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Homesite attendance based on sex, breeding status, and number of helpers in gray wolf packs

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We studied gray wolf (*Canis lupus*) homesite attendance rates using global positioning system locations of 17 GPS-radiocollared wolves from 7 packs in Idaho. Nonbreeding wolves attended homesites more once pups were weaned and we hypothesize this is a behavior that benefits subsequent pup-rearing. The breeding status and sex of the wolf was the strongest predictor of homesite attendance in the preweaning period but the dominant predictor postweaning was the number of helpers in the pack. We estimated that each additional helper in a pack decreased an individual's attendance rate by 7.5%. Because helpers can either attend or provision pups, our results suggest that small packs invest in protecting pups at the expense of having additional adults foraging.

Key words: attendance, *Canis lupus*, cooperative breeding, den, helper, homesite, pup-rearing, rendezvous site, wolf pack

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Gray wolves (*Canis lupus*) are cooperative breeders that roam widely across large territories (Fuller et al. 2003); pack movements are constrained, however, during the pup-rearing season as adults provision and protect relatively immobile pups kept at homesites (i.e., dens during preweaning and rendezvous sites postweaning). The percentage of time spent at homesites can vary greatly among pack members (Potvin et al. 2004; Thurston 2002). Studies have shown that breeding females have the highest attendance rates at dens but that attendance at rendezvous sites drops off markedly as the pups are weaned and the female returns to foraging (Ballard et al. 1991; Harrington and Mech 1982). The roles of nonbreeding wolves with regard to homesite attendance are more variable and not well understood (Ballard et al. 1991). Past studies, although limited by small sample sizes, have suggested that homesite attendance by nonbreeding wolves increases once pups are weaned (Ballard et al. 1991; Harrington and Mech 1982; Thurston 2002) because nonbreeding wolves begin to provision pups with food and provide protection from intruders. Thurston (2002) found that nonbreeding females attended the homesite more than did nonbreeding males. Information on homesite attendance, particularly at rendezvous sites during the summer, is lacking because previous studies either ended approximately mid-July (Potvin et al. 2004; Thurston 2002) or were based on observations of just 1 or 2 animals (Harrington and Mech 1982).

Attendance rates also are influenced by pack size and composition (Ballard et al. 1991). The presence of an adequate number of helpers (i.e., nonbreeding wolves $>$ 12 months old) may permit increased attendance at homesites, as has been shown for painted hunting dogs (*Lycaon pictus*—Courchamp et al. 2002). Alternatively, increased pack size may create increased food demands for all individuals in the pack and attendance may be lower in large packs because individuals must forage more frequently. Conceivably, if the number of helpers within a pack is small, per capita attendance rates at the homesite would be lower because helpers would need to be hunting to keep pups provisioned.

We used locations of GPS-radiocollared gray wolves from multiple packs in central and northern Idaho to calculate homesite attendance rates for collared wolves over the entire pup-rearing season. We assessed the influence of sex, breeding status, pack membership, and number of helpers within each pack on attendance rates by collared individuals. We

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Table 1.—Homesite attendance data for gray wolves ($n = 17$) at dens and rendezvous sites (RSs) in 7 packs in Idaho (2007–2009). GPS = global positioning system; NA = not available.

Breeding status–sex	Pack name	No. helpers in pack	Period of observation	Total no. GPS locations	% locations at den[a]	% locations at RS[a]	% locations at homesites[b]
Breeding female	Packer John	4	15 April–6 August 2008	371	89.6	45.4	65.0
Breeding female	Archie Mountain	5	15 April–15 September 2009	404	80.8	6.7	21.0
Breeding female	Wapiti	6	1 May–15 September 2009	415	86.4	21.3	34.0
Breeding male	Wapiti	6	1 May–15 September 2009	386	33.8	10.7	14.8
Breeding male[c]	Archie Mountain	7	15 April–16 June 2008	187	7.0	NA	7.0
Nonbreeding female	Archie Mountain	7	15 April–15 September 2008	409	24.9	5.3	15.9
Nonbreeding female	Archie Mountain	5	15 April–15 September 2009	214	17.2	5.1	8.4
Nonbreeding female	Timberline	5	15 April–15 September 2009	280	22.5	11.3	16.8
Nonbreeding female	Timberline	5	15 April–15 September 2009	385	30.2	12.0	20.0
Nonbreeding female	Timberline	5	15 April–15 September 2009	398	27.2	10.7	17.8
Nonbreeding female	Timberline	5	15 April–15 September 2008	344	NA	38.1	38.1
Nonbreeding female	Moyer Basin	10	15 April–3 May 2008	64	14.1	NA	14.1
Nonbreeding female	Marble Mountain	4	4 June–28 July 2008	134	22.2	37.5	31.3
Nonbreeding male	Jureano Mountain	6	3 July–15 September 2007	225	NA	4.4	4.4
Nonbreeding male	Archie Mountain	7	15 April–15 September 2008	376	18.6	5.6	12.5
Nonbreeding male	Timberline	5	15 April–15 Septermber 2008	424	NA	12.0	12.0
Nonbreeding male	Archie Mountain	5	15 April–15 September 2009	198	0.0	6.6	5.6

[a] Within 500 m.

[b] Den and RS combined, within 500 m.

[c] Probable breeding male.

hypothesized that breeding females would spend less time at the homesite once pups were weaned and that nonbreeding wolves would increase their attendance postweaning as a result. We also speculated that postweaning, breeding status, sex, and pack membership would not affect attendance rates of individual wolves significantly, and that the number of helpers in the pack would be the main predictor of attendance. We hypothesized that the number of helpers would influence individual attendance rates in 1 of 2 ways: the number of helpers would be positively correlated with attendance rates because helpers beyond those required for provisioning would be available for homesite attendance, or alternatively, the number of helpers would be negatively correlated with attendance rates because food requirements of large packs require increased per capita hunting effort, reducing the number of helpers available for homesite attendance.

Materials and Methods

Wolves were captured and fitted with GPS radiocollars (Lotek Inc., Newmarket, Ontario, Canada, or Telonics Inc., Mesa, Arizona) as part of collaborative wolf research between the Nez Perce Tribe, Idaho Department of Fish and Game, and the University of Montana (United States Fish and Wildlife Service et al. 2008, 2009). All captures were accomplished in 2007–2009 using either padded foothold traps in summer or by darting from helicopters in January. Sex and breeding status were determined either from previous very-high-frequency radiotelemetry monitoring of the pack or observations during capture and handling. Swollen testes, body size, weight, and age derived from teeth condition (Gipson et al. 2000) allowed us to determine which males were breeders, and age and behavior provided indications of breeding status of females, which was later confirmed during denning season from very-high-frequency telemetry monitoring from either aircraft or the ground. Global positioning system collars were programmed with fix intervals of either 6 h ($n = 4$) or 7.5 h ($n = 13$). Animal handling followed guidelines of the American Society of Mammalogists (Sikes et al. 2011) as well as an animal care and use protocol approved by the University of Montana.

We mapped the locations of gray wolves in central and north-central Idaho during the pup-rearing season (15 April–15 September) and classified each collared wolf by its sex and breeding status for analysis (i.e., breeding male, breeding female, nonbreeding male, or nonbreeding female; Table 1). Although all data on homesite attendance were collected remotely via GPS transmitters, homesite locations and pack and litter sizes were determined in the field. We identified homesites (den and rendezvous sites) by monitoring collared wolves using very-high-frequency telemetry from both the ground and from aircraft. We considered an area a homesite if we observed pups or heard their howling and observed their sign (tracks or scats) at the site. Although wolf packs may use several rendezvous sites each year, we only found evidence of 1 rendezvous site for the time period examined for each pack. We determined pack and litter sizes from rendezvous site surveys (Ausband et al. 2010; United States Fish and Wildlife Service et al. 2008, 2009) and from visual observations from very-high-frequency telemetry monitoring of study packs from aircraft (United States Fish and Wildlife Service et al. 2008, 2009). We defined helper wolves as the nonbreeding members of the pack (>12 months old).

We used ArcGIS 9.3 (ESRI, Redlands, California) to find the percentage of global positioning system locations during the pup-rearing season that were within a 500-m radius of the known homesite during the time it was estimated to have been

Table 2.—Homesite attendance (%) based on sex and breeding status of gray wolves ($n = 17$) in 7 packs in Idaho (2007–2009).

	Breeding females	Breeding males	Nonbreeding females	Nonbreeding males
Den attendance	86.7	14.1	24.5	16.0
Rendezvous site attendance	21.6	10.7	18.1	8.3
Overall homesite attendance	39.2	12.2	20.6	9.7

used. We chose to use a buffer of 500 m because according to Frame et al. (2004), movements greater than this distance from the homesite are considered foraging bouts. We assumed that each pack began using a den site on 15 April and later relocated to a rendezvous site. We estimated the date of abandonment of the natal den by analyzing the latest date in which a global positioning system location was within 500 m of the den and the 1st date in which a location appeared within this distance of the rendezvous site. We considered the time period when wolves were at the den site to be the preweaning period and we considered the time spent at rendezvous sites the postweaning period. To determine how attendance changed throughout the pup-rearing season, we pooled data for each breeding status–sex class into 2-week periods from 15 April to 15 September. We considered intervals of 2 weeks to be short enough to detect subtleties in attendance change while still maintaining an adequate sample size in each interval. We then calculated the amount of time each breeding status–sex class was present at its homesite during each 2-week period. When breeding females are in dens underground satellite reception may be lost and location data may be missing for this time period (Nielson et al. 2009). This occurred for 2 breeding females in our sample during the typical time of parturition for wolves in Idaho. To provide a better estimate of attendance rates for these 2 breeding females in our analyses, when we encountered continuous missed fixes during the time of parturition, we assumed the breeding females were in dens and treated the missed fixes as locations at the homesite in our analyses. Ignoring these gaps of data during the critical denning period would have greatly reduced the validity of our analyses.

Null hypotheses comparing equality of proportions of fixes among breeding status–sex classes of wolves were evaluated with a Pearson's chi-square test using SYSTAT 12 (SYSTAT Software, Inc., Chicago, Illinois). We used multiple regression (De Veaux et al. 2004) to model individual attendance rates based on breeding status–sex, pack membership, and number of helpers within each individual's pack during both pre- and postweaning periods. We included a dummy variable (i.e., 1–7) to represent pack membership and test whether we could make valid comparisons between individuals that belonged to different packs.

Results

We analyzed a total of 5,214 global positioning system locations of 17 wolves from 7 packs comprising 1,932 wolf days (Table 1). Attendance rates differed by sex and breeding status ($\chi^2{}_3 = 356.57$, $P < 0.001$). Over the entire pup-rearing season breeding females had the highest attendance rates (39.2%; Table 2), but attendance declined from 86.7% during the preweaning period to 21.6% postweaning (Table 2) with a marked ~20% dip coinciding with the time when pups would have just been weaned. Breeding wolves displayed the highest attendance rates in the period immediately after parturition, whereas the attendance of nonbreeding wolves peaked slightly later in summer (Fig. 1). All 4 breeding and sex classes showed a general decline in homesite attendance throughout the puprearing season and the decrease was most marked for breeding females, but they still had the highest overall attendance rates of any individuals (Fig. 1). By early September, no wolves were located within 500 m of their pack's rendezvous site. Our preweaning model explained nearly 80% of the variation in attendance rates between individuals ($R^2 = 0.77$; adjusted $R^2 = 0.70$; $y = -23.1$(breeding status–sex) $-$ 3.1(number of helpers) + 1.1(pack membership)). Preweaning, the breeding status–sex of the wolf was the dominant predictor of attendance ($P < 0.001$) and neither pack membership ($P = 0.63$) nor number of helpers in the pack ($P = 0.31$) contributed appreciably to the model. Postweaning, our model explained nearly 50% of the variation in attendance rates between individual wolves ($R^2 = 0.47$; adjusted $R^2 = 0.32$; $y = -2.9$(breeding status–sex) $-$ 7.5(number of helpers) + 1.1(pack membership)). During the postweaning period the number of helpers in the pack was by far the strongest predictor of attendance ($P = 0.05$), whereas pack membership ($P = 0.39$) and breeding status–sex ($P = 0.35$) contributed little to the model. Once pups were weaned, each additional helper decreased an individual's attendance rate by 7.5% given that breeding status–sex and pack membership remained fixed.

Discussion

Wolves are social carnivores that exhibit cooperative breeding behavior; we show that individuals within a pack vary greatly in their attendance rates at homesites throughout the pup-rearing season. We found strong support for the hypothesis that breeding females would attend homesites more than other pack members but that they would display a sharp drop in attendance when the pack shifted from using dens (preweaning) to subsequent rendezvous sites (postweaning). Although breeding females attended homesites more often than other individuals, the drop in attendance postweaning suggests that once pups are weaned, the breeding female can contribute more to food acquisition for the pack, as has been found for other cooperatively breeding canids (Courchamp et al. 2002). Pup provisioning and ultimately survival may be enhanced if breeding females, which have higher hunting success rates than nonbreeding wolves (Mech and Boitani 2003), take on a more

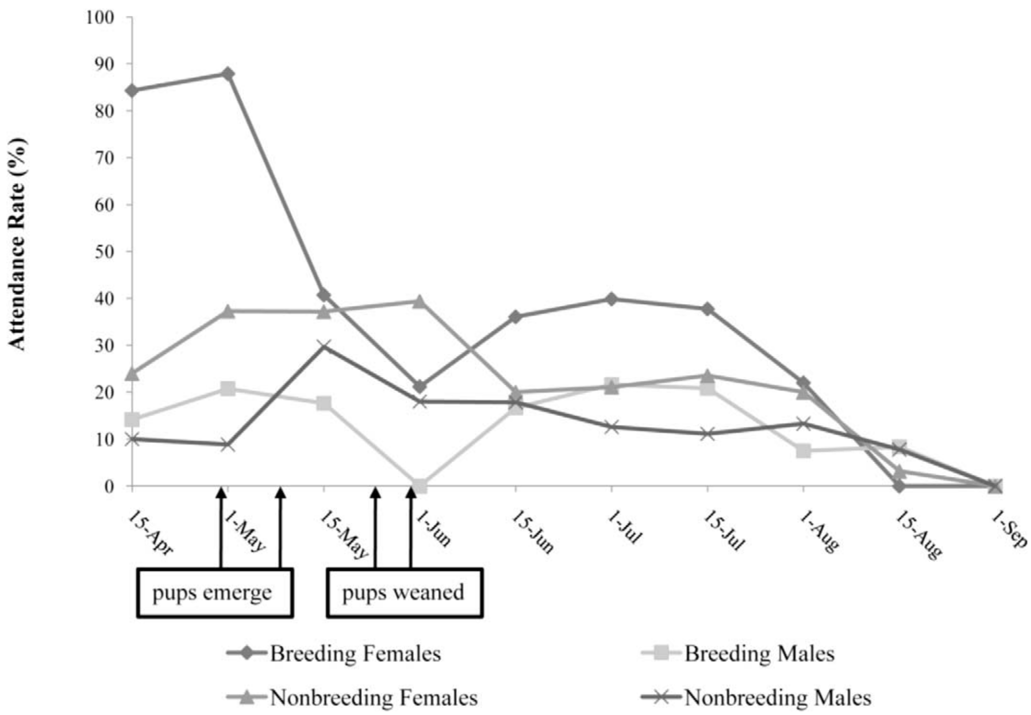

Fig. 1.—Attendance rates (%) for each breeding and sex class at homesites within 2-week intervals during the pup-rearing season for 17 wolves in 7 packs in Idaho, 2007–2009. Date ranges indicated by arrows on the x-axis represent timing of pup emergence from the den and pups being weaned within our study area.

active role in hunting following weaning. The cost of reproduction and nursing is high for breeding females and they displayed a marked dip in attendance coinciding with the time when pups would be weaned in our area (∼21 May–1 June; Fig. 1). Breeding females may be more actively foraging during this time to replenish reserves lost during the taxing reproductive period or to simply be away from the energetic young pups.

Attendance rates of both breeding males and breeding females were generally highest during the 2-week time period immediately after parturition, but the attendance of nonbreeding wolves (both male and female) did not peak until 2–4 weeks later. This suggests that once pups emerged from the den, nonbreeding wolves assumed a more active role in pup-rearing. Nonbreeding wolves may be learning to care for pups, offering them a fitness advantage in the event they eventually breed, as has been shown in other cooperatively breeding mammals (Solomon and French 1997). If nonbreeding wolves are related to the pups they attend, they would also gain an indirect fitness advantage if the care they provided increased pup survival. Not all nonbreeding wolves, particularly nonbreeding females, attended homesites regularly, however. We found marked variation in attendance rates within nonbreeding female wolves postweaning (5–38%; Table 1), suggesting that certain helpers take on pup-guarding duties whereas others do not. These differences may be a function of age, as found for common marmosets (*Callithrix jacchus*), or relatedness between nonbreeders and young, as found in golden lion tamarins (*Leontopithecus rosalia*—Tardif 1997).

Homesite attendance can be viewed as an investment made by the wolf pack that involves trade-offs between protecting pups at the homesite and leaving the homesite to hunt for food. During the preweaning period the number of helpers had little influence on attendance rates. Once pups were weaned this pattern switched; the number of helpers became a strong predictor of attendance rates and other members in the pack other than the breeders began to play a more active role in pup-rearing. Our alternative hypothesis on the effects of the number of helpers on postweaning homesite attendance was supported; individuals living in packs with more helpers attended the homesite less. We hypothesize 2 possible explanations: having additional members in the pack creates more food demands and this constraint requires wolves to forage more often and attend the homesite less; and wolf packs may need few adults guarding the pups at any particular time, therefore, per capita attendance rates in a large pack will necessarily be low because the workload is shared among many individuals. Because helpers can either attend or provision pups, our results suggest that small packs invest in protecting pups at the expense of having additional adults foraging. This trade-off between provisioning and protecting pups has been noted in packs of cooperatively breeding painted hunting dogs (Courchamp et al. 2002).

Our best model for predicting individual attendance rates postweaning left approximately 50% of the variation in the data unexplained, indicating that other factors also influence attendance rates. Harrington et al. (1983) hypothesized that food availability may influence homesite attendance rates by wolves because when prey is scarce helpers may be unwilling or unable to remain at the homesite for protection and instead spend their time foraging. Additionally, Griffin and West (2003) showed that in many cooperatively breeding species, individuals provisioned and cared for young less if they were more distant relatives or unrelated. Lastly, older, nonbreeding individuals of callitrichids participated more in pup-rearing than did younger nonbreeders (Tardif 1997). Although the necessary data were unavailable, we may have been able to explain more variation in homesite attendance if we had included data on prey availability, relatedness of individuals, and more-precise estimates of individual ages within each pack.

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