

Direct Estimation of Early Survival and Movements in Eastern Wolf Pups

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ABSTRACT Determining juvenile survival and recruitment rates is essential to assess status and viability of animal populations. Currently, the demographic attributes of juvenile carnivores, specifically wolves (*Canis lycaon*), are poorly known but of considerable conservation interest. We measured survival and dispersal rates for 51 juvenile (age 3.5–31 weeks) wolves in Algonquin Provincial Park, Canada, from 2004 to 2005, using implantable very high frequency transmitters. Monthly pup survival was high (0.970, 95% CI = 0.951–0.990) and constant from June to November, and most pup mortality was from natural causes. Pups dispersed as early as age 15 weeks, and monthly dispersal rates were high for young pups (min. = 0.008, 95% CI = 0.000–0.019; max. = 0.030, 95% CI = 0.010–0.050). We failed to detect any influence of pack or litter size on pup survival or probability of dispersal. Radiotelemetry offers an individual-based monitoring technique capable of providing direct assessment of wolf pup survival and movements, with rigorous estimation of survival and dispersal rates and quantification of cause-specific mortality. (JOURNAL OF WILDLIFE MANAGEMENT 72(4):949–954; 2008)

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Basic demographic attributes, such as survival and dispersal, are difficult to measure in juvenile mammals, thus their contribution to population dynamics often remains unclear (Laurenson 1994, Echols et al. 2004). Yet, juvenile survival and dispersal should play an important role in determining population trend and viability among carnivores (DelGiudice et al. 1991, Laurenson 1994, Fuller et al. 2003). Theory suggests that carnivore populations should have high juvenile survival, particularly among social species where juvenile dispersal is often delayed and nonbreeding helpers assist in food provisioning (Moehlman 1979, Harrington et al. 1983, Jennions and Macdonald 1994, Russell et al. 2002). However, these conclusions are largely speculative because few studies have estimated survival and dispersal of juvenile carnivores using robust methods before the age where individuals can safely be marked with radiocollars (i.e., <4 months for wolves; Van Ballenberghe and Mech 1975, Mech 1977). Thus, there is a critical need for improved estimation of the demographic attributes of juvenile carnivores.

Survival rates of juvenile wolves (*Canis lycaon*) have been difficult to estimate. Most studies of wolf pup survival are based on passive monitoring techniques that may provide potentially biased measures of survival (e.g., Rausch 1967, Van Ballenberghe and Mech 1975, Harrington et al. 1983, Fuller 1989, Smith et al. 2006). For example, litter counts (e.g., Fuller 1989, Smith et al. 2006) only provide estimates of apparent survival because fate of individuals lost to follow-up (i.e., death or dispersal) cannot be determined.

This is of particular concern in studies where mortality appears to be elevated for young pups (e.g., Mech and Goyal 1993, Johnson et al. 1994, Smith et al. 2006). In addition, there is little direct knowledge of wolf pup dispersal patterns during the early juvenile period (i.e., <8 months of age) except for a few telemetry studies conducted in late summer that suggest such events are uncommon (Gese and Mech 1991, Mech and Boitani 2003). Documenting detailed movements of wolf pups should also be important from the standpoint of understanding social dynamics and susceptibility to mortality.

We investigated survival and dispersal among juvenile eastern wolves in Algonquin Provincial Park (APP), Canada, using intraperitoneal radiotransmitters surgically implanted in 4–6-week-old wolf pups. We predicted that survival for pups aged 1–7 months would be low based on previous surveys suggesting consistently low pup recruitment in APP (Theberge and Theberge 2004). We also predicted that early dispersal rates would be low and that movements would increase progressively during the early postweaning period as pups matured and became more mobile (e.g., Joslin 1967, Mech and Boitani 2003).

STUDY AREA

Algonquin Provincial Park lay at the southern edge of the Canadian Shield and the ecotone between boreal and Great Lakes–St. Lawrence forests in south-central Ontario, Canada (45°N, 78°W; 7,571 km²; Pimlott et al. 1969, Patterson et al. 2004). The western side of the Park was dominated by tolerant hardwood species (sugar maple [*Acer saccharum*], American beech [*Fagus grandifolia*], yellow birch [*Betula alleghaniensis*], and eastern hemlock [*Tsuga canadensis*]), and was characterized by glacial till over rugged terrain and elevations up to 580 m (Pimlott et al. 1969, Patterson et al. 2004, Quinn 2004). The western uplands

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transitioned to sandy outwash and rolling to flat terrain in the eastern third of the APP, which was dominated by conifer species (eastern white pine [*Pinus strobus*], red pine [*P. resinosa*], and jack pine [*P. banksiana*]), intolerant hardwoods (paper birch [*Betula papyrifera*], quaking aspen [*Populus tremuloides*], northern red oak [*Quercus rubra*], sugar maple, and red maple [*Acer rubrum*]) and lower elevations (180–380 m; Pimlott et al. 1969, Cook 1999, Quinn 2004). Population densities and basic dynamics of wolves within the Park were consistent from 2002 to 2007, when an intensive study was conducted on the adult wolf population (B. Patterson, Ontario Ministry of Natural Resources, unpublished data).

METHODS

We identified wolf den sites in spring via monitoring of radiocollared adults (2004: $n = 11$ packs, 2005: $n = 15$ packs; Crawshaw et al. 2007). We captured pups manually at the den 4–6 weeks after the date that collared adult wolves first localized at the den site. We weighed, sexed, and implanted a very high frequency radiotransmitter with a mortality sensor (Advanced Telemetry Systems, Isanti, MN, or Telonics, Mesa, AZ) in the peritoneal cavity of each pup (Crawshaw et al. 2007). All capture and implanting procedures were approved by Trent University and Ontario Ministry of Natural Resources Animal Care Committees. We estimated pup age in weeks using body size and degree of tooth eruption at the time of capture (Rutter and Pimlott 1968, Van Ballenberghe and Mech 1975). We collected blood from the cephalic vein of each pup, and serum was tested for antibodies to canine parvovirus-2 (CPV-2) by hemagglutination inhibition and to canine distemper (CD) by virus neutralization at the Animal Health Laboratory (University of Guelph, Guelph, ON, Canada). We returned pups to the den when they became ambulatory following surgery, and we monitored the den after evacuating the site to ensure that pups were not abandoned by adults. We continued monitoring transmitted pups for survival via ground or aerial telemetry every 2–3 days after capture until the end of August and weekly thereafter. We determined cause of death for each pup using evidence at the mortality site and detailed necropsies conducted by personnel from the Canadian Cooperative Wildlife Health Centre, University of Guelph.

We estimated survival rates using a generalized Kaplan–Meier survival model with staggered entry (Pollock et al. 1989). In all models, the mean estimated whelping date for both years constituted day 1 of the study (i.e., the entry day for all transmitted pups into the risk set), and we calculated monthly survival rates through 30 November of each year, at which time we right-censored all pups known to still be alive. We obtained cause-specific mortality estimates via the nonparametric cumulative incidence function estimator as described by Heisey and Patterson (2006). We also fit a parametric Weibull survival analysis to test the hypothesis of constant survival rate during the study period (McCallum 2000, Murray 2006).

We analyzed effects of ecological factors on wolf pup survival using Cox Proportional Hazards (CPH) regression models (Cox 1972). Variables we included in CPH models were the natal pack of each pup, gender of the pup, and number of adult members in the natal pack (i.e., max. no. of individuals verified to be with the pack on >1 occasion during the previous winter). We also included litter size as a time-dependent covariate in survival analyses. Because pup survival within litters might not be independent, we used clustering to identify littermates in all CPH analyses to achieve robust variance estimation (Lin and Wei 1989).

We defined dispersal as emigration from the natal territory without returning for the remainder of the study period (Gese and Mech 1991). We used generalized Kaplan–Meier estimators with staggered entry to generate residency rates, and we then calculated dispersal rates at $1 - \text{residency rates}$ (Pollock et al. 1989, Patterson and Messier 2001). Some pups disappeared from their natal territory after exhibiting predispersal behavior (e.g., they were last located apart from any transmitted littermate or ad pack member) but before the anticipated expiry of transmitter batteries and were not subsequently relocated following extensive aerial and ground searches within the natal territory. We considered such individuals probable dispersers and included them with known dispersers to obtain a maximum dispersal rate (Pollock et al. 1989). Inclusion of probable dispersers is supported by the disparity between the long distances moved by all known dispersers shortly after leaving their natal territory (20–40 km) and the limited reception range of implanted transmitters (4–7 km during aerial telemetry; Crawshaw et al. 2007). We also calculated a minimum dispersal rate using only individuals that were verified to have dispersed (Pollock et al. 1989). We used CPH models with clustered littermates to analyze effects of natal pack, gender, litter size (time dependent), and pack size on dispersal using the data set that included probable dispersers.

We recorded the succession of homesites that each monitored litter used throughout summer as well as the number of days spent at each homesite and the linear distance moved between successive homesites. We described movement characteristics of aging pups by dividing the study period into 4 intervals: 1) denning (age < 6 weeks), 2) early rendezvous (age = 6–11 weeks), 3) late rendezvous (age = 12–17 weeks), and 4) rendezvous abandonment (age ≥ 18 weeks). We then used each interval in a repeated-measures analysis of variance (ANOVA) to examine effects of age class, natal pack, litter size, and pack size on the described movement metrics. We did not include occupancy times for disturbed homesites in analyses because the pack subsequently abandoned these sites (Argue et al., in press). Likewise, we did not include distances moved from disturbed homesites in analyses.

We also recorded the date that each litter abandoned rendezvous sites, and we used simple multiple regression to determine the relationship between natal pack, year, pack size, and litter size on the timing of rendezvous site

abandonment. We defined litter cohesion as the proportion of the litter located together at a given time, and we quantified this parameter via repeated-measures ANOVA using the same age classes and dependent variables as in movement analyses. We log-transformed all movement and homesite occupancy data before analysis to promote normality.

RESULTS

We estimated average birth date of pups in APP to be 29 April \pm 1.9 days for 2004 and 2005 (SE; range = 18 Apr–11 May). However, estimated parturition date for pups born in 2005 (27 Apr \pm 2.8 days) was earlier than in 2004 (4 May \pm 2.2 days; $t_{11} = 2.37$, $P = 0.04$). We conducted pup captures from 29 May to 16 June during both years. We implanted 53 pups from 13 litters with transmitters (2004: $n = 20$ pups from 5 litters; 2005: $n = 33$ pups from 8 litters). Mean age of captured pups was 5.5 \pm 0.4 weeks (range = 3.5–8 weeks), mean litter size was 4.6 \pm 0.6 pups (range = 2–7, $n = 10$, we excluded 3 partial litters), and sex ratio of marked pups was close to parity (27:26 M:F). Adults returned to each den site shortly after our departure and relocated pups to a new den site, usually 0.4–2.0 km away. We found no evidence of pup abandonment following transmitter implanting and only 2 cases (3.8% of pups implanted) where our handling procedure may have contributed to negative impacts on pup survival (Crawshaw et al. 2007). We censored these 2 littermates from all subsequent analyses.

Monthly survival of wolf pups (all yr combined) was 0.970 (95% CI = 0.951–0.990), and survival for the entire 31-week study period was 0.806 (95% CI = 0.699–0.930). We recorded 9 pup mortalities, 6 from natural causes and one human caused; the cause was not determinable for 2 deaths. Causes of natural mortality included drowning ($n = 2$), conspecific strife ($n = 1$), black bear predation ($n = 1$), and other causes (e.g., intrapack strife, $n = 1$). No mortalities were attributed to CPV-2 or CD based on findings at necropsy and limited evidence for active infection of CPV-2 in pups. The single human-caused mortality was due to shooting. Cumulative hazard rate estimates were 0.125 (95% CI = 0.046–0.205) for natural deaths and 0.025 (95% CI = –0.015–0.066) for human-caused deaths for the entire 31-week study period.

Weibull survival analysis revealed that mortality risk was relatively constant for the June–November period (all yr combined; $P = 1.68$, 95% CI = 0.93–3.02, $z_1 = 1.73$, $P = 0.084$; Fig. 1). However, no pup mortalities occurred before the age of 11 weeks (18 Jul), after which mortalities occurred at a constant rate. The CPH revealed that litter size, pack size, and gender did not affect pup mortality risk (all $P \geq 0.31$). Mortality risk was marginally different between packs (all yr combined; $z = 1.64$, $P = 0.100$), with packs experiencing pup mortality ranging from 0–50% of the litter in any given year. We were unable to identify specific factors predisposing pups to higher mortality risk within particular packs.

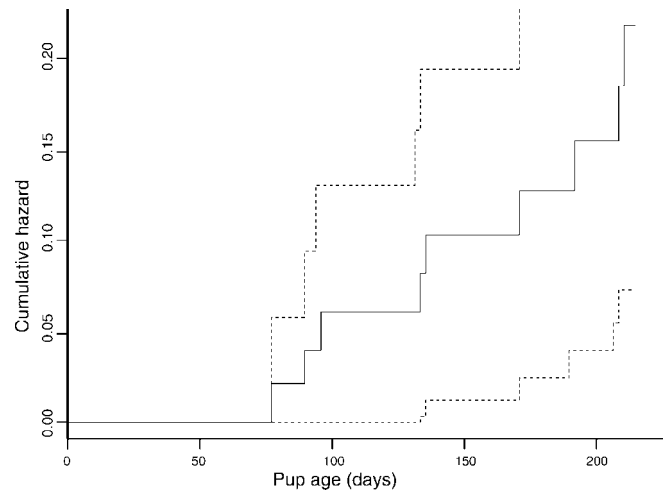


Figure 1. Nelson–Aalen cumulative hazard function (\pm 95% CI) for wolf pups monitored in Algonquin Provincial Park, Ontario, Canada ($n = 51$; 2004–2005). We calculated cumulative hazard using all observed mortalities, excluding 2 pups that died from capture-related disturbance.

We considered that 9 of 51 pups dispersed during the study period; 3 of these events were confirmed and 6 were suspected based on criteria described in the methods. Estimated maximum monthly dispersal rate was 0.030 (95% CI = 0.010–0.050) during the study period and was 0.198 (95% CI = 0.072–0.307) for the entire 31 weeks. Minimum monthly dispersal rate was 0.008 (95% CI = 0.000–0.019) and was 0.055 (95% CI = 0.000–0.129) for the entire study period. The youngest age that we verified any pup to have dispersed was 15 weeks (19 Aug). Natal pack, gender, litter size, and pack size did not affect dispersal tendencies for pups (all $P \geq 0.17$). No known disperser formed or joined an existing pack before 30 November. One disperser was killed by conspecifics in a territory adjacent to its natal territory within days following dispersal. Another spent much of the autumn localized near a municipal garbage dump approximately 20 km from its natal territory. The remaining verified disperser survived past 30 November, spent the winter >30 km from its natal territory and returned to its natal pack in June of its second year.

Dens and early rendezvous sites were occupied longer than rendezvous sites used later in summer ($F_{3,36} = 163.9$, $P < 0.01$; Fig. 2a). Number of days that litters spent at individual homesites was positively correlated to pack size ($F_{3,36} = 3.0$, $P = 0.03$), but the effect size was small and probably of limited biological relevance (increase of 0.53 days/ad individual in the pack). Natal pack and litter size were not important determinants of homesite occupancy (all $P \geq 0.19$).

Litters were moved very short distances, if at all, in their first 6 weeks. However, movement distance increased progressively as pups became older ($F_{3,36} = 55.2$, $P < 0.01$; Fig. 2b). Natal pack, litter size, and pack size did not affect movement distance (all $P \geq 0.64$). Litters showed decreased cohesion during and after abandoning rendezvous sites relative to when pups were younger ($F_{2,9} = 5.7$, $P =$

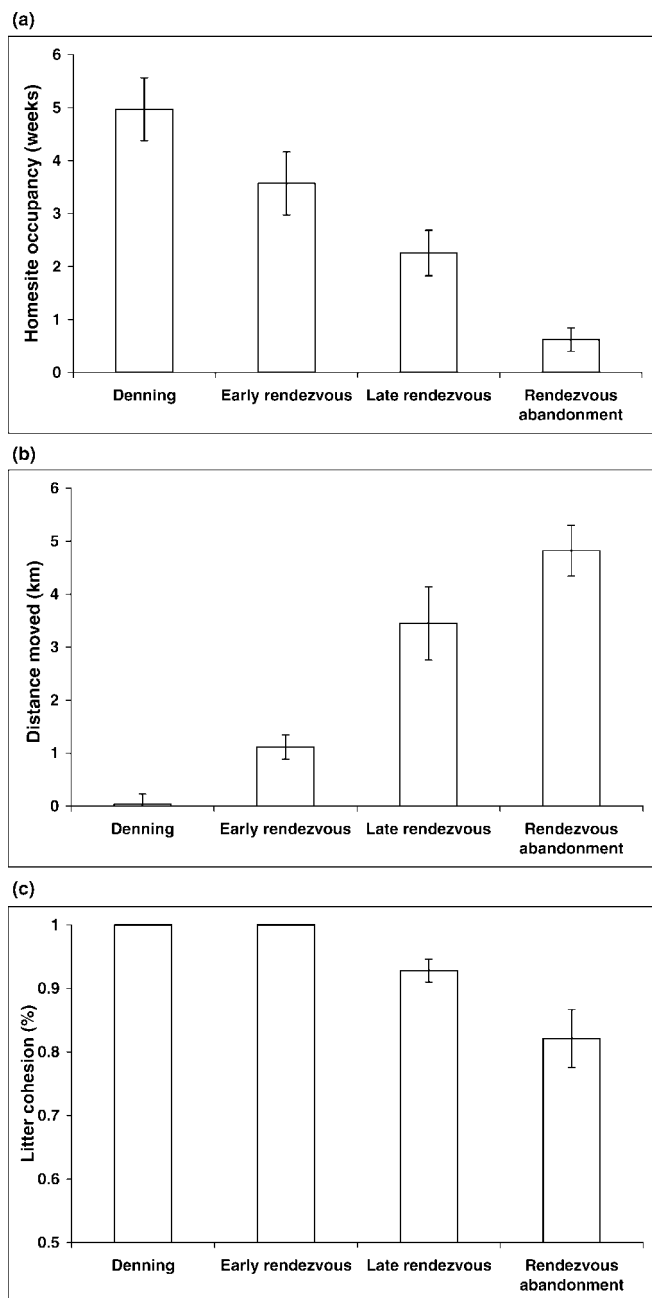


Figure 2. Wolf pup age separated into 4 increasing age classes (denning, early rendezvous, late rendezvous, and rendezvous abandonment), and mean (\pm SE) (a) duration of homesite occupancy, (b) distance moved between homesites or relocations, and (c) litter cohesion expressed as the percentage of the litter that was together, for 13 wolf litters implanted with intraperitoneal radio transmitters in Algonquin Provincial Park, Ontario, Canada, 2004–2005.

0.03; Fig. 2c). Litter cohesion was not affected by natal pack, litter size, or pack size (all $P \geq 0.38$).

Litter cohorts showed annual variation in the age that they abandoned rendezvous sites ($F_{1,12} = 8.85$, $P = 0.02$), with the 2005 litter cohort doing so 3.4 weeks younger than the 2004 cohort (2004: 20.7 ± 0.8 weeks or 25 Sep; 2005: 17.3 ± 0.7 weeks or 26 Aug). Natal pack and pack size did not affect age at which litters abandoned rendezvous sites (all $P \geq 0.45$), but litter size showed a marginally significant

inverse relationship with age when rendezvous sites were abandoned ($F_{1,12} = 4.62$, $P = 0.07$).

DISCUSSION

Our study is the first to document wolf pup survival and movements from weaning to beginning of their first winter and thus presents the only individual-based estimate of pup survival and dispersal for the summer and early-fall. Summer pup survival in APP was high but within the large range of apparent survival rates reported previously for wolf pups (i.e., 0.36–0.91; Fuller et al. 2003). Timing of pup deaths suggests that mortality risk is greater after pups are fully weaned and become more independent. Most deaths were due to natural causes, and mortality appeared to be independent of commonly inferred risks in juvenile canids, such as starvation or CPV-2 infections. The only covariate that may have affected pup mortality risk was the natal pack of the litter, indicating that packs likely vary in their ability to raise pups to independence.

We detected pups dispersing from natal packs at an earlier age than recorded previously for wolves (Mech and Boitani 2003). We did not identify any social, physical, or environmental factors promoting early juvenile dispersal. Therefore, detection of early dispersal for pups in APP may merely reflect the advantage of monitoring juveniles intensively in their first months. Conversely, given the alleged genetic distinction between eastern wolves and gray wolves and the evolutionary relatedness of eastern wolves and coyotes, early dispersal among eastern wolves in APP may reflect differences in life history patterns (Harrison 1992, Gese et al. 1996, Wilson et al. 2000, Grewal et al. 2004). Regardless of the mechanism, we would have misinterpreted the reduction in litter size due to dispersal as probable mortality events had we estimated pup survival using indirect techniques. Although early juvenile dispersal usually begets low survival and production, ≥ 1 pup that dispersed before November survived past the age of 24 months (Gese and Mech 1991, Schauster et al. 2002). Thus, at least some early dispersers have the opportunity to establish or join packs. Our findings suggest additional research is needed to determine 1) survival and success of early dispersers in terms of their demographic contribution to the population, and 2) the mechanisms promoting early dispersal of wolf pups.

As pups aged, we found that the distance moved between homesites increased and the duration of stay at homesites and cohesiveness of litters decreased. This decrease in occupancy times and cohesiveness at later homesites parallels the waning dependence of pups on homesites and may expose pups to additional mortality factors. Pup movements were largely independent of differing social factors, such as pack size, litter size, and the natal pack of the litter, suggesting that these homesite shifts are governed by other undetermined factors, such as prey availability. Litter size may have affected age at which litters abandoned rendezvous sites, but it was likely more a function of the stage of pup development, which can vary annually but could not be assessed directly (Harrington and Mech 1982).

We present the first comprehensive direct estimates of wolf pup survival, cause-specific mortality, dispersal, and movements from weaning through beginning of winter. The demonstrated safety of capture and implanting protocols (i.e., Crawshaw et al. 2007) should alleviate concerns related to den disturbance and thus encourage other researchers to adopt these methods when seeking to estimate early survival and dispersal or to elucidate causes of death in juvenile carnivores.

Management Implications

Our study revealed that pup production and survival for APP wolves was higher than that estimated previously (Theberge and Theberge 2004). This disparity may be due to temporal change in APP wolf population dynamics or simply due to improvement in estimation of basic demographic parameters. Regardless, our study demonstrates that it is possible to obtain individual-based demographic information on juvenile wolves that may play a critical role in developing more robust and defensible management strategies. Specifically, the direct estimates of juvenile survival we obtained will assist in development of more realistic population models for wolves in central Ontario. Future research on mammal populations should monitor the demographics of all age cohorts within the study population to fully assess status and allow for proper management (see also DelGiudice et al. 2006).

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LITERATURE CITED

Argue, A. M., K. J. Mills, and B. R. Patterson. In press. Behavioural response of eastern wolves (*Canis lycaon*) to disturbance at homesites and its effects on pup survival. *Canadian Journal of Zoology*.
Cook, S. J., D. R. Norris, and J. B. Theberge. 1999. Spatial dynamics of a

migratory wolf population in winter, south-central Ontario (1990–1995). *Canadian Journal of Zoology* 77:1740–1750.
Cox, D. R. 1972. Regression models and life tables (with discussion). *Journal of the Royal Statistical Society, Series B* 34:187–220.
Crawshaw, G. J., K. J. Mills, C. Mosley, and B. R. Patterson. 2007. Field implantation of intraperitoneal radiotransmitters in eastern wolf (*Canis lycaon*) pups using inhalation anesthesia with sevoflurane. *Journal of Wildlife Diseases* 43:711–718.
DelGiudice, G. D., J. Fieberg, M. R. Riggs, M. Carstensen-Powell, and W. Pan. 2006. A long-term age-specific survival analysis of female white-tailed deer. *Journal of Wildlife Management* 70:1556–1568.
DelGiudice, G. D., L. D. Mech, and U.S. Seal. 1991. Gray wolf density and its association with weights and hematology of pups from 1970 to 1988. *Journal of Wildlife Diseases* 27:630–636.
Echols, K. N., M. R. Vaughan, and H. D. Moll. 2004. Evaluation of subcutaneous implants for monitoring American black bear cub survival. *Ursus* 15:172–180.
Fuller, T. K. 1989. Population dynamics of wolves in north-central Minnesota. *Wildlife Monographs* 105.
Fuller, T. K., L. D. Mech, and J. F. Cochrane. 2003. Wolf population dynamics. Pages 161–191 in L. D. Mech and L. Boitani, editors. *Wolves: behavior, conservation, and ecology*. University of Chicago Press, Chicago, Illinois, USA.
Gese, E. M., and L. D. Mech. 1991. Dispersal of wolves (*Canis lupus*) in northeastern Minnesota, 1969–1989. *Canadian Journal of Zoology* 69:2946–2955.
Gese, E. M., R. L. Ruff, and R. L. Crabtree. 1996. Social and nutritional factors influencing the dispersal of resident coyotes. *Animal Behaviour* 52:1025–1043.
Grewal, S. K., P. J. Wilson, T. K. Kung, K. Shami, M. T. Theberge, J. B. Theberge, and B. N. White. 2004. A genetic assessment of the eastern wolf (*Canis lycaon*) in Algonquin Provincial Park. *Journal of Mammalogy* 85:625–632.
Harrington, F. H., and L. D. Mech. 1982. Fall and winter homesite use by wolves in northeastern Minnesota. *Canadian Field-Naturalist* 96:79–84.
Harrington, F. H., L. D. Mech, and S. H. Fritts. 1983. Pack size and wolf pup survival: their relationship under varying ecological conditions. *Behavioral Ecology and Sociobiology* 13:19–26.
Harrison, D. J. 1992. Dispersal characteristics of juvenile coyotes in Maine. *Journal of Wildlife Management* 56:128–138.
Heisey, D. M., and B. R. Patterson. 2006. A review of methods to estimate cause-specific mortality in presence of competing risks. *Journal of Wildlife Management* 70:1544–1555.
Jennions, M. D., and D. W. Macdonald. 1994. Cooperative breeding in mammals. *Trends in Ecology and Evolution* 9:89–93.
Johnson, M. K., D. K. Boyd, and D. H. Pletscher. 1994. Serologic investigations of canine parvovirus and canine distemper in relation to wolf (*Canis lupus*) pup mortalities. *Journal of Wildlife Diseases* 30:270–273.
Joslin, P. W. B. 1967. Movements and home sites of timber wolves in Algonquin Park. *American Zoologist* 7:279–288.
Laurenson, M. K. 1994. High juvenile mortality in cheetahs (*Acinonyx jubatus*) and its consequences for maternal care. *Journal of Zoology, London* 234:387–408.
Lin, D. Y., and L. J. Wei. 1989. The robust inference for the Cox proportional hazards model. *Journal of the American Statistical Association* 84:1074–1079.
McCallum, H. 2000. Population parameters: estimation for ecological models. Blackwell-Science, Oxford University Press, New York, New York, USA.
Mech, L. D. 1977. Productivity, mortality, and population trends of wolves in northeastern Minnesota. *Journal of Mammalogy* 58:559–574.
Mech, L. D., and L. Boitani. 2003. Wolf social ecology. Pages 1–34 in L. D. Mech and L. Boitani, editors. *Wolves: behavior, conservation, and ecology*. University of Chicago Press, Chicago, Illinois, USA.
Mech, L. D., and S. M. Goyal. 1993. Canine parvovirus effect on wolf population change and pup survival. *Journal of Wildlife Diseases* 29:330–333.
Moehlman, P. D. 1979. Jackal helpers and pup survival. *Nature* 277:382–383.
Murray, D. L. 2006. On improving telemetry-based survival estimation. *Journal of Wildlife Management* 70:1530–1543.

- Patterson, B. R., and F. Messier. 2001. Social organization and space use of coyotes in eastern Canada relative to prey distribution and abundance. *Journal of Mammalogy* 82:463–477.
- Patterson, B. R., N. W. S. Quinn, E. F. Becker, and D. B. Meier. 2004. Estimating wolf densities in forested areas using network sampling of tracks in snow. *Wildlife Society Bulletin* 32:938–947.
- Pimlott, D. H., J. A. Shannon, and G. B. Kolenosky. 1969. The ecology of the timber wolf in Algonquin Provincial Park. Ontario Department of Lands and Forests, Fish and Wildlife Research Report 87, Toronto, Ontario, Canada.
- Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. *Journal of Wildlife Management* 53:7–15.
- Quinn, N. W. S. 2004. The presettlement hardwood forests and wildlife of Algonquin Provincial Park: a synthesis of historic evidence and recent research. *The Forestry Chronicle* 80:705–717.
- Rausch, R. A. 1967. Some aspects of the population ecology of wolves, Alaska. *American Zoologist* 7:253–265.
- Russell, A. F., T. H. Clutton-Brock, P. N. M. Brotherton, L. L. Sharpe, G. M. McIlrath, F. D. Dalerum, E. Z. Cameron, and J. A. Barnard. 2002. Factors affecting pup growth and survival in co-operatively breeding meerkats *Suricata suricata*. *Journal of Animal Ecology* 71:700–709.
- Rutter, R. J., and D. H. Pimlott. 1968. The world of the wolf. J. B. Lippincott, Philadelphia, Pennsylvania, USA.
- Schauster, E. R., E. M. Gese, and A. M. Kitchen. 2002. Population ecology of swift foxes (*Vulpes velox*) in southeastern Colorado. *Canadian Journal of Zoology* 80:307–319.
- Smith, D. W., D. R. Stahler, and D. S. Guernsey. 2006. Yellowstone wolf project: annual report, 2005. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming, USA.
- Theberge, J. B., and M. T. Theberge. 2004. The wolves of Algonquin Park: a 12 year ecological study. University of Waterloo, Department of Geography Publication Series 56, Waterloo, Ontario, Canada.
- Van Ballenberghe, V., and L. D. Mech. 1975. Weights, growth, and survival of timber wolf pups in Minnesota. *Journal of Mammalogy* 56:44–63.
- Wilson, P. J., S. Grewal, I. D. Lawford, J. N. M. Heal, A. G. Granacki, D. Pennock, J. B. Theberge, M. T. Theberge, D. R. Voigt, W. Waddell, R. E. Chambers, P. C. Paquet, G. Goulet, D. Cluff, and B. N. White. 2000. DNA profiles of the eastern Canadian wolf and the red wolf provide evidence for a common evolutionary history independent of the gray wolf. *Canadian Journal of Zoology* 78:2156–2166.

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