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Dog days of summer: influences on decision of wolves to move pups

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For animals that forage widely, protecting young from predation can span relatively long time periods due to the inability of young to travel with and be protected by their parents. Moving relatively immobile young to improve access to important resources, limit detection of concentrated scent by predators, and decrease infestations by ectoparasites can be advantageous. Moving young, however, can also expose them to increased mortality risks (e.g., accidents, getting lost, predation). For group-living animals that live in variable environments and care for young over extended time periods, the influence of biotic factors (e.g., group size, predation risk) and abiotic factors (e.g., temperature and precipitation) on the decision to move young is unknown. We used data from 25 satellite-collared wolves (*Canis lupus*) in Idaho, Montana, and Yellowstone National Park to evaluate how these factors could influence the decision to move pups during the pup-rearing season. We hypothesized that litter size, the number of adults in a group, and perceived predation risk would positively affect the number of times gray wolves moved pups. We further hypothesized that wolves would move their pups more often when it was hot and dry to ensure sufficient access to water. Contrary to our hypothesis, monthly temperature above the 30-year average was negatively related to the number of times wolves moved their pups. Monthly precipitation above the 30-year average, however, was positively related to the amount of time wolves spent at pup-rearing sites after leaving the natal den. We found little relationship between risk of predation (by grizzly bears, humans, or conspecifics) or group and litter sizes and number of times wolves moved their pups. Our findings suggest that abiotic factors most strongly influence the decision of wolves to move pups, although responses to unpredictable biotic events (e.g., a predator encountering pups) cannot be ruled out.

Key words: *Canis lupus*, gray wolves, movement, offspring, predation, rendezvous sites

Protecting young from predation is an important life history strategy particularly for long-lived animals with relatively long gestation and rearing times. Parents exhibit a wide range of behaviors to protect young from predation, including aggressive defense, occupying cavities, nests or dens, alarm calling, and even feigning injury to lure predators away from young (Theberge and Pimlott 1969; Smythe 1977; Hofer and East 1993; Hollen and Radford 2009). Cryptic coloration and precocial growth patterns of young also aid in escaping predation (Davies et al. 2012). For terrestrial carnivores that forage widely for patchy resources, protecting young from predation can span relatively long time periods due to the inability of young to travel far, participate in foraging, and thus be protected by their parents. Carnivores that live in groups often leave an adult group member with the offspring to guard them from predation (Moehlman 1979; Ruprecht et al. 2012). Spotted hyenas (*Crocuta crocuta*), for example, will care for young during their first 12 months of life largely at communal dens. Multiple females within a hyena clan will move their 2-week-old young to these sites and leave adults to guard them while the clan forages (Hofer and East 1993). Hyena females give birth separately in natal dens and high-ranking females have natal dens that are closer to communal den sites than do lower ranking females, suggesting that moving young is dangerous

and it is advantageous to make movements as short as possible (Boydston et al. 2006).

If moving young exposes them to increased mortality risk, then the benefits of moving them should, on the average, outweigh the costs of the increased risk of mortality. For example, moving young may be risky but keeping them at a site, where accumulated scents can attract predators, parasite loads can increase, or distance to patchily distributed food and water resources becomes too great, may be more costly than moving. Additionally, abiotic factors such as temperature and precipitation may influence movements directly because of their effects on availability of water (or, indirectly on the effects of water availability on prey). For animals that live in groups, benefits and costs of the decision to move young can all be affected by group size. The relative influence of biotic factors such as group size and predation risk, and abiotic factors such as temperature and precipitation on the decision of group-living animals to move young reared over long time periods is unknown.

Gray wolves (*Canis lupus*) are a useful species for studying the influences on decisions to move pups. Wolves in protected or lightly harvested populations generally live in family groups comprising a breeding pair and 2–3 generations of their offspring. Wolves have large territories and forage widely, thus pups born in dens are often moved among rendezvous sites for their first 4–5 months of life until they are large enough to travel with the group. The decision to move offspring does not appear to be due solely to pup age because wolves vary widely in the frequency and timing of such movements. Litter and group sizes, as well as predation risk from other carnivores (e.g., grizzly bears, *Ursus arctos*—Hayes and Baer 1992), also vary widely among wolf groups.

Because scents that attract predators and ectoparasite loads (Boydston et al. 2006) potentially increase over time at pup-rearing sites, we hypothesized that litter size and the number of adults in the group would positively influence the number of times wolves moved pups during the pup-rearing season. Because presence of grizzly bears, exposure to humans, and high densities of wolves threaten pup survival, we hypothesized that each would positively influence how frequently young were moved. Lastly, wolves require ample amounts of water to digest high-protein diets (Unger et al. 2009) and they generally choose pup-rearing sites with standing but ephemeral water sources (Ausband et al. 2010). We thus hypothesized that wolves would move pups more often when it was hot and dry because they need to find new sites with sufficient water as occupied pup-rearing sites dry.

Materials and Methods

Study area.—Our 3 study areas were in Idaho, Montana, and Yellowstone National Park (YNP), Wyoming. Generally, Idaho and Montana are mountainous and dominated by a mix of ponderosa pine (*Pinus ponderosa*), lodgepole pine (*P. contorta*), and spruce (*Picea englemannii*) forests and sagebrush (*Artemisia tridentata*) steppe. Annual precipitation ranges from 89 to 178 cm and temperatures range from −34°C in winter to 38°C in summer (Western Regional Climate Center 2014). Wolves were common and at moderate-to-high densities in both Idaho and Montana during our study. Groups within our study areas in Idaho did not overlap the range of grizzly bears, whereas some, but did for some of our groups in Montana and all of our groups in YNP. Black bears (*U. americanus*), cougars (*Puma concolor*), and coyotes (*C. latrans*) were present in all of our study areas. Wolf harvest began in both Idaho and Montana in 2009. YNP is dominated by lodgepole pine forests and expansive meadow systems. YNP is relatively dry and precipitation averages 47 cm annually and temperature fluctuations range from −39°C in winter to 30°C in summer at Yellowstone Lake (Western Regional Climate Center 2014). Wolves and grizzly bears exist at high densities inside YNP where no hunting by humans is allowed.

Field and analysis methods.—During 2003–2012, wolves were immobilized and fitted with satellite collars (Lotek, Newmarket, Ontario, Canada and Telonics, Mesa, Arizona) as part of population monitoring efforts or research being conducted by Idaho Department of Fish and Game, Montana Fish, Wildlife and Parks, and YNP (USFWS 2004, 2005, 2006, 2007, 2008, 2009, 2010, 2011, 2012, 2013). Animal handling followed ASM guidelines (Sikes et al. 2011). Collars were set to collect 3–48 locations per day. We considered 15 April to 1 September the pup-rearing season (Ruprecht et al. 2012) and plotted wolf locations for each year using a Geographic Information System (GIS; Arc 10.2; ESRI, Redding, California). Where den and rendezvous site locations were not known from ground surveys and monitoring work, we defined a cluster of GPS locations as a pup-rearing site when ≥ 10 locations from at least 1 satellite-collared group member were within 500 m of one another for ≥ 6 days. We considered sites to be abandoned when GPS locations from at least 1 satellite-collared group member became consistently frequent at a different location, suggesting they were in the process of moving pups to a new location. We excluded unsuccessful GPS location attempts in our assessment of site abandonment. Wolves may have clusters of locations that are kill sites, but 85% of kills are abandoned after 3 days and none have been found active after 5 days (Metz et al. 2011).

Group and litter size counts were obtained visually (generally from the air) as part of annual population monitoring efforts or in some cases from genotypes of individuals derived from fecal samples collected at rendezvous sites (Ausband et al. 2010; Stenglein et al. 2011; Stansbury et al. 2014). We used presence of grizzly bears in areas occupied by wolf groups as an index of predation risk by grizzlies. We used the number of roads and trails within 500 m of each pup-rearing site calculated using Topologically Integrated Geographic Encoding and Referencing (TIGER) roads layer as an index of predation risk or disturbance by humans. We used density of wolves as an index of predation risk by wolves; counts of wolves were sufficient to estimate density (wolves/1,000 km^2) only in YNP. To represent abiotic effects, we calculated relative temperature and precipitation as the ratio of monthly temperatures and precipitation to long-term averages to represent abiotic factors; we averaged mean daily precipitation and temperature for each

2 km^2 area containing a pup-rearing site while occupied, then divided it by the 30-year averages (i.e., normal conditions; PRISM Climate Group, Corvallis, Oregon). We rounded to the nearest month and used that month's relative precipitation and temperature effects as covariates in our model. (e.g., we used the average precipitation and temperature ratios for July for wolves using a pup-rearing site from 22 June to 22 July). Relative precipitation and temperature values > 1.0 indicated conditions above normal, whereas values < 1.0 indicated conditions below normal.

We used a generalized linear model and a Poisson distribution with a log-link function to model the effects of study area, group size, litter size, presence of grizzly bears, density of roads and trails, and relative precipitation and temperature on the number of times wolves moved their pups over the pup-rearing season. We used the same model structure with number of days at each site as the response variable to examine movement patterns within the pup-rearing season. We used Akaike's Information Criteria corrected for small sample size (AIC_c—Burnham and Anderson 2002) to compare candidate models, and likelihood ratio tests to compare candidate model fit against intercept-only models. We used linear regression to evaluate the relationship between density of wolves in YNP and the number of times wolves moved their pups over the pup-rearing season.

Results

Twenty-five groups of wolves had ≥ 1 satellite-collared group member for the duration of pup-rearing seasons (15 April to 1 September). Collared wolves were located 2.4 (median) times daily. Groups included an average of 7.6 adults (*SD* = 3.4) and 4.7 pups (*SD* = 2.0), occupied 3.8 pup-rearing sites/season (*SD* = 1.5), and moved their pups 2.8 times (*SD* = 1.4) over the course of the pup-rearing season. Days spent at pup-rearing sites were highly variable but generally declined as summer progressed and pups grew (Fig. 1). The global model containing all covariates did not explain the number of times wolves moved pups better than more parsimonious models. We found no evidence of an effect of study area, presence of grizzly bears, or number of nearby roads and trails on the number of times wolves moved their pups (Table 1). Models with the number of adults and litter size did not perform better than models including only precipitation and temperature effects. A model using only relative temperature was the most supported model of all we considered (Table 1). Relative temperature was strongly and negatively correlated with the number of times wolves moved their pups ($\beta = -3.5$; $P = 0.01$). Density of wolves in YNP was unrelated to the number of times wolves moved their pups ($R^2 < 0.01$; $P = 0.94$).

Models containing only abiotic factors best explained the number of times wolves moved their pups, but the effect of these variables on days spent at each pup-rearing site varied. The number of days spent at a den site was negatively correlated with relative temperature and weakly with relative precipitation (Table 2). In contrast, after leaving the natal den, relative temperature and precipitation were both strongly and positively correlated with the number of days spent at the second pup-rearing site (i.e., rendezvous site 1; Table 2). Relative precipitation was strongly and positively related to the number of days spent at subsequent pup-rearing sites (Table 2). Sample sizes for groups that used > 4 pup-rearing sites were small ($N \leq 7$), we therefore did not model the number of days at sites after the 4th pup-rearing site.

Discussion

Moving young can expose them to increased mortality risk through predation, accidents (e.g., drowning), or young becoming separated and lost during movement bouts. The benefits of moving can outweigh the costs and pup relocation as evolved in wolves as well as other species (Hofer and East 1993). We found little influence of predation risk but strong effects of abiotic factors on the number of times wolves moved their pups. Monthly temperatures and precipitation that were relatively high (i.e., > 30-year average) appear to have strongly

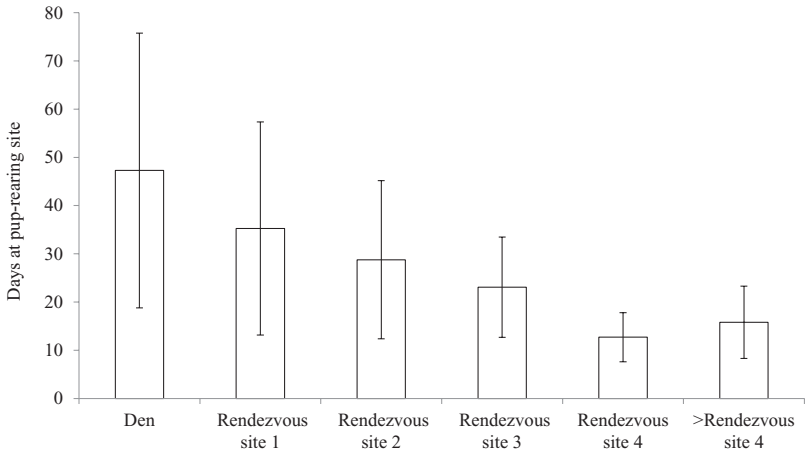

Fig. 1.—Days spent at pup-rearing sites for groups of wolves (*Canis lupus*) in Idaho, Montana, and Yellowstone National Park, United States, 2006–2012. Error bars represent the *SD*.

Table 1.—Number of parameters (K), Akaike's Information Criterion (AIC_c), ΔAIC_c value, Akaike weight (w_i), and likelihood ratio test χ^2, and P-value for model predicting number of times gray wolves (*Canis lupus*) move their pups during pup-rearing season. Precipitation and temperature variables are relative to long-term trends (ratio of monthly observations to 30-year averages).

Model	K	AIC_c	ΔAIC_c	w_i	Likelihood ratio χ^2 (P)
Temperature	2	86.35	0	0.60	6.78 (0.01)
Precipitation + temperature	3	88.60	2.25	0.19	7.13 (0.03)
Precipitation	2	90.38	4.03	0.08	2.75 (0.10)
No. of adults + precipitation + temperature	4	91.18	4.83	0.05	7.41 (0.06)
No. of pups + precipitation + temperature	4	91.31	4.96	0.05	7.28 (0.06)
No. of pups + no. of adults	3	95.06	8.71	0.01	0.67 (0.72)
Grizzly bears + no. of pups	3	95.43	9.08	0.01	0.30 (0.86)
No. of roads and trails + no. of pups	3	95.70	9.35	0.01	0.03 (0.99)
Grizzly bears + no. of pups + no. of adults	4	97.60	11.25	0.00	0.98 (0.81)
Study area + precipitation + temperature + no. of adults	5	97.67	11.32	0.00	7.58 (0.18)
Study area + precipitation + temperature + no. of pups	5	97.75	11.40	0.00	7.50 (0.19)
Study area + grizzly bears + no. of roads and trails + precipitation + temperature + no. of pups + no. of adults	8	110.85	24.50	0.00	7.74 (0.46)

Table 2.—Direction (+ or −) and statistical significance (P-value) of variables from top models predicting number of days wolves spent at pup-rearing sites in Idaho, Montana, and Yellowstone National Park, United States, 2006–2012. Precipitation and temperature variables are relative to long-term trends (ratio of monthly observations to 30-year averages).

Variable	Den	Rendezvous site 1	Rendezvous site 2	Rendezvous site 3
Precipitation	− (0.07)	+ (< 0.01)	+ (< 0.01)	+ (< 0.01)
Temperature	− (< 0.01)	+ (< 0.01)	+ (0.62)	− (0.86)

influenced when and how often to move pups, whereas group and litter sizes did not.

Contrary to our hypothesis, we found that wolves moved their pups less often when temperatures were relatively high. This trend was especially evident at the rendezvous sites used immediately after leaving the natal den. Conceivably, relatively high temperatures could affect wolves in several ways. Wolves occupying pup-rearing sites with adequate water may stay at these sites as long as possible because equivalent sites are limited and moving may be physiologically taxing in such years. The positive relationship between relative precipitation and days spent at pup-rearing sites over the summer appears to support this. Alternatively, wolves in the Rocky Mountains may not have to forage as widely and move pups as frequently to be near patches of prey during warm years because their primary prey, elk (*Cervus elaphus*), are concentrated along streams and rivers in much of our study areas (M. Hurley, IDFG, pers. comm.). We suggest this is unlikely, however, given the ease with which wolves travel and the relatively short distances they moved pups ($\bar{X}$ = 3.29 km, SD = 2.22). Our results were not consistent with the notion that ectoparasites may be more abundant in warm years (Merino and Potti 1996), thus providing incentive to move pups frequently.

We found no relationship between our measures of perceived predation risk (grizzly bear presence, density of roads and trails, and wolf density) and the number of times wolves moved their pups. Although grizzly bears are known to kill wolves (Hayes and Baer 1992), the probability of predation by grizzlies may be low enough that movement of pups does little to reduce it. Alternatively, simple presence of grizzly bears may have been insufficient to capture an effect of bears on the movement of pups. Encounters between humans and wolves are likely also improbable during the pup-rearing season. Further, because hunting and trapping by humans do not generally overlap the pup-rearing season in our study areas, people encountering wolves at that time of year may pose little threat to pups and thus no incentive to move them. Alternatively, density of roads and trails may not be proportional to risks of human-caused mortality or disturbance. Wolves will kill pups of other wolves at pup-rearing sites (Smith et al. 2010); conceivably, risk of this happening should increase with density of wolves. YNP has the highest wolf densities in the U.S. Rocky Mountains (Smith et al. 2003) and was the only area where we could obtain reliable estimates of wolf densities during the pup-rearing season. Although our sample size was limited (n = 8), we found no relationship between wolf density and the number of times wolves moved their pups (Fig. 2). Some movements of pups we observed could have been due to chance encounters between predators and pup-rearing sites (Smith et al. 2015), an interaction we could not detect. Because our measures of predation risk were coarse, further work is needed to dismiss the density or distribution of sympatric predators as relatively unimportant to the decision by wolves to move pups. Further, predation risk may not have affected within-year decisions to relocate pups, but it could affect between-year decisions. For example, Tengmalm's owls (*Aegolius funereus*) will move and have subsequent clutches in new nest cavities if a clutch is lost to predation (Sonerud 1985). Anecdotally, however, it does not appear that wolves in YNP

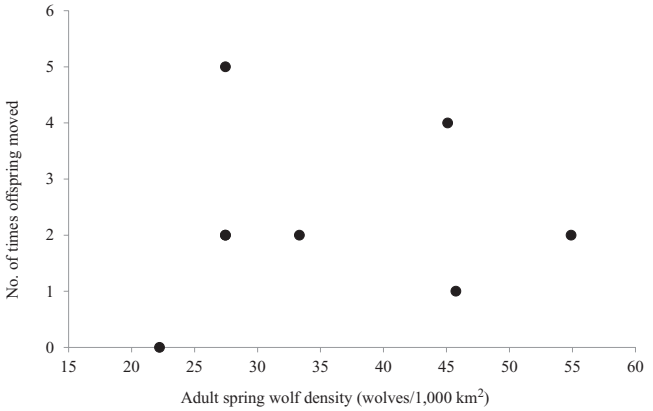

Fig. 2.—Relationship ($R^2 < 0.01$; $P = 0.94$) between number of times wolves (*Canis lupus*) moved pups and density of adult wolves (wolves/1,000 km^2) during the pup rearing season (15 April to 1 September) in Yellowstone National Park's northern range (2003–2012).

always avoid former pup-rearing sites after prior predation of pups at those sites (D. Stahler, YNP, pers. comm.).

We hypothesized that large litters would leave abundant sign and scent for predators to detect and increase ectoparasite transfer and abundance (Boydston et al. 2006; but see also Almberg et al. 2015), providing incentive to move large litters frequently. We also hypothesized that large groups would move pups more frequently because of ample help. We found no support for these hypotheses. Whereas large litters may potentially increase detection by predators or infestation by ectoparasites, moving large litters without pups becoming separated and lost may be sufficiently difficult to outweigh the risks of staying. Number of adults in groups may have not been influential because help moving pups does not increase with group size; e.g., mothers move very young pups by carrying them one at a time (Boydston et al. 2006), and pups become mobile enough to follow their mothers as the pup-rearing season progresses.

Decision-making related to reproduction in gray wolves, like other cooperatively breeding species, can be affected by dynamic interactions between biotic and abiotic factors (Ruprecht et al. 2012; Creel and Creel 2015). Our results suggest that abiotic factors were most influential in the decision by wolves in the U.S. northern Rocky Mountains to move pups, whereas biotic factors were not. If true, wolves make decisions to move pups in response to environmental conditions and constraints (e.g., avoiding heat stress) and potentially the availability of water resources. Biologists who use pup-rearing sites as a means of monitoring and studying wolf populations (Ausband et al. 2010; Iliopoulos et al. 2014) may need to consider that groups will move relatively little in warm years and the ability to detect them at multiple locations will be low. Relatively high precipitation during the pup-rearing season strengthens this pattern. Lastly, given the influence of relative temperature on pup relocation that we observed, accounting for variability in abiotic factors on detection probability would be useful when estimating population parameters based on surveys of pup-rearing sites.

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