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Demma, Dominic J. and Mech, L. David, "Wolf, *Canis lupus*, Visits to White-tailed Deer, *Odocoileus virginianus*, Summer Ranges: Optimal Foraging?" (2009). *USGS Northern Prairie Wildlife Research Center*. 361.

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Wolf, *Canis lupus*, Visits to White-tailed Deer, *Odocoileus virginianus*, Summer Ranges: Optimal Foraging?

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Demma, Dominic J., and L. David Mech. 2009. Wolf, *Canis lupus*, visits to White-tailed Deer, *Odocoileus virginianus*, summer ranges: optimal foraging? *Canadian Field-Naturalist* 123(4): 299–303.

We tested whether Wolf (*Canis lupus*) visits to individual female White-tailed Deer (*Odocoileus virginianus*) summer ranges during 2003 and 2004 in northeastern Minnesota were in accord with optimal-foraging theory. Using GPS collars with 10- to 30-minute location attempts on four Wolves and five female deer, plus eleven VHF-collared female deer in the Wolves' territory, provided new insights into the frequency of Wolf visits to summer ranges of female deer. Wolves made a mean 0.055 visits/day to summer ranges of deer three years and older, significantly more than their 0.032 mean visits/day to ranges of two-year-old deer, which generally produce fewer fawns, and most Wolf visits to ranges of older deer were much longer than those to ranges of younger deer. Because fawns comprise the major part of the Wolf's summer diet, this Wolf behavior accords with optimal-foraging theory.

Key Words: Wolf, *Canis lupus*, White-tailed Deer, *Odocoileus virginianus*, predation, optimal foraging, Minnesota.

Two aspects of optimal-foraging theory involve optimal choice of food patches and optimal allocation of time to food patches of different value (Pyke et al. 1977). Wolves (*Canis lupus*) feeding on deer fawns (*Odocoileus* spp.) during summer are faced with such optimal foraging decisions, but heretofore it has been impossible to study this problem. Now new technology has made it possible, and we report a preliminary study as an example of what can now be accomplished.

Northern White-tailed Deer (*Odocoileus virginianus*) migrate to individual traditional summer ranges during spring (Ozoga et al. 1982; Nelson and Mech 1984; Nelson et al. 2004), and fawns are born there during an annual birth pulse that peaks in early June (Kunkel and Mech 1994). Parturient does space out from conspecifics and greatly restrict their movements as fawning approaches, and they continue to maintain exclusive sites during fawn-rearing (Nelson and Mech 1981). This behavior facilitates bonding between the mother and fawn(s), but also constitutes an optimum defense strategy against predators while young fawns are particularly vulnerable (Nelson and Mech 1981; Mech 1984; Kunkel and Mech 1994).

Reproductive performance in White-tailed does differs between young and older age classes. Because of

lower pregnancy and fecundity rates, two-year-olds produce fewer fawns per doe than older (three years and older) deer (Ozoga et al. 1982; Ozoga and Verme 1986; DelGuidice et al. 2007). Fawns are the primary prey of Wolves in White-tailed Deer range during summer (Frenzel 1974; Van Ballenberghe et al. 1975; Nelson and Mech 1986; Kunkel and Mech 1994).

Demma et al. (2007) characterized movements of five GPS-collared members of a Wolf pack in relation to summer ranges of GPS-collared female deer. All summer ranges of GPS-collared deer within the Wolf pack territory were visited by at least one GPS-collared pack member. Wolves visited the summer ranges of GPS-collared deer frequently (one Wolf visit per 3–5 days on average), and the amount of time GPS-collared Wolves spent in the summer ranges of GPS-collared deer varied from 1 to 22 hours.

Almost nothing else is known about summer Wolf interactions with deer because of the difficulty of studying this subject, but GPS collars afford a new opportunity to address the issue. Any piece of added information will begin to better elucidate the subject. Thus we present new information about the rate of visits by Wolves to the ranges of female deer of different ages. Because two-year-old female deer would generally

be accompanied by fewer fawns than older deer, optimal foraging theory predicts that Wolves would visit the ranges of the younger deer less often, other factors being equal. Thus we used GPS collars on Wolves and GPS and VHF collars on deer during the Demma et al. (2007) study to compare frequency of Wolf visits to the summer ranges of deer of both ages.

Study Area

We conducted this study during the summers of 2003 and 2004 in the 240-km² territory of the Pike Lake Wolf pack in the Superior National Forest of northeastern Minnesota (48°N, 92°W) (Figure 1). Nelson and Mech (1981) provided a detailed description of the study area. Wolves occurred throughout the study area at densities of 28–36/1000 km² (L. D. Mech, unpublished data). The area is near the northern limit of deer range, and density was an estimated 12–15 deer/10 km² (M. H. Dexter, Minnesota Department of Natural Resources, unpublished report).

Methods

During May–July 2003 and 2004, we live-trapped and anesthetized Wolves using standard techniques (Mech 1974; Demma et al. 2007). Wolves were examined for general condition, sexed, weighed, ear-tagged, and aged by tooth wear (Gipson et al. 2000). We took measurements of testes and teats to assess reproductive status (Mech 2006), and administered antibiotics.

We fitted the Wolves with GPS radio-collars that we programmed to obtain locations at either 10-min or 15-min intervals, 24 hours per day (Televilt, Lindesberg, Sweden, and Advanced Telemetry Systems, Inc. [ATS], Isanti, Minnesota, USA). The GPS collars contained either drop-off mechanisms that we programmed to release after 110 or 130 days post start-up (Televilt) or that we could release at will (ATS) by a remotely operated transceiver (Mech and Gese 1992).

We captured adult female deer during March 2003 and 2004 in collapsible Clover traps (McCullough 1975). The captured deer were anesthetized, examined, and sampled using standard techniques (Mech et al. 1985; Kreeger 1996; Nelson 2001). We attached a VHF radio-collar or releasable ATS GPS collar (Merrill et al. 1998). We programmed the deer GPS collars to obtain one location per week until 15 May and one location per 30 min thereafter. We remotely released the collars from the deer after the GPS battery level dropped below the threshold required to obtain fixes.

To minimize any potential movement bias resulting from capture and immobilization, we arbitrarily excluded Wolf GPS locations collected during the first five days post capture. We plotted all GPS data in ArcMap (ESRI, Inc., Redlands, California) and used Hawth's Analysis Tools (www.spatialecology.com) to calculate minimum convex polygons for deer (MCPs; Mohr 1947). We used this common method because

TABLE 1. Background data on VHF- and GPS-collared deer with home ranges that overlapped with GPS-collared Wolves during summer 2003 and 2004 in the Superior National Forest of northeastern Minnesota.

Year	Deer No.	Age	Number of locations	Collar type
2003	8066	3	9	VHF
2003	8070	7	11	VHF
2003	8076	2	9	VHF
2003	8080	2	7	VHF
2003	8082	5	11	VHF
2003	8084	2	803	GPS
2003	8094	3	2808	GPS
2003	8104	3	1359	GPS
2003	8110	2	739	GPS
2004	8066	4	9	VHF
2004	8070	8	11	VHF
2004	8076	3	9	VHF
2004	8080	3	7	VHF
2004	8082	6	11	VHF
2004	8110	3	7	VHF
2004	8114	3	7	VHF
2004	8118	7	12	VHF
2004	8126	7	11	VHF
2004	8142	3	10	VHF
2004	8144	2	9	VHF
2004	8158	8	1403	GPS

the MCPs of our GPS-collared deer included 739–2808 locations (Table 1) without large voids, thus minimizing two of the main MCP biases (White and Garrott 1990). We defined summer ranges of GPS-collared deer as MCPs comprising all locations from 15 May to 15 August. The MCPs generally contained dense point clusters with a few outliers that we arbitrarily excluded if they were >200 m away. The mean proportion of GPS locations excluded was 1%. Because many fewer locations were available for VHF-collared deer, we did not exclude outliers for MCP calculations. We combined 2003 and 2004 summer VHF locations for deer studied during both summers because female deer in this area use the same ranges each summer (Nelson 1979; Nelson and Mech 1984). We used a two-sample *t* test to compare mean MCP area calculated using GPS and VHF locations.

We calculated the frequency of Wolf visits to the summer range of each radio-collared deer by dividing the number of GPS Wolf visits by the number of GPS Wolf days. We calculated GPS Wolf days for each deer summer range by summing the study tenures of all GPS Wolves whose summer territories overlapped the deer ranges. We considered Wolf locations to be within deer MCP boundaries as visits, and we counted each visit as separate if Wolf locations and approximated travel paths (lines connecting successive locations) indicated that the Wolf left the deer summer range and had traveled >500 m away before revisiting or if it

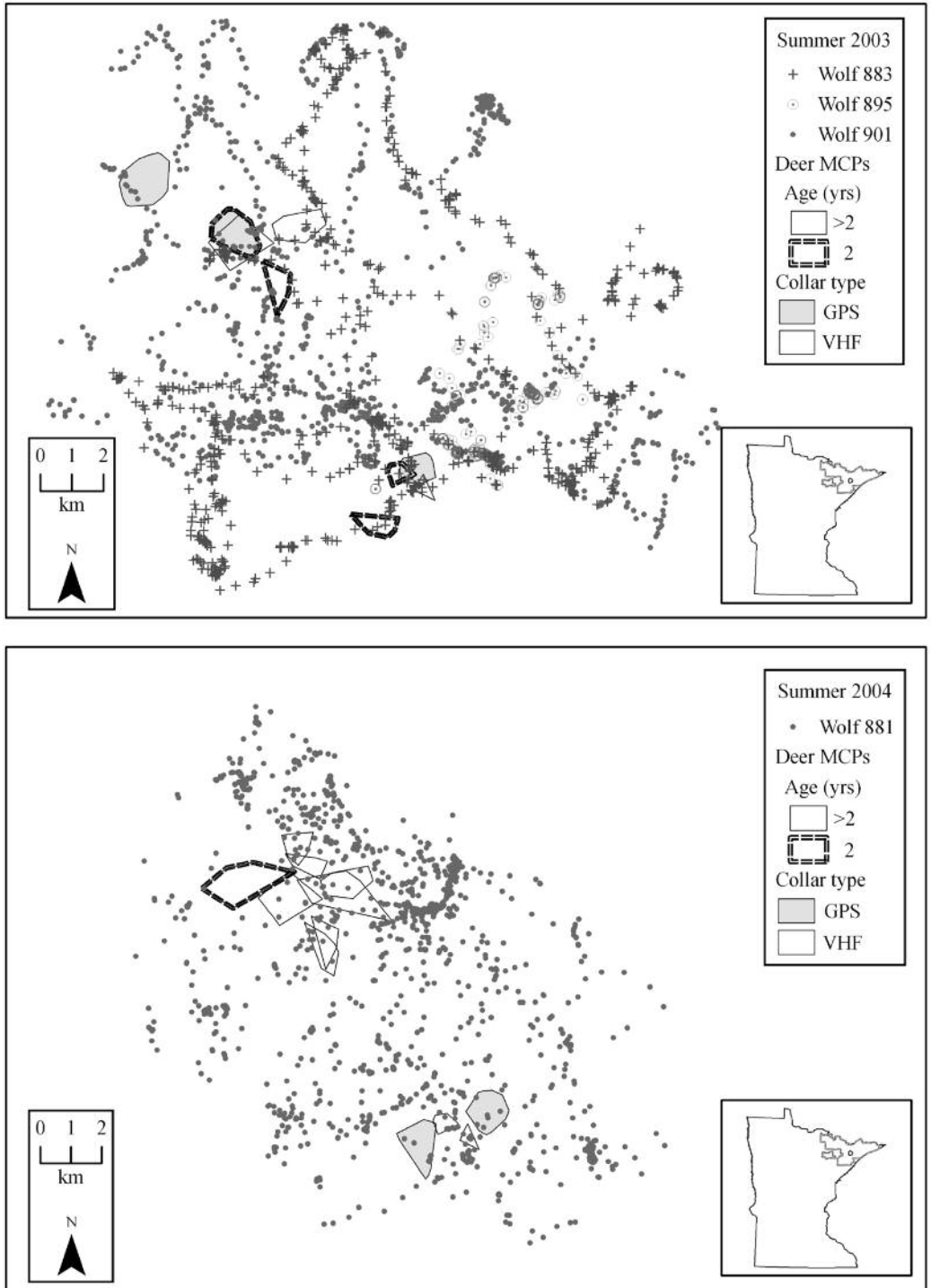


FIGURE 1. Locations of GPS-collared Wolves and locations of minimum convex polygons (MCPs) of VHF- and GPS-collared deer within Wolf pack territory during summers 2003 and 2004 in the Superior National Forest of north-eastern Minnesota.

returned ≥ 12 hours later. We also calculated Wolf visits to within 200 m of the boundaries of a deer MCP in case our deer MCPs were incompletely described (White and Garrott 1990).

We used a two-sample *t* test to test for differences in the mean frequencies of Wolf visits to young (two-year-old) versus older (three years old and older) deer and to test for differences in the mean time spent visiting each. We defined significance as $P < 0.05$.

Results

We captured and instrumented three Wolves in 2003 and one Wolf in 2004 to study Wolf visits to deer summer ranges (Demma et al. 2007; Table 1). The study Wolves consisted of two females and two males, 1 to 8 years old. All Wolves were determined to be non-breeders (Mech 2006), with the exception of Wolf 881, an eight-year-old breeding male. Mean GPS study period per Wolf was 34 days ($SD = 10$, $n = 4$) and number of locations per Wolf averaged 1960 ($SD = 804$, $n = 4$).

We captured and instrumented with ATS GPS collars four deer in March 2003 and one deer in March 2004. Each deer migrated to summer ranges that overlapped spatially and temporally with GPS Wolf territories (Table 1). The GPS tenure of deer averaged 91 days ($SD = 4$), and the mean number of GPS locations per deer was 1422 ($SD = 833$). Mean area of summer MCPs, which included a nearby GPS-collared deer that did not overlap with any GPS-collared Wolves, averaged 137 ha ($SD = 37$).

We captured, aged, and instrumented with VHF collars five deer in winter 2003 and six deer in winter 2004. Each deer migrated to summer home ranges that overlapped with GPS Wolf territories (Table 1). All five of the VHF-collared deer studied during 2003 returned to those summer ranges in 2004. The mean VHF MCP area (109 ha, $SD = 78$) was less than, but not significantly different from ($t_{15} = 0.81$; $P = 0.43$), the mean GPS MCP area (137 ha, $SD = 15$). The combination of the GPS and VHF radio-collared deer yielded a sample of five deer summers of data for two-year-old deer and 16 deer summers for deer three years old and older.

Our GPS-collared Wolf pack members visited the summer ranges of all radio-collared deer within the territory (Figure 1). Wolves made a total of 50 visits to summer ranges of GPS-collared and VHF-collared deer, with a mean of two ($SE = 0.2$) GPS-collared Wolf visits per deer. Wolf 883 visited 9 of 9 deer summer ranges during a 33-day period, and Wolf 901 visited six of six deer summer ranges during a 32-day period, both in 2003. Wolf 895 had a study period of only five days and visited summer ranges of two of four radio-collared deer before dispersing from the territory in late June 2003 (Figure 1). Wolf 881 visited 12 of 12 known deer summer ranges in the territory during a 48-day study period in 2004. Although multiple Wolf pack members were radio-collared during 2003, the number of summer ranges of radio-collared deer over-

lapping each Wolf's range was different. This was due in part to temporal differences in Wolf study periods as well as to individual Wolf summer movement patterns within the territory.

Wolves visited summer ranges of two-year-old deer an average of 0.032 times/day and visited the summer ranges of older deer an average of 0.055 times/day ($t_{19} = 2.1$; $P = 0.05$). Wolves also spent much less average time visiting younger deer ranges (1.8 vs. 10.1 hours), although that difference was not significant ($t_{3,3} = 1.5$; $P = 0.22$). We also compared daily visits of Wolves to within 200 m of deer summer ranges in case our deer MCPs were incompletely described (White and Garrott 1990). Wolves made 0.044 visits/day to the 200 m-buffered MCPs of two-year-old deer and 0.075 visits/day to those of older deer ($t_{19} = 2.0$; $P = 0.06$).

Discussion

Our GPS-collared Wolves visited the summer ranges of all radio-collared deer within their territory (Demma et al. 2007). They visited the summer ranges of deer three years old and older more frequently than those of two-year-old deer and most spent more time there, although average difference in time spent was not significant. Because deer three years old and older tend to produce more fawns than two-year-olds do (Ozoga et al. 1982; Verme and Ullrey 1984; Ozoga and Verme 1986; DelGuidice et al. 2007), the greater number of Wolf visits we observed to ranges of older deer is consistent with the assumed food value of those ranges. Older deer can produce one to three fawns per year, so multiple Wolf visits to summer ranges of older deer, even after a Wolf kills a fawn there, could lead to another kill. Thus return trips of Wolves to deer home ranges where fawns had already been killed would not necessarily result in reduced hunting success.

The amount of overlap among our deer summer ranges varied, and because not every deer in the Wolf territory was collared, we could not determine actual densities of prey patches in each deer MCP. The ranges of three of the five two-year-old deer did not overlap with any older radio-collared deer, but one other overlapped 38% with the range of an older deer and another overlapped 74% with the range of an older deer. Because such overlap could have confounded our analyses, we tested our results after eliminating those from the two younger deer that overlapped with the older ones, and the results were still significant.

Our estimated number of Wolf visits to deer home ranges increased with the addition of the 200-m buffer. However, most Wolf visits were within the core MCP boundaries of GPS- and VHF-collared deer, and comprised 71 and 73% of total visits, respectively. We feel that the addition of the 200-m buffers (and corresponding Wolf visits) to the deer home ranges, albeit somewhat arbitrary, is a reasonable method to estimate Wolf visits to deer home ranges that may be underestimated by location data.

With or without the buffer, the behavior of the Wolves we studied accords with optimal foraging theory (Pyke et al. 1977), and suggests that even Wolves facing their initial summer of hunting deer fawns soon learn which food patches to visit more frequently.

Acknowledgments

This study was supported by the Biological Resources Discipline, U.S. Geological Survey, U.S. Department of Agriculture North Central Research Station, the W & M Foundation, the University of Minnesota, and Valerie Gates. We thank numerous volunteer technicians for completing long hours of field work in often challenging conditions, and Shannon Barber-Meyer and Dan MacNulty for critiquing the manuscript.

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Received 13 January 2009

Accepted 2 July 2010