WILDLIFE BIOLOGY

Research article

Single visits to active wolf dens do not impact wolf pup recruitment or pack size

Thomas D. Gable[1], Sean M. Johnson-Bice[2], Austin T. Homkes[1] and Joseph K. Bump[1]

[1]Department of Fisheries, Wildlife and Conservation Biology, University of Minnesota, St. Paul, MN, USA
[2]Department of Biological Sciences, University of Manitoba, Winnipeg, Manitoba, Canada

Correspondence: Thomas D. Gable (thomasd.gable@gmail.com)

Wildlife Biology
2024: e01195
doi: 10.1002/wlb3.01195

Subject Editor: Douglas Smith
Editor-in-Chief: Ilse Storch
Accepted 8 December 2023

Evaluating methods used to capture and mark neonates is necessary for ensuring research methods are ethical, follow best practices, and do not have long-term unintended impacts on neonates or populations. We used a quasi-experimental approach (reference versus treatment) to determine whether visiting wolf dens and marking wolf *Canis lupus* pups affects important wolf population metrics. Specifically, we examined whether pup recruitment and pack size differed between packs where we visited dens and handled pups ('disturbed packs' = treatment group) and those where we did not visit dens ('undisturbed packs' = reference group). During 2019–2023, we studied 43 wolf packs and litters, 19 of which were disturbed packs and 24 of which were undisturbed. We found no difference in recruitment or pack size between disturbed and undisturbed wolf packs. However, we did observe substantial annual variation in recruitment and pack size, which indicated that other ecological factors (e.g. prey abundance) were likely responsible for annual changes in recruitment and pack size. Our findings are consistent with several other studies, and together this research indicates that wolf dens can be visited once and wolf pups handled briefly for research purposes without having a measurable effect on recruitment and pack size.

Keywords: handling, pup survival, recruitment, wolf dens, wolf pack, wolf pups

Introduction

Understanding the life-history of wildlife species and how key population parameters (e.g. survival, mortality) vary with age are crucial for understanding the population dynamics of species (Gotelli 2008). Collecting these data is relatively straightforward and non-invasive for species that are readily observable. However, for cryptic species that are challenging to observe, researchers must use alternative methods to collect data and understand the life-history of a species (Smith and Pinter-Wollman 2021). This is particularly true when researchers design studies to investigate the mortality and survival of neonates – both important population parameters that often drive larger population dynamics (Gaillard et al. 1998, Gude et al. 2012).

Researchers commonly capture and handle neonates to count, mark, tag, otherwise distinguish and/or collar individuals in an effort to study neonatal survival and mortality (Benson et al. 2013, Leonard et al. 2017, Severud et al. 2019, Engebretsen et al. 2023). The methods used to do so are often species-specific, as are the responses of wildlife to researchers handling neonates. Some species are sensitive to human disturbance, and handling of young can directly cause mortality via stress (capture myopathy) (Höfle et al. 2004, Seguel et al. 2013) or by causing parents to abandon neonates (Donadio et al. 2012, DelGiudice et al. 2018). However, neonates of many wildlife species can be handled with little-to-no observable adverse effects (e.g. decreasing survival or recruitment of neonates) (Vashon et al. 2003, Powell et al. 2005, Beck et al. 2009, Leonard et al. 2017). Nonetheless, evaluating the methods used to capture and handle neonates is necessary to ensure research methods are ethical, follow best practices, and do not have unintended effects on neonates or populations (Sikes and Bryan 2016, Horning et al. 2019).

Gray wolves *Canis lupus* are a cryptic species that are challenging to study in many areas during the summer when pups are reared. Wolves are particularly difficult to study in densely-forested systems where visibility during summer is extremely limited and reliably observing wolves is not possible. As a result, wolf pup survival, movement, and behavior during this period remains poorly understood in most forested ecosystems (Fuller et al. 2003, Schmidt et al. 2008, Palacios and Mech 2010). To evaluate wolf pup survival and collect data on other important population parameters, researchers often visit dens and extract pups to determine sex and litter size, record morphometrics, and mark individuals before placing pups back in dens (we refer to this process as 'handling pups' hereafter) (Crawshaw et al. 2007, Beck et al. 2009). In other instances, researchers visit dens in an effort to increase endangered wolf populations by introducing captive born pups to wild born litters through cross-fostering efforts (Harding et al. 2016, Gese et al. 2018).

Although several studies have examined how human disturbance and/or handling of pups influences pup survival or recruitment, few have used an experimental approach with control/reference groups (i.e. undisturbed packs) and treatment groups (i.e. disturbed packs) (though see Frame et al. 2007). Rather, most prior work has examined how survival rates of handled pups has changed after capture/marking to understand possible handling-related effects (Crawshaw et al. 2007, Argue et al. 2008, Beck et al. 2009). The lack of an experimental approach is understandable because studying the direct survival of pups in 'control' or 'reference' groups is very difficult – if not practically impossible – in systems where pups are not easily observed.

We have handled pups while visiting active wolf dens in the Greater Voyageurs Ecosystem (GVE), MN, USA for several years to study litter size and wolf pup survival, and to mark wolf pups for identification during subsequent GPS-collaring or monitoring efforts. Using these data in addition to other collected population metrics, we used a unique quasi-experimental approach to evaluate the effects that single visits to dens to mark pups has on pup recruitment (pups added per pack) and pack size (wolves per pack). We examined pack size to specifically assess whether marking pups influences the size of packs in ways other than recruitment. We examined whether pup recruitment and pack size measured later that year were different between packs where we visited dens and marked pups (treatment) versus packs where we did not visit dens and mark pups (reference). Our approach was advantageous because recruitment and pack size can be estimated non-invasively using remote camera arrays. Thus, our study provides a novel and useful assessment of what effects, if any, visiting wolf dens and marking pups may have on wolf pup recruitment and pack size.

Study area

The Greater Voyageurs Ecosystem

The GVE is a 1966 km^2 southern boreal ecosystem situated in the Laurentian Mixed Forest Province. The landscape is typified by dense forests (deciduous, coniferous and mixed) and abundant lakes, bogs, and wetlands interspersed with outcrops and rocky ridges from glacial activity (Gable et al. 2018). The northern portion of the GVE is made up of Voyageurs National Park (882 km^2). The rest of the GVE south of Voyageurs National Park is federal, state, county, timber company, and privately-owned land. Much of the land outside of Voyageurs National Park is actively logged, which results in a landscape of clear-cuts, young forests, wetlands, and mature forests. The GVE has sustained high wolf densities for the past 30 years and average density since 2015 has been 60 wolves 1000 km^{-2} (Gable et al. 2022, 2023), despite wolf hunting and trapping to the north in Canada. Wolves in the GVE were a threatened species per the United States Endangered Species Act for the duration of our study except for a brief period in 2021–2022, when wolves were temporarily delisted (although no legal harvest occurred during this delisting period).

Material and methods

Locating dens

We captured adult wolves using rubber-padded foothold traps, and fitted them with GPS-collars programmed to take locations every 20 min or 6 h. We identified active wolf dens based on the movement of these GPS-collared wolves (Walsh et al. 2016). We generally visited wolf dens during the first two weeks of May when pups were ~ 3–5 weeks old (average date of parturition is 11 April; Voyageurs Wolf Project unpubl. data). Once at dens, we removed pups from the den and placed all pups in a burlap sack together. We then sexed, weighed, and collected biological samples (hair/blood) from each pup individually. We also inserted a passive integrated transponder tag into the scruff of each pup, and ear-tagged pups in 3 of 19 litters. After handling, we placed all pups back in the den together. Total time spent at dens was generally < 30–60 min.

In several instances, we were unable to see the entirety of a den's interior and thus were not certain whether we had observed and/or marked all pups from inside the den. To confirm or update our litter size observations, we placed remote cameras outside of dens to record videos of pups after marking. We estimated average litter size for wolves in the GVE using data from litters where we felt confident that we had observed and counted all pups in a den (e.g. instances where we could observe all pups in a den or where we had repeated trail camera observations of the same number of pups at dens). We considered litter size to be the number of pups observed at a den 3–5 weeks after parturition. We only visited active dens one time, and only returned to dens to recover cameras once dens were abandoned by wolves. All capture and handling of pups and adults was evaluated and approved by Institutional Animal Care and Use Committees at the National Park Service and University of Minnesota (protocols: MWR_VOYA_WINDELS_WOLF and UMN 1905-37051A).

Estimating recruitment and pack size

During 2019–2023, we studied recruitment and pack size for packs where we visited dens and handled pups ('disturbed packs') versus packs where we did not visit dens and handle pups ('undisturbed packs'). To do this, we used remote cameras deployed year-round in strategic locations within pack territories to obtain as many observations of packs traveling together during late summer, fall and winter (Ausband et al. 2022). The number of cameras deployed in our study area increased each year from ~ 50–60 cameras deployed during 2019–2020 to ~ 210–220 cameras deployed during 2022–2023. We studied both disturbed and undisturbed packs in each year of our study to account for the possibility of annual variation in recruitment and pack size estimates (Table 1).

We considered pack size to be the number of wolves in each pack at the end of the biological year, which ends at parturition (Borg and Schirokauer 2022). We therefore estimated pack sizes by obtaining repeated observations of wolf packs using remote cameras (average of eight independent observations per pack; Gable et al. 2022) during our winter monitoring period (1 December–10 April). For more details about methods and effort, see Gable et al. (2022, 2023). We used the repeated observations of wolf packs collected during our winter monitoring period to determine pack composition including the number of surviving pups in each pack (Gable et al. 2022, 2023). We considered recruitment to be the number of pups in each pack that survived their first biological year. Because we could not observe wolves precisely at the end of the biological year (10 April), we assumed that pups that survived through January were recruited (similar to Gude et al. 2012). Mortality risk for pups is highest in late summer and fall (Fuller et al. 2003), and if pups survive to winter, their probability of survival is high which is why pack size in the GVE is almost identical in mid-winter (December) and late winter (March) just before pups are born (Gable et al. 2022, Cassidy et al. 2023). We determined the number of pups in each pack using remote camera video footage because pups are readily distinguishable – based on facial structure and development, pelage, and size (depending on time of year) – from adults for most of the year (Fig. 1, Peterson and Page 1988, Gable et al. 2022). When available, we also used information on wolf pack composition from GPS-collared wolves and pack size/composition data from the previous biological year to help determine the number of pups recruited. In five instances, we were unsure how many pups were recruited in a pack because we did not obtain trail camera footage of sufficient quality to conclusively determine the precise number of pups (Table 1). In such instances, we used all available information on the social composition of a pack during the winter monitoring period (e.g. information from collared wolves, knowledge of breeding pair or adult subordinates in a pack, any observations of pups, etc.) to determine how many pups at a minimum were in a given pack and how many could possibly be in that pack. For example, in 2020, the Huron Pack consisted of four wolves: two of which we knew were the breeding pair – the breeding male was collared and the female readily identified from her appearance – and one subordinate that was clearly a pup. We did not have clear footage of the fourth pack member so we concluded that at a minimum one pup survived and at a maximum two pups survived.

We only included packs for which reproduction occurred or could be confidently assumed to have occurred (e.g. lactating female or pups observed on cameras). We did this because packs that did not reproduce cannot recruit pups in that year and thus were not relevant to this study. We did not include packs if we could not determine whether reproduction occurred (e.g. a new pair of wolves taking over an existing territory in winter).

Table 1. The distribution of wolf packs studied by year and treatment group (disturbed versus undisturbed) in the Greater Voyageurs Ecosystem, MN, USA.

Year	Disturbed	Undisturbed	Total
2019–2020	3*	5	8
2020–2021	6	4†	10
2021–2022	6†	6†	12
2022–2023	4	9	13
Total	19	24	43

*We had minimum and maximum estimates of recruitment for two packs because of uncertainty; one pack recruited a minimum of one pup and maximum of two pups, and the other a minimum of three and maximum of four pups.†We had minimum and maximum estimates of recruitment for one pack in that group. In 2020–2021, one undisturbed pack recruited 1–2 pups. In 2022, one disturbed pack recruited 4–5 pups and one undisturbed pack recruited 1–3 pups.

Analysis

We used a mixed-effect Poisson model to assess whether visiting dens and marking pups affected recruitment. The

Figure 1. An example of how recruited wolf pups in the Greater Voyageurs Ecosystem, MN, USA can be distinguished from adult wolves during winter. All four wolves in this figure were in the same pack and captured on the same remote camera within a 2.5-week period from mid-February to early March 2022. Panel A is a recruited wolf pup (~ 10 months old) and is easily distinguished from adult wolves based on its facial structure and development, and overall appearance (Mech 1970, Peterson and Page 1988). Panel B is the breeding male (~ 3 years old) of the pack, Panel C the breeding female (unknown age), and Panel D a subordinate wolf (2 years old). The wolves in panel A and D were both marked with microchips as ~ 4-week-old pups.

model structure for recruitment was as follows: number of pups recruited was the dependent variable, 'treatment' (disturbed/undisturbed) and 'year' (2019–2020, 2020–2021, 2021–2022 and 2022–2023; we examined year as a categorical variable and used 2020–2021 as the reference level) were independent variables, and wolf pack ID was a random intercept term. We did this analysis using both the minimum and maximum estimates of recruitment to determine if doing so affected our findings and conclusions. Because our pack size data consisted of non-zero count data, we used a truncated Conway–Maxwell–Poisson model to assess whether visiting dens and marking pups affected pack size. Our pack size model had a similar model structure to the recruitment model, except pack size was the dependent variable instead of recruitment. All analyses were performed in program R and we used the 'DHARMa' package to perform residual diagnostic checks on both models and ensure both models were specified correctly (Hartig 2022). We used an alpha-level of 0.05 to determine statistical significance.

Results

We studied 43 packs in this analysis: 8 in 2019–2020, 10 in 2020–2021, 12 in 2021–2022, and 13 in 2022–2023 (Table 1). Of the 43 packs studied, we visited dens and handled pups of 19 packs (disturbed packs). We did not visit dens or handle pups of the other 24 packs (undisturbed packs).

We did not detect a difference in recruitment between disturbed and undisturbed packs ($p = 0.16$; $\beta_{undisturbed} = -0.35$; 95% confidence interval [CI] = −0.86 to 0.15, Fig. 2). However, recruitment was higher ($p < 0.005$) in 2021–2022 (2.3 pups/pack; $p < 0.005$, $\beta_{2021-2022} = 1.39$, 95% CI = 0.58–2.39) and 2022–2023 (2.3 pups/pack; $p < 0.005$, $\beta_{2022-2023} = 1.42$, 95% CI = 0.60–2.41) than in 2020–2021 (0.6 pups/pack) (Fig. 3). We did not detect a difference in recruitment between 2019–2020 and 2020–2021 (0.9 pups versus 0.6 pups; $p = 0.42$; $\beta_{2019-2020} = 0.45$; 95% CI = −0.66 to 1.59). We derived minimum and maximum estimates of recruitment for five packs for which we were not certain of

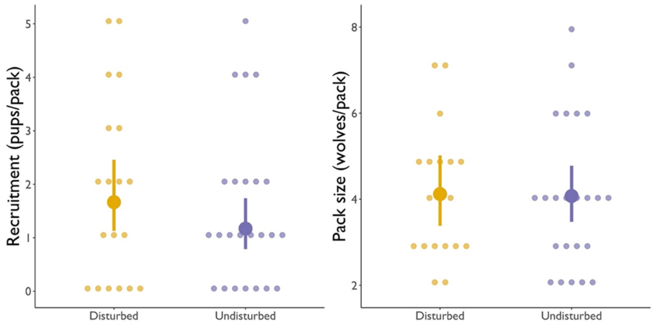

Figure 2. Recruitment and pack size for packs in the Greater Voyageurs Ecosystem, MN, USA where we visited dens and handled pups ('disturbed packs'; orange) versus packs where we did not visit dens and handle pups ('undisturbed packs'; purple). The larger points are estimates of recruitment and pack size for disturbed and undisturbed packs with associated 95% confidence intervals. The smaller points represent raw data collected from individual packs.

the number of pups recruited. Although our results above used the minimum estimates, our results did not change when we excluded these five instances or when we used the maximum estimates of recruitment.

We did not detect a difference in pack size between disturbed and undisturbed packs ($p = 0.93$; $\beta_{undisturbed} = -0.01$; 95% confidence interval [CI] = −0.24 to 0.22, Fig. 2). However, pack size was higher in 2021–2022 (4.7 wolves; $p < 0.05$, $\beta_{2021-2022} = 0.33$, 95% CI = 0.02–0.65) and 2022–2023 (5.0 wolves; $p < 0.05$, $\beta_{2022-2023} = 0.40$, 95% CI = 0.09–0.71) than in 2020–2021 (3.3 wolves) (Fig. 3). We did not detect a difference in pack size between 2019–2020 and 2020–2021 (3.3 vs 3.4; $p = 0.83$, $\beta_{2019-2020} = -0.04$, 95% CI = −0.43 to 0.34).

We observed and counted 21 litters during 2019–2022: 19 via the den visits described above and two from remote cameras placed near dens > 1 month prior to parturition. Mean litter size during 2019–2022 was 5.0 ± 0.3 pups (SE).

Discussion

Our work indicates that a single visit to wolf dens to count and mark wolf pups for research does not impact wolf pup recruitment or wolf pack size. Indeed, there was no difference in recruitment or pack size for disturbed and undisturbed packs. We assumed average litter size was the same for disturbed and undisturbed wolf packs, and therefore comparing recruitment between these groups was an appropriate method to measure human impacts on pups (i.e. that recruitment was directly related to survival). We think this is a valid assumption and there is no reason to our knowledge to expect a difference in litter size between disturbed and undisturbed packs. We primarily detected dens using GPS-collared wolves and attempted to keep 1–2 functional collars in each pack each year. However, due to myriad uncontrollable circumstances (e.g. collar failure, wolf dispersal/mortality) that rarely happened. Thus, the packs that had a wolf with a functional collar during spring were seemingly random and not for any identifiable reason. As such, our assumption regarding average litter size among packs appears robust.

Given our study design, recruitment should be strongly related, if not directly related, to wolf pup survival. We sampled disturbed and undisturbed packs in each year and explicitly modelled annual differences, thus accounting for any inter-annual differences in litter size. Other studies have demonstrated that recruitment and survival rates of wolves are strongly related. For example, in Idaho, recruitment and survival were clearly correlated and followed similar patterns over a five-year period (Fig. 2, 4 in Ausband et al. 2015). By demonstrating that visiting dens once to mark pups does not appear to impact recruitment, we therefore transitively conclude that these research activities likely do not impact pup survival either.

However, there clearly were substantial annual changes in recruitment during our study (Fig. 3). Namely, in 2019–2020 and 2020–2021 recruitment (0.6–0.9 pups/pack) was similarly low for disturbed and undisturbed packs. Assuming a mean litter size of 5.0 pups (see results), pup survival ranged from 0.12–0.18 during those years. However, recruitment more than doubled in 2021–2022 and 2022–2023 to 2.3 pups/pack in both years, which presumably increased survival to 0.46–0.47. The increase in pup recruitment and survival led to larger wolf packs in 2021–2022 and 2022–2023 (4.7–5.0 wolves/pack) compared to 2019–2020 and 2020–2021 (3.3–3.4 wolves/pack). These patterns and data clearly indicate that: 1) other annual factors (e.g. prey biomass; Harrington et al. 1983) likely drive changes in annual pup recruitment (Fig. 2), and consequently pack size and 2) changes in recruitment and pack size were not related to visiting dens and handling of wolf pups.

Our findings are consistent with most other studies that examined the impact of human disturbance of wolf dens. Indeed, studies on the topic in India (Habib and Kumar 2007) as well as those across Canada (Northwest Territories [Frame et al. 2007]; Ontario [Crawshaw et al. 2007, Argue et al. 2008]), and the US (Alaska [Ballard et al. 1987, Person and Russell 2009]; North Carolina [red wolves *Canis rufus*; Beck et al. 2009, Gese et al. 2018]; Arizona [Harding et al. 2016]; Wisconsin [Thiel et al. 1998]) have all concluded that human disturbance at dens and/or handling pups for research purposes does not negatively impact the survival of wolf pups. We only visited dens a single time but other experimental work showed that repeated human disturbance over the course of three days did not impact pup survival (Frame et al. 2007). This collective research indicates that wolves can tolerate some levels of human disturbance at dens (Thiel et al. 1998). The primary reason why visiting dens does not have an impact is because wolves have strong fidelity to their offspring and they do not readily abandon their pups (Mills et al. 2008). However, visiting dens and handling pups is a short-term disturbance and most studies have found that wolves will likely relocate pups to a new den nearby once humans leave (Frame et al. 2007, Habib and Kumar 2007, Nonaka 2011). Relocating pups to new dens does not appear to increase mortality risk for pups

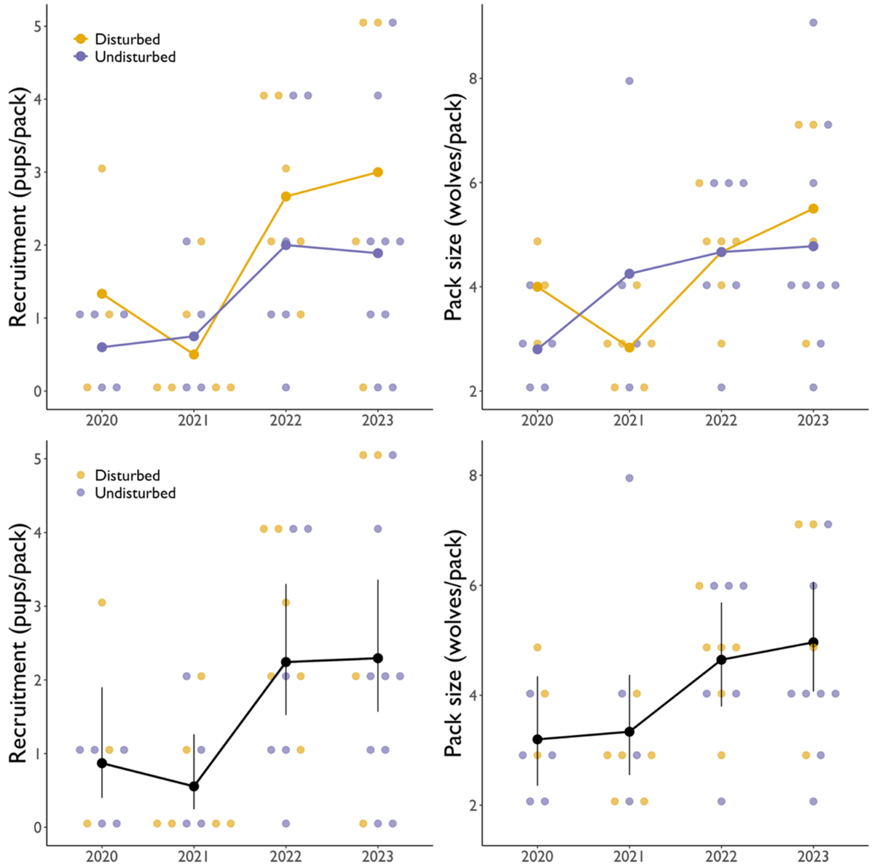

Figure 3. Annual variation in recruitment and pack size for wolves in the Greater Voyageurs Ecosystem, MN, USA during 2019–2023. The year on the x-axis refers to the biological year examined (e.g. 2020 refers to biological year spanning April 2019–April 2020). The smaller points are the raw data collected from individual packs where we visited dens and handled pups ('disturbed packs'; orange) versus packs where we did not visit dens and handle pups ('undisturbed packs'; purple). The top two panels show mean annual recruitment and pack size for disturbed and undisturbed packs. The bottom panels show the modelled estimates of recruitment and pack size for each year with associated 95% confidence intervals. Worth noting: the difference in pack size of disturbed and undisturbed packs in 2021 is driven by one pack that was much larger (8 wolves) than all others studied in 2021.

(Frame et al. 2007, Habib and Kumar 2007), which is not surprising because wolves readily move pups to new dens for reasons unrelated to humans (Mills et al. 2008, Nonaka 2011, Ausband et al. 2016). Experimental work in Northwest Territories (Frame et al. 2007) and detailed observational work in India (Habib and Kumar 2007) identified no pup mortalities due to human-induced relocations. However, in Algonquin Provincial Park, two young pups drowned after a human-induced relocation, which the authors state may or may not have been related to human disturbance (Crawshaw et al. 2007).

The only study we are aware of that has concluded human disturbance negatively affects pup survival is Sidorovich et al. (2016) in Belarus. However, the methods Sidorovich et al. (2016) used to estimate survival were questionable at best and should be viewed with caution. Specifically, they estimated survival in late fall, in part, by examining wolf tracks and identifying surviving pups based on the size of tracks and number of tracks observed. We are not aware of any data or evidence to indicate that this approach is valid, and we would argue that it is unreliable at best. By late fall, pups are generally approaching the size of adult wolves, and there is little to suggest their feet, and therefore tracks, are considerably smaller than adults at this time (Van Ballenberghe and Mech 1975, Mech 2008). We have examined many wolf tracks (> 100–200) in fall and early winter and have not seen any evidence that indicates pups can be readily and reliably differentiated from adults based on tracks alone.

Although the data from our study and numerous others indicate that researchers can visit dens once to handle pups without measurable effects on recruitment and pack size, researchers must give careful consideration as to whether visiting dens is necessary and warranted. Human visits to dens are a short-term disturbance for wolves and we argue dens should only be visited for defensible reasons (Sikes and Bryan 2016). Of course, what is defensible will vary and depend on many considerations. One key consideration should be (and was explicitly addressed in our animal welfare permitting process): can the data of interest be collected in some other way without visiting active dens and disturbing wolves?

In our case, the primary reasons for visiting dens were to collect data on litter size to estimate pack-level pup survival rates in an effort to understand population dynamics, as well as to mark individual pups to study them as adults. We are not aware of less invasive ways to mark pups or other methods to record accurate litter size data for individual packs without visiting dens (the two litter size estimates we obtained via remote camera were only obtained by guessing which den(s) the pack might use for reproduction, but den fidelity is generally low in our study area). Non-invasive, genetic approaches have been used to estimate litter size/pup survival but these generally require researchers to wait until pups are older (~ 3 months; Ausband et al. 2015). However, some pups have died by this age so estimates of litter size are likely underestimated via this approach while estimates of pup survival are likely overestimated (Voyageurs Wolf Project unpubl.). Wolf pup survival has been enigmatic in forested systems for decades (Fuller et al. 2003), in part, because finding dens and recording litter sizes is challenging. Thus, we think visiting dens to understand pup survival and address this key life-history knowledge gap is defensible. On the other hand, visiting active dens to collect genetic samples, take photographs, or to simply document dens is less defensible because all of these activities can be done once wolves have abandoned the site for reasons other than human disturbance (Stenglein et al. 2011). Regardless of the reasons for the research, there is substantive evidence that demonstrates a single visit to active dens to mark or handle pups does not have a measurable deleterious effect on wolf pup recruitment or pack size.

Acknowledgements – Foremost, we want to thank the National Park Service and their staff for efforts studying wolves in Voyageurs National Park since 1975. We also thank the Minnesota Environment and Natural Resources Trust Fund, the University of Minnesota, Northern Michigan University, the Van Sloun Foundation, Voyageurs Conservancy, Rainy Lake Conservancy, Wolf Conservation Center, International Wolf Center, The 6 Legacy, the National Wolfwatcher Coalition, Big Bad Project, Wildlife Science Center, Arc'teryx, NatureSpy, Vectronic-Aerospace, and 6067 individual donors who have supported the work of the Voyageurs.
Funding – We thank the Minnesota Environment and Natural Resources Trust Fund, National Park Service, the University of Minnesota, Northern Michigan University, the Van Sloun Foundation, Voyageurs Conservancy, Rainy Lake Conservancy, Wolf Conservation Center, International Wolf Center, The 6 Legacy, the National Wolfwatcher Coalition, Big Bad Project, Wildlife Science Center, Arc'teryx, NatureSpy, Vectronic-Aerospace, and 6067 individual donors who have supported the work of the Voyageurs Wolf Project.

Author contributions

Thomas D. Gable: Conceptualization (lead); Data curation (equal); Formal analysis (lead); Funding acquisition (equal); Methodology (lead); Project administration (equal); Writing – original draft (lead); Writing – review and editing (equal). **Sean M. Johnson-Bice:** Conceptualization (supporting); Formal analysis (supporting); Methodology (supporting); Writing – review and editing (equal). **Austin T. Homkes:** Conceptualization (supporting); Data curation (equal); Formal analysis (supporting); Methodology (supporting); Project administration (supporting); Writing – review and editing (equal). **Joseph K. Bump:** Conceptualization (supporting); Funding acquisition (equal); Project administration (equal); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at https://publons.com/publon/10.1002/wlb3.01195.

Data availability statement

Data are available from: https://conservancy.umn.edu/handle/11299/259159 (Gable et al. 2024).

References

Argue, A. M., Mills, K. J. and Patterson, B. R. 2008. Behavioural response of eastern wolves (*Canis lycaon*) to disturbance at homesites and its effects on pup survival. – Can. J. Zool. 86: 400–406.
Ausband, D. E., Stansbury, C. R., Stenglein, J. L., Struthers, J. L. and Waits, L. P. 2015. Recruitment in a social carnivore before and after harvest. – Anim. Conserv. 18: 415–423.
Ausband, D. E., Mitchell, M. S., Bassing, S. B., Nordhagen, M., Smith, D. W. and Stahler, D. R. 2016. Dog days of summer: influences on decision of wolves to move pups. – J. Mammal. 97: 1282–1287.
Ausband, D. E., Lukacs, P. M., Hurley, M., Roberts, S., Strickfaden, K. and Moeller, A. K. 2022. Estimating wolf abundance from cameras. – Ecosphere 13: 1–8.
Ballard, W. B., Whitman, J. S. and Gardner, C. L. 1987. Ecology of an exploited wolf population in south-central Alaska. – Wildl. Monogr. 98: 3–54.
Beck, K. B., Lucash, C. F. and Stoskopf, M. K. 2009. Lack of impact of den interference on neonatal red wolves. – Southeast. Nat. 8: 631–638.
Benson, J. F., Mills, K. J., Loveless, K. M. and Patterson, B. R. 2013. Genetic and environmental influences on pup mortality risk for wolves and coyotes within a Canis hybrid zone. – Biol. Conserv. 166: 133–141.
Borg, B. L. and Schirokauer, D. W. 2022. The role of weather and long-term prey dynamics as drivers of wolf population dynamics in a multi-prey system. – Front. Ecol. Evol. 10: 791161.
Cassidy, K. A., Borg, B. L., Klauder, K. J., Sorum, M. S., Thomas-Kuzilik, R., Dewey, S. R., Stephenson, J. A., Stahler, D. R., Gable, T. D., Bump, J. K., Homkes, A. T., Windels, S. K. and Smith, D. W. 2023. Human-caused mortality triggers pack instability in gray wolves. – Front. Ecol. Environ. 21: 356–362.
Crawshaw, G. J., Mills, K. J., Mosley, C. and Patterson, B. R. 2007. Field implantation of intraperitoneal radiotransmitters in eastern wolf (*Canis lycaon*) pups using inhalation anesthesia with sevoflurane. – J. Wildl. Dis. 43: 711–718.
DelGiudice, G. D., Severud, W. J., Obermoller, T. R. and St-Louis, V. 2018. Gaining a deeper understanding of capture-induced abandonment of moose neonates. – J. Wildl. Manage. 82: 287–298.

Donadio, E., Ruiz Blanco, M., Crego, R. D., Buskirk, S. W. and Novaro, A. J. 2012. Capturing and radio ear-tagging neonatal vicuñas. – Wildl. Soc. Bull. 36: 119–123.
Engebretsen, K. N., DeBloois, D. and Young, J. K. 2023. Use of radio-linked VHF technology to monitor neonate carnivores. – Wildl. Soc. Bull. 47: e1438.
Frame, P. F., Cluff, H. D. and Hik, D. S. 2007. Response of wolves to experimental disturbance at homesites. – J. Wildl. Manage. 71: 316–320.
Fuller, T. K., Mech, L. D. and Cochrane, J. F. 2003. Wolf population dynamics. – In: Mech, L. D. and Boitani, L. (eds), Wolves: behavior, ecology, and conservation. Univ. Chicago Press, pp. 161–191.
Gable, T. D., Windels, S. K., Bruggink, J. G. and Barber-Meyer, S. M. 2018. Weekly summer diet of gray wolves (*Canis lupus*) in northeastern Minnesota. – Am. Midl. Nat. 179: 15–27.
Gable, T. D., Homkes, A. and Bump, J. 2022. 2021–2022 Greater Voyageurs Ecosystem wolf pack and population size report. – Univ. Minnesota Digital Conservancy.
Gable, T. D., Homkes, A. and Bump, J. 2023. 2022–2023 Greater Voyageurs Ecosystem wolf population report. – Univ. Minnesota Digital Conservancy.
Gable, T. D., Johnson-Bice, S. M., Homkes, A. T. and Bump, J. K. 2024. Data from: Single visits to active wolf dens do not impact wolf pup recruitment or pack size. – https://conservancy.umn.edu/handle/11299/259159.
Gaillard, J. M., Festa-Bianchet, M. and Yoccoz, N. G. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. – Trends Ecol. Evol. 13: 58–63.
Gese, E. M., Waddell, W. T., Terletzky, P. A., Lucash, C. F., McLellan, S. R. and Behrns, S. K. 2018. Cross-fostering as a conservation tool to augment endangered carnivore populations. – J. Mammal. 99: 1033–1041.
Gotelli, N. J. 2008. A primer of ecology. – Sinauer Associates Incorporated.
Gude, J. A., Mitchell, M. S., Russell, R. E., Sime, C. A., Bangs, E. E., Mech, L. D. and Ream, R. R. 2012. Wolf population dynamics in the U. S. Northern Rocky Mountains are affected by recruitment and human-caused mortality. – J. Wildl. Manage. 76: 108–118.
Habib, B. and Kumar, S. 2007. Den shifting by wolves in semi-wild landscapes in the Deccan Plateau, Maharashtra, India. – J. Zool. 272: 259–265.
Harding, L. E., Heffelfinger, J., Paetkau, D., Rubin, E., Dolphin, J. and Aoude, A. 2016. Genetic management and setting recovery goals for Mexican wolves (*Canis lupus baileyi*) in the wild. – Biol. Conserv. 203: 151–159.
Harrington, F. H., David Mech, L. D. and Fritts, S. H. 1983. Pack size and wolf pup survival: their relationship under varying ecological conditions. – Behav. Ecol. Sociobiol. 13: 19–26.
Hartig, F. 2022. Dharma: residual diagnostics for hierarchical (multi-level /mixed) regression models. – R package ver. 0.4.6, http://florianhartig.github.io/DHARMa/.
Höfle, U., Millán, J., Gortázar, C., Buenestado, F. J., Marco, I. and Villafuerte, R. 2004. Self-injury and capture myopathy in net-captured juvenile red-legged partridge with necklace radiotags. – Wildl. Soc. Bull. 32: 344–350.
Horning, M. et al. 2019. Best practice recommendations for the use of external telemetry devices on pinnipeds. – Anim. Biotelemetry 7: 20.
Leonard, J. L., Inselman, W. M., Perkins, L. B., Grovenburg, T. W., Lammers, D. J. and Jenks, J. A. 2017. Capturing neonatal bison with a net gun from a utility terrain vehicle. – J. Fish Wildl. Manage. 8: 255–259.
Mech, L. D. 1970. The wolf: the ecology and behavior of an endangered species. – Univ. Minnesota Press.
Mech, L. D. 2008. Weight changes in wild wolves, *Canis lupus*, from ages 2 to 24 months. – Can. Field Nat. 122: 173.
Mills, K. J., Patterson, B. R. and Murray, D. L. 2008. Direct estimation of early survival and movements in eastern wolf pups. – J. Wildl. Manage. 72: 949–954.
Nonaka, Y. 2011. Response of breeding wolves to human disturbance on den sites – an experiment. – Uppsala Univ., Sweden.
Palacios, V. and Mech, L. D. 2010. Problems with studying wolf predation on small prey in summer via global positioning system collars. – Eur. J. Wildl. Res. 57: 149–156.
Person, D. K. and Russell, A. L. 2009. Reproduction and den site selection by wolves in a disturbed landscape. – Northwest. Sci. 83: 211–224.
Peterson, R. O. and Page, R. E. 1988. The rise and fall of Isle Royale wolves, 1975–1986. – J. Mammal. 69: 89–99.
Powell, M. C., DelGiudice, G. D. and Sampson, B. A. 2005. Low risk of marking-induced abandonment in free-ranging white-tailed deer neonates. – Wildl. Soc. Bull. 33: 643–655.
Schmidt, K., Jędrzejewski, W., Theuerkauf, J., Kowalczyk, R., Okarma, H. and Jędrzejewska, B. 2008. Reproductive behaviour of wild-living wolves in Bialowieza Primeval Forest (Poland). – J. Ethol. 26: 69–78.
Seguel, M., Paredes, E., Pavés, H. and Gottdenker, N. L. 2013. Capture-induced stress cardiomyopathy in South American fur seal pups (*Arctophoca australis gracilis*). – Mar. Mamm. Sci. 30: 1149–1157.
Severud, W. J., Obermoller, T. R., DelGiudice, G. D. and Fieberg, J. R. 2019. Survival and cause-specific mortality of moose calves in northeastern Minnesota. – J. Wildl. Manage. 83: 1131–1142.
Sidorovich, V., Schnitzler, A., Schnitzler, C. and Rotenko, I. 2016. Wolf denning behaviour in response to external disturbances and implications for pup survival. – Mamm. Biol. 87: 89–92.
Sikes, R. S. and Bryan, J. A. 2016. 2016 Guidelines of the American society of mammalogists for the use of wild mammals in research and education. – J. Mammal. 97: 663–688.
Smith, J. E. and Pinter-Wollman, N. 2021. Observing the unwatchable: integrating automated sensing, naturalistic observations and animal social network analysis in the age of big data. – J. Anim. Ecol. 90: 62–75.
Stenglein, J. L., Waits, L. P., Ausband, D. E., Zager, P. and Mack, C. M. 2011. Estimating gray wolf pack size and family relationships using noninvasive genetic sampling at rendezvous sites. – J. Mammal. 92: 784–795.
Thiel, R. P., Merrill, S. and Mech, L. D. 1998. Tolerance by denning wolves, *Canis lupus*, to human disturbance. – Can. Field Nat. 122: 340–342.
Van Ballenberghe, V. and Mech, L. D. 1975. Weights, growth, and survival of timber wolf pups in Minnesota. – J. Mammal. 56: 44–63.
Vashon, J. H., Vaughan, M. R., Vashon, A. D., Martin, D. D. and Echols, K. N. 2003. An expandable radiocollar for black bear cubs. – Wildl. Soc. Bull. 31: 380–386.
Walsh, P. B., Sethi, S. A., Lake, B. C., Mangipane, B. A., Nielson, R. and Lowe, S. 2016. Estimating denning date of wolves with daily movement and GPS location fix failure. – Wildl. Soc. Bull. 40: 663–668.