number of wolves present in the Watana pack, we expected overall activity to be higher at the Watana den than at the Susitna den. Overall, activity was twice as great as that recorded for the Susitna pack, but this difference was not significant ($t' = 1.17$, $df = 5$, $P = 0.30$).

The Watana alpha female (W-308) was the most active (8.9 hours/day pre-weaning and 9.2 hours/day post-weaning) of any of the wolves studied (Table

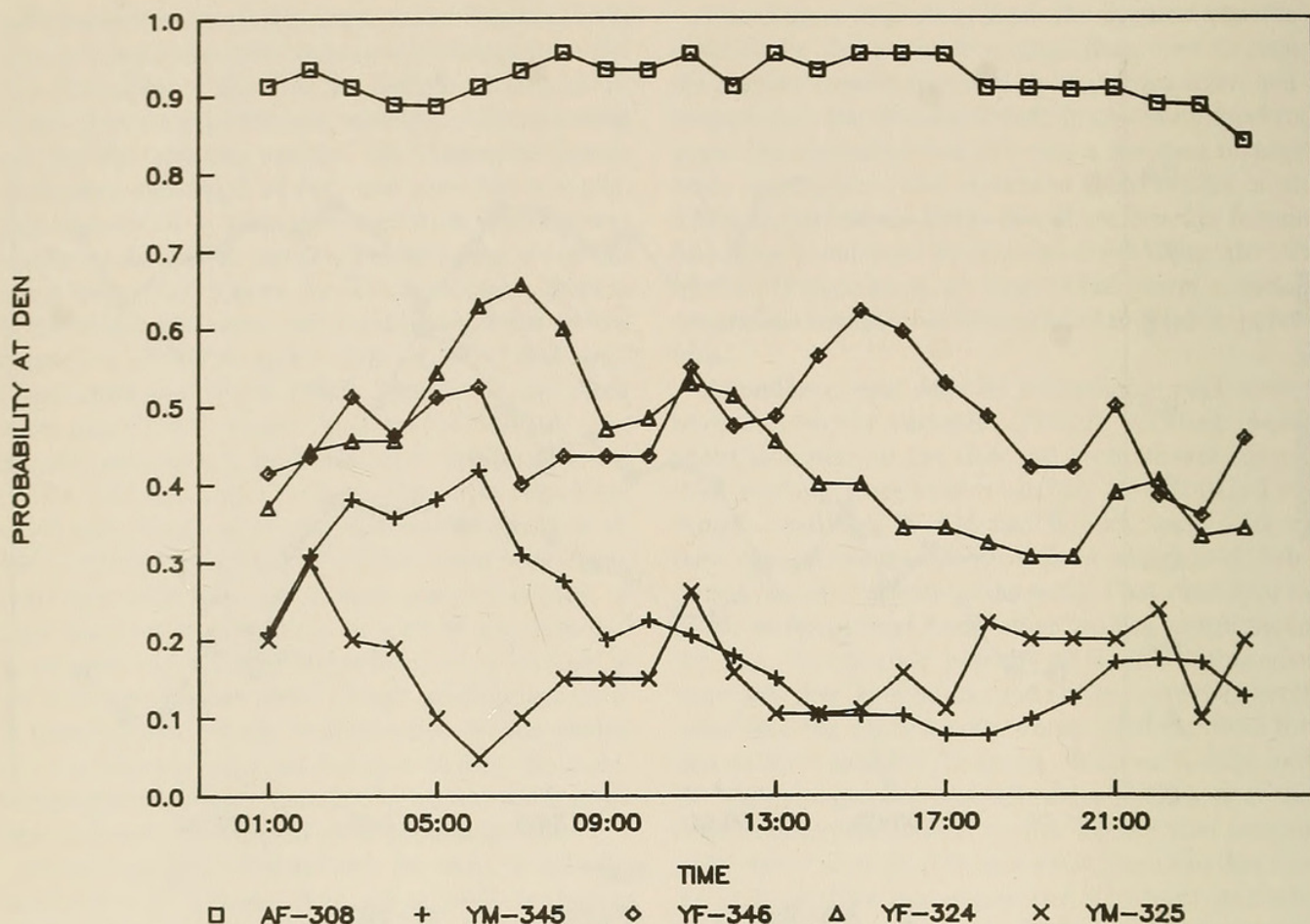


FIGURE 2. Probability of finding individual radio-collared wolves on an hourly basis at the Watana wolf den as determined from continuous monitoring of radio signals from 8 May through 21 June 1981 in southcentral Alaska (AM = adult male, AF = adult female, YF = yearling female, and YM = yearling male).

1). She was active more than 13 hours on 8 days and was never less active than 4 hours per day. On days she was relatively inactive (< 9 continuous hours/day), wolves W-324, W-325, or W-346 were present and were active 10-16 hours per day. In comparison, the Susitna alpha female (S-295) was active for > 7 hours on only 1 of 16 days and was active less than 4 hours on 8 days. Wolf S-295's absences from the den averaged 1 hour/day more than those of Watana female W-308, but she rested significantly more than the Watana female ($t = 4.258$, $P < 0.001$).

Harrington and Mech (1982) concluded that groups of wolves most likely would be found at dens near dawn, less frequently at dusk, and few would occur during the day (about 0800 to 2000 hours). Alpha females in our study had higher probabilities of being found at dens during all hours than other sex and age classes of wolves (Figures 1 and 2). Yearling females had the second highest probability of being found at den sites followed by yearling males, but probabilities of specific hours of attendance or absence were variable and not predictable.

In contrast to Harrington and Mech's (1982) findings, there was a relatively high probability that groups of wolves could be found at the den during

the day. We concur with Harrington and Mech (1982) that some of these reported differences may be related to different lighting conditions in Alaska. During the denning season in Alaska, there are no periods of complete darkness, and, although prey may be more active during crepuscular hours, the differences may not be as pronounced as farther south. Also, because the Minnesota population was food stressed, wolves in that area may have been forced to hunt during all daylight hours (Harrington and Mech 1982).

Even though not the sire of the pups, Susitna male S-305 appeared to be the primary food provider because he was responsible for three of the four known ungulate kills and he was absent from the den more than other wolves. Susitna male S-305 was absent from the den site from 31 to 37 hours every 2.5 days. No other wolves in either pack were absent from the den as much. Based upon aerial observations we surmised that S-305's absences from the den were related to extended hunting forays. We expected a similar pattern of den attendance for the alpha male from the Watana pack but he was not radio-collared. Groups of yearling wolves appear to be largely unsuccessful at killing large ungulate prey

without the leadership of more experienced adults, particularly alpha males (Ballard et al. 1987: 23). Therefore, pack age structure appears to be important in determining the type, sex, and age of prey and perhaps the frequency of ungulate kills. The attendance pattern of alpha male S-305 fit the general pattern described by Harrington and Mech (1982) except that S-305 was present at the den more often and on a more regular basis than those in Minnesota, perhaps reflecting greater prey availability in the Alaskan study.

Strip-chart and ground observations suggested that when pups were 2 to 7 weeks of age they were left alone at the den about 15% of the time. However, yearling female S-306 was not monitored by either strip-chart or ground scanning. All monitored yearlings from both packs were observed alone at the den. Therefore, 15% was the maximum time pups were left unattended at the Susitna den. Pups were left unattended at the Watana den about 5% of the time in 1981.

Harrington and Mech (1982) and Chapman (1977) reported that pups were frequently left unattended for long periods. Chapman (1977) reported that in three Alaskan packs, pups were left unattended from 40 to 73% of the time depending on pack size and composition. In contrast, our data indicate that packs numbering 4 to 8 adults inhabiting areas of plentiful food resources seldom left pups unattended. The duration and frequency that pups are left unattended at dens appears highly variable among areas and may depend on a number of factors including age of pups, available food resources, and sex and age composition of the pack. Measurement of potential causative factors is required before any conclusions can be made.

The death of the Susitna alpha male and a large yearling male prior to denning allowed us to study possible impacts of losses of key individuals on denning behavior and pup survival. Although both Peterson et al. (1984) and Ballard et al. (1987) found no significant relationship between number of surviving pups and numbers of adults in packs, it seems reasonable that quality and quantity of food delivered to the den is related to pack size and age structure in some manner. However, identification of the threshold level at which survival is influenced has not been determined. Packs composed of several adults would not require the assistance of alpha females in killing large prey. Such females could provide continuous care to pups rather than leaving at regular intervals. Packs composed of only one adult may not be able to provide optimal quantities or quality of food without the assistance of the alpha female. Ballard et al. (1981) report one case where a single adult female successfully raised 3 to 4 pups. This litter size was less than the average of 5.3

reported by Ballard et al. (1987) and was near the 1975 average of 3.7 when the density of ungulate prey was lowest. In our study both packs of 4 and 8 adult wolves each successfully raised litters of 6 pups. Neither pack left the den unattended for long periods as was found in areas of lower food resources (Harrington and Mech 1982; Chapman 1977). In smaller packs it appears that alpha females must take a more active role in obtaining prey compared to packs with more adult wolves if length of time away from the den means more time hunting. Also with smaller packs, there was less den attendance by yearlings. If subordinate yearlings are not as capable hunters as adults (Ballard et al. 1987), then perhaps in relatively large packs yearlings may spend more time at the den begging excess food (Harrington et al. 1983). There may be a shortage of excess food in smaller packs accounting for lower attendance rates by yearlings at den sites.

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