Behavioural response of eastern wolves (*Canis lycaon*) to disturbance at homesites and its effects on pup survival

A.M. Argue, K.J. Mills, and B.R. Patterson

Abstract: Human disturbance at wolf dens and rendezvous sites (homesites) may have direct effects on pup survival and could result in the alteration of homesite-use characteristics. During a demographic study of eastern wolves (*Canis lycaon*) in Algonquin Provincial Park, Ontario, we entered active homesites to tag pups with VHF radio transmitters. Homesite attendance and pup survival data collected in 2003–2005 were used to determine (*i*) the immediate response of wolves to disturbance at homesites, (*ii*) whether distance moved between homesites was influenced by disturbance, (*iii*) if pup survival was compromised by researcher disturbance, and (*iv*) whether reuse in subsequent years differed between disturbed and undisturbed den sites. Packs tended to relocate pups after a disturbance, though we did not detect a difference in distances travelled between natural homesite shifts and those following disturbance. Disturbed homesites were reused in following years at a similar frequency as undisturbed homesites (6 of 15 vs. 8 of 22 homesites, respectively). Although postcapture mortality risk was slightly elevated for pups, we could not detect long-term effects of disturbance. This resilience to disturbance, and our documentation of effective techniques for radio-tagging young pups, demonstrate that research on wolf pup demography can be performed effectively without causing unacceptable negative impacts on wolf behaviour or mortality.

Résumé : La perturbation par les humains des terriers et des lieux de rencontre (de résidence) des loups peut avoir des effets directs sur la survie des louveteaux et peut entraîner une altération des caractéristiques d'utilisation de ces lieux de résidence. Au cours d'une étude démographique des loups de l'est (*Canis lycaon*) au parc provincial Algonquin en Ontario, nous avons pénétré dans des lieux de résidence occupés par les loups afin de munir des louveteaux de transmetteurs radio VHF. Les données sur l'utilisation des lieux de résidence et sur la survie des louveteaux récoltées en 2003–2005 nous ont servi (*i*) à déterminer la réaction immédiate des loups à la perturbation de leurs lieux de résidence, (*ii*) à connaître l'influence de la perturbation sur la distance de déménagement entre les lieux de résidence, (*iii*) à savoir si la perturbation causée par les chercheurs compromet la survie des louveteaux et (*iv*) à découvrir si l'utilisation répétée du site durant les années subséquentes différait entre les sites des terriers perturbés et non perturbés. Après une perturbation, les meutes ont tendance à déplacer les louveteaux, bien que nous soyons incapables de détecter une différence dans les distances parcourues lors de changements naturels de lieu de résidence et les déplacements consécutifs à une perturbation. Les lieux de résidence perturbés sont réutilisés les années subséquentes à une même fréquence que les sites non perturbés (respectivement 6 de 15 sites et 8 de 22 sites). Bien que le risque de mortalité après la capture soit légèrement accru chez les louveteaux, nous ne décelons aucun effet à long terme de la perturbation. Cette résilience à la perturbation et la démonstration de l'efficacité de nos techniques pour munir les jeunes louveteaux d'étiquettes radio assurent qu'il est possible de mener avec succès des études démographiques sur les louveteaux sans causer d'impacts négatifs inacceptables sur le comportement et la mortalité des loups.

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Introduction

Anthropogenic disturbance such as vehicle traffic, forestry operations, research activities, and other human activity can have significant, often negative, impacts on wildlife (Kerley et al. 2002; Fortin and Andruskiw 2003; Wichrowski et al. 2005). Such disturbances may cause permanent movement away from a natal site, territory, or other resource (Ellison and Cleary 1977; Walker et al. 2005), abandonment of young by parents (Thomson 1992), or decreased survival of offspring or reproductive success (Frederick and Collopy 1989; Giese 1996; Smith 1998; Walker et al. 2005; Mills et al. 2008). Few studies have focused specifically on the effects of research activities on free-ranging mammals, although such activities may also impact behaviour or survival (Chapman 1977, Laurenson and Caro 1994; Wolski et al. 2004; Frame et al. 2007; Habib and Kumar 2007). These studies, and anecdotal evidence from other studies (e.g., Harrison and Gilbert 1985; Mowat et al. 1996; Way et al. 2001), suggest that mammals typically react adversely to disturbance at homesites on a short temporal scale that does

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generally not affect subsequent survival or reproduction. Yet few have quantified behavioural responses and longer term effects of disturbance (but see Chapman 1977; Laurenson and Caro 1994; Frame et al. 2007; Habib and Kumar 2007).

Wolf den and rendezvous sites (collectively called homesites; Joslin 1967) are generally the centre of activity for packs during the pup-rearing season (Mech and Boitani 2003). Although wolves tend to select specific habitats when choosing homesites (Norris et al. 2002; Theuerkauf et al. 2003; Trapp 2004), no studies have investigated whether pup survival is related to den-site characteristics (Trapp 2004). However, repeated, multiannual use of homesites is common (Chapman 1977; Fuller 1989; Ballard et al. 1991), and may be reinforced when wolves successfully rear pups at a particular site (Fuller 1989).

Concerns regarding the status of eastern wolves (*Canis lycaon*; Wilson et al. 2000) in Algonquin Provincial Park, Ontario, prompted research on the demography of adult and juvenile wolves within the Park (e.g., Patterson et al. 2004; Mills et al. 2008). Assessment of juvenile demography required capture of young pups at homesites to deploy radio transmitters for subsequent monitoring (Mills et al. 2008). Because most researchers have actively avoided disturbing homesites owing to the perceived detrimental effects on wolf behaviour and pup survival (Mech 1977), the effects of pup capture and handling at homesites have not been studied. In general, reports in the literature suggest that wolves are often sensitive to homesite disturbance (Chapman 1977; Smith 1998; Frame et al. 2007), yet they can also show a high level of tolerance for human activities in and around homesites (Chapman 1977; Thiel et al. 1998). Frame et al. (2007) documented wolf reproductive success, abandonment of homesites, and reuse of homesites after experimental human disturbance in the Northwest Territories, Canada. The disturbance in their study consisted of a single intruder approaching a homesite, and they found no measureable adverse effects on wolves. Responses of wolves may differ when exposed to disturbances of longer duration, involving a greater number of intruders, or involving capture and handling of pups.

As wolves continue to recolonize much of their historic range in North America and Europe (Mech and Boitani 2003), and human development encroaches farther into remote wilderness areas, human disturbance at wolf homesites could become increasingly common. Further investigations of the response of wolves to disturbance are important to better understand potential modifications of wolf behaviour and homesite selection that may affect pup survival (Chapman 1977; Walker et al. 2005). It is also important to document adverse effects caused by disturbance at homesites to assess the acceptability of intrusive research when considering future work on wolf pup demography.

We tested whether human disturbance at homesites significantly altered homesite selection by eastern wolves. If human disturbance altered homesite selection, then significantly fewer disturbed sites should have been reused in subsequent years than undisturbed sites and (or) the distance moved among homesites following a disturbance should have been different than the distance moved among undisturbed sites. We also directly monitored radio-tagged pups following disturbance to assess the immediate response of disturbed wolf packs and any impacts on the subsequent survival of pups.

Materials and methods

Algonquin Provincial Park, Ontario, Canada, is located at the southern edge of the Canadian Shield (45°N, 78°W), and has an area of 7571 km^2 (Pimlott et al. 1969; Patterson et al. 2004). The Park is characterized by mixed forests of maple (*Acer* L.), birch (*Betula* L.), pine (*Pinus* L.), and cottonwood (*Populus* L.), and is the largest protected area in the range of eastern wolves (Grewal et al. 2004).

We trapped adult wolves and fitted them with very high frequency (VHF) radio collars or global positioning system (GPS) collars from 2002 to 2006 (for protocols see Patterson et al. 2004). In 2004 and 2005, we monitored radio-collared adults via aerial and ground telemetry at least three times weekly from 15 April to 29 May to locate den sites. We entered these den sites from 29 May to 16 June each year (3.5–8 weeks after birth), captured pups, and surgically implanted intraperitoneal VHF radio transmitters to monitor survival (n = 53; Crawshaw et al. 2007; Mills et al. 2008). The approximate length of time spent at each den ranged from 1 to 6 h. We also captured 25 pups belonging to 19 litters from July to November of each year (2002–2006) using padded foothold traps (Victor Softcatch #1.5 and #3) and fitted them with either a VHF ear-tag transmitter (M3400; Advanced Telemetry Systems, Isanti, Minnesota) or a padded VHF radio collar (LMRT3; Lotek Engineering, Inc., Newmarket, Ontario). Cumulative time spent at the homesite for trapping efforts generally ranged from 1 to 2 h. All capture and handling protocols were approved by the Ontario Ministry of Natural Resources Wildlife Animal Care Committee (permit Nos. 02-75, 03-75, 04-75, 05-75, and 06-75).

Immediate response

We monitored transmittered pups and pack members via ground and aerial-based VHF telemetry following capture to determine whether wolves abandoned the disturbed homesite. In some cases, we entered den sites but did not capture or handle pups because trapping attempts were unsuccessful or pups were too young for transmitter deployment. Therefore, we categorized disturbance as low level if the homesite was entered once and pups were not handled, or high level if the homesite was entered multiple times or if pups were handled. For each disturbance event we categorized the number of researchers involved as <4 individuals and ≥4 individuals, and the duration of the disturbance event as <1 or ≥1 h. Low-level disturbance generally involved 1–3 researchers entering the site for 0.1–1 h and high-level disturbance involved ≥4 researchers occupying the site for >1 h. We defined cases where disturbed packs abandoned homesites as "abandoned" and cases where packs remained at the disturbed homesite as "no response". We then compared the rates of abandonment to disturbance intensity, group size involved in disturbance, and duration of the disturbance using Fisher's exact test (Zar 1999).

Pup age can also affect the response of a pack to human disturbance at the homesite (Chapman 1977; Frame et al. 2007; Habib and Kumar 2007). We therefore tested for differences in response according to pup age, categorized as ≤4 and >4 weeks (below and above weaning age, respectively; Frame et al. 2007) for homesites exposed to both levels of human disturbance using Fisher's exact test (Zar 1999).

Homesite reuse

We documented all homesites used by each litter of pups fitted with surgically implanted transmitters until they left rendezvous sites and began moving with their pack in early fall. We used den and rendezvous sites that were occupied by packs on or before 19 July to determine patterns of homesite reuse, as this was the latest date that any pack was found at a den. We restricted our analysis to early sites because homesite selection in later summer might be strongly influenced by short temporal events such as weather or the existence of an ungulate carcass (Chapman 1977; Peterson 1977). In addition, the number of rendezvous sites reused in the late summer was low (K.J. Mills, unpublished data), thus there were insufficient data for analysis. We classified each homesite as "undisturbed" if it was not approached by researchers (or anyone else to the best of our knowledge) and "disturbed" if researchers entered the site and (or) handled pups. We further classified each homesite as "reused" if the wolf pack denned or established a rendezvous site within a 100 m radius of that site in a following year, or "not reused" if the pack never re-established a homesite there during consecutive years. We compared the frequency of reuse for disturbed and undisturbed sites using Pearson's χ^2 test.

Displacement distance

We calculated displacement distance as the straight-line distance between subsequent homesites. Only homesite locations from packs with implanted litters were included in these analyses because we were unable to determine all homesites for pups marked using other transmitters. We classified each homesite as undisturbed or disturbed using the criteria identified above. We categorized homesites by pup age to account for changes in pup movements as they increase in age (Mills et al. 2008). The two age categories used were denning (age <6 weeks) and early rendezvous (age 6–11.9 weeks) to reflect aspects of homesite use during these age ranges (Mills et al. 2008). Analyses involving older pups (age ≥12 weeks) were not possible because of the small sample sizes for disturbed homesites. We used ANOVA to determine if displacement distances differed between disturbed and undisturbed sites in each of the three age categories.

Pup survival

We monitored pup survival via telemetry every 2–3 days for the duration of the summer and at least once per week during the fall. We collected dead pups promptly and determined the time and cause of death using evidence found at the mortality site and necropsies performed at the Canadian Cooperative Wildlife Health Centre, University of Guelph. We calculated the instantaneous hazard for the pups using the computer program PHMPL (Joly et al. 1999) to assess whether mortality risk was elevated immediately following capture. We set the date of capture as day 1, and examined the instantaneous hazard as time progressed from this point.

Table 1. Distribution of eastern wolf (*Canis lycaon*) homesites that were abandoned or not abandoned (i.e., no response) after low- and high-level disturbance in Algonquin Provincial Park between 2003 and 2006.

	Low	High	Total
No response	4	0	4
Abandoned	5	20	25
Total	9	20	29

We considered the hazard functions for pups captured manually at dens and pups captured using foothold traps separately to avoid potential confounding effects owing to different capture techniques and timing of capture (i.e., early summer vs. late summer and fall, respectively). We also considered individual pups as the sample unit because we documented only one case where >1 litter mate succumbed to the same mortality event. In all remaining cases the fate of individual pups varied markedly within packs. Instantaneous hazard for pups captured manually from dens was measured for the first 120 days postcapture, which approximately extended from June to the end of September. The hazard for pups trapped using footholds could only be measured for 60 days postcapture because of the small sample sizes and reduced monitoring of pups in December. We visually assessed the hazard curves for any obvious changes in slope or elevation to infer the relative effects of capture and handling versus natural (background) mortality occurring during the monitoring period.

Results

Immediate response

We subjected 9 homesites to low-level disturbance and 20 homesites to high-level disturbance during our research (Table 1). Packs abandoned disturbed homesites in all cases of high-level disturbance regardless of pup age, and in 5 of 9 cases of low-level disturbance (Fisher's exact test, P = 0.005). Abandonment always occurred within 24 h of the disturbance (i.e., generally the night following disturbance). The number of individuals involved in disturbing the homesite had little effect on the tendency towards abandonment (6 of 9 cases with <4 individuals vs. 18 of 21 cases with ≥4 individuals; Fisher's exact test, P = 0.237). However, wolves responded differently based on the duration of homesite disturbance and abandoned homesites in only 4 of 8 cases following <1 h of disturbance vs. 20 of 22 cases following ≥1 h of disturbance (Table 2; Fisher's exact test, P = 0.029). Pups >4 weeks of age were moved from 4 of 5 low-level disturbed homesites compared with pups ≤4 weeks of age being relocated from only 1 of 4 low-level disturbed homesites (Fisher's exact test, P = 0.159). Pups were always moved from high-level disturbed homesites, regardless of age.

Homesite reuse

We documented 37 early homesites from 15 wolf packs with surgically implanted pups (Table 3). We found no difference in the frequency of homesite reuse in subsequent

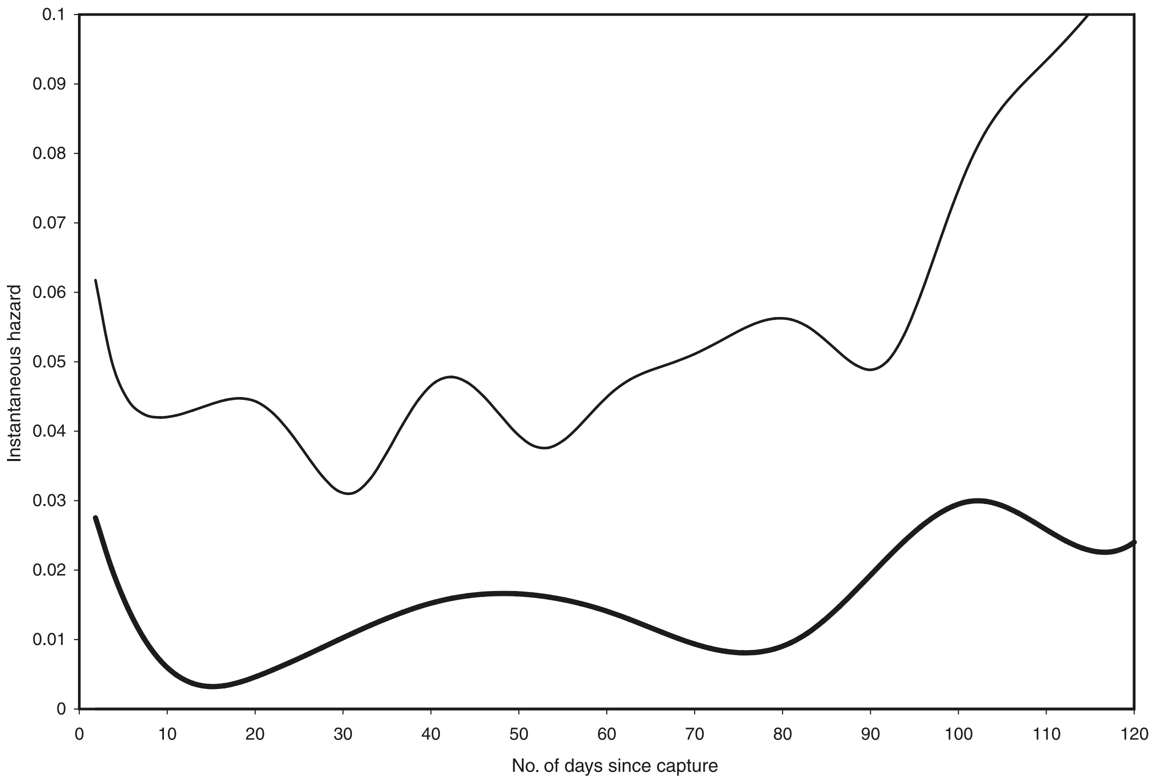
Table 2. Distribution of eastern wolf (*Canis lycaon*) homesites that were abandoned or not abandoned (i.e., no response) after disturbance durations of <1 and ≥1 h in Algonquin Provincial Park between 2003 and 2006.

	<1 h	≥1 h	Total
No response	4	2	6
Abandoned	4	20	24
Total	8	22	30

Table 3. Distribution of disturbed and undisturbed homesites that were reused and not reused by eastern wolf (*Canis lycaon*) packs monitored in Algonquin Provincial Park between 2003 and 2006 (n = 37).

	Disturbed	Undisturbed	Total
Reused	6	8	14
Not reused	9	14	23
Total	15	22	37

Fig. 1. Instantaneous hazard (thick line) (±95% CI (thin line)) for eastern wolf (*Canis lycaon*) pups following manual capture at den sites in Algonquin Park, Ontario, for implant procedures. The day of capture is day 0 and the lower 95% CI limit was zero for the entire period.



years between disturbed (6 of 15) and undisturbed (8 of 22) homesites (χ^2 = 0.0147, P = 0.90).

Displacement distance

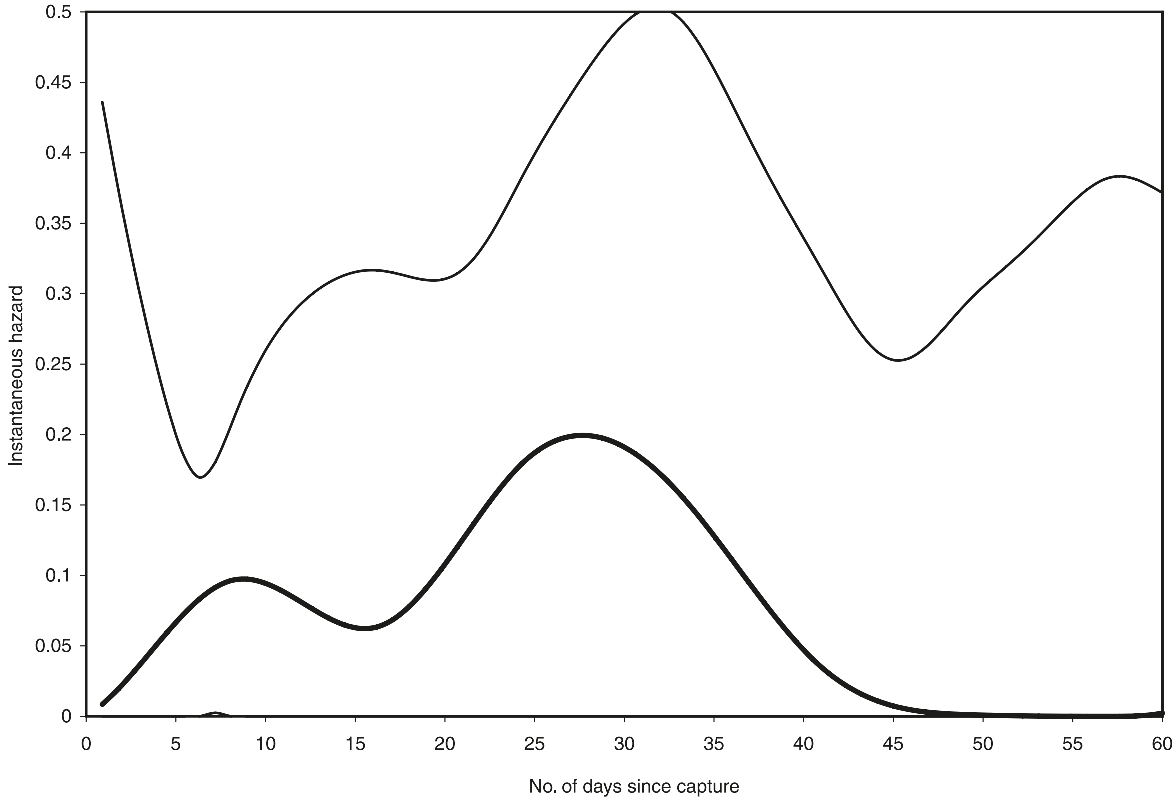
The mean (±SE) displacement distance was not different between disturbed (1.23 ± 0.35 km, n = 6) and undisturbed (1.03 ± 0.20 km, n = 6) sites for litters in the denning age (P = 0.593) or early-rendezvous age categories (1.41 ± 0.37 km, n = 7 vs. 1.64 ± 0.19 km, n = 25 for disturbed and undisturbed sites, respectively; P = 0.583).

Pup survival

We manually captured 53 pups from 12 dens in early summer and subsequently used foothold traps to capture 25 additional pups (i.e., n = 78) during 2002–2006 combined. The instantaneous hazard for pups captured manually and implanted at den sites was slightly elevated for the first 5 days but did not exceed natural mortality that occurred later in the fall (e.g., at 100 days postcapture; Fig. 1). This slightly elevated mortality risk resulted from two litter mates dying within 3 days postcapture when they were relocated to a flooded den. Necropsies indicated no negative physiological response to the implant or implant procedure and confirmed the cause of death as drowning.

Initial mortality risk for pups captured using foothold traps was low but increased after 7 days postcapture with three mortalities occurring between days 7 and 9 (Fig. 2). Two of these pups were in poor condition at the time of capture, characterized by emaciation (i.e., protruding skeletal features and little discernable subcutaneous fat) in both cases, and significant hair loss in one case, probably owing to sarcoptic mange. A third pup that died 8 days postcapture appeared healthy at time of capture and was consumed prior to recovery, which precluded the definitive identification of cause of death. The peak mortality risk observed ~10 days postcapture was approximately half the maximum mortality risk observed at 28 days postcapture (Fig. 2) at which time causes of death were clearly unrelated to capture (Mills et al. 2008). No other direct adverse effects of pup capture or

Fig. 2. Instantaneous hazard (thick line) (±95% CI (thin line)) for eastern wolf (*Canis lycaon*) pups following capture with foothold traps in and around Algonquin Park, Ontario. The day of capture is day 0 and the lower 95% CI limit overlapped zero for most of the study period.



handling, such as rejection or abandonment by pack members, were documented.

Discussion

Wolves exhibited variable behavioural responses depending on the intensity and duration of disturbance at homesites. In all cases where pups were captured and handled, adult wolves moved pups to a new homesite. Wolves abandoned homesites less frequently (5 of 9 cases) when subjected to lower intensity disturbance (i.e., no direct contact with pups, and typically a single visit to the site). The duration of homesite disturbance also positively affected the tendency of wolves to abandon homesites, while the number of researchers involved in the disturbance was not significant. Because high-level disturbance where pups were handled typically involved a longer stay at the disturbed site, we cannot be certain whether it is the handling of pups or the length of disturbance (or both) that is more important in inducing homesite abandonment. We did not detect a significant effect of pup age on the tendency of packs to relocate pups following low-level disturbance, but given the data (i.e., 4 of 5 vs. 1 of 4 litters moved for pups >4 and ≤4 weeks of age, respectively) this likely reflects small sample sizes rather than a true lack of effect. Qualitatively, these results support the findings of Frame et al. (2007) and Habib and Kumar (2007), who found age of pups at the time of disturbance to be important in influencing abandonment of disturbed homesites. Adult pack members may resist moving young pups because it is more risky owing to their small size, low mobility, and lack of independence (Packard 2003; Frame et al. 2007). In fact, the two pups that drowned following capture were only 3.5 weeks of age, and represented the youngest pups captured during the study. We recommend that manual capture at the den site only be attempted if pups are known to exceed 4 weeks of age. The date that collared adults localize at den sites is generally accurate and could be used as a benchmark for timing pup captures. Note, however, that in some cases localization at a den site can precede whelping by up to 2 weeks (Mills et al. 2008).

Movement distances to new homesites were not affected by disturbance. However, straight-line distances measured between homesites may not reflect actual distance travelled because movement paths between homesites may be convoluted if wolves have to search for new sites following disturbance. Because wolves appear to have a detailed knowledge of their territories as judged by their intense use of many areas within their territory (Mech and Boitani 2003), it is likely that they also possess prior knowledge of the locations of alternative homesites. Thus, movements to those homesites are probably quite direct. If so, there should be no additional increase in energy expenditure owing to excessive movements or time spent during site selection following disturbance.

No pups were abandoned by pack members following capture, which shows the resiliency of wolves to human disturbance and pup handling (Thiel et al. 1998; Schultz et al. 1999). Nonetheless, although negative effects on pup survival owing to disturbance have not been documented (Frame et al. 2007; Habib and Kumar 2007), disturbance at homesites and pup capture directly caused the death of 2 of the 53 pups we implanted. Although undesirable, this level of capture-related mortality was within the acceptable thresholds identified for capture techniques applied to adult wolves (Arnemo et al. 2006). Furthermore, some level of pup mortality would be expected to occur naturally during normal homesite shifts, as pups would be susceptible to mortality while moving through unfamiliar territory and traversing obstacles such as rivers (Smith 1998).

In addition to the two pups that died immediately following relocation, capture may have been a proximate cause of death for three additional pups (12.0%, n = 25) captured with foothold traps. However, these pups were captured during the period when natural mortality is expected to be highest for young pups (August–September; Van Ballenberghe and Mech 1975), and indeed two of these pups were in very poor condition when captured. In these cases, capture likely further compromised their already poor condition and thus may be considered the proximate, but likely not the ultimate, mortality factor. Both of these pups were manually restrained without use of chemicals and processing times were short (≤15 min). Pups in poor physical condition may also be more susceptible to capture because food-based baits were generally used to target pups. As such our sample of trapped pups may have been biased towards those in poor condition and thus experiencing an elevated risk of mortality.

Similar to Frame et al. (2007), we found that disturbance did not affect the tendency for packs to reuse homesites in subsequent years. In fact, the Spoor Lake pack returned to a disturbed den site <1 week after pups were captured there. The McKaskill Lake pack also used the same homesite (two dens, one rendezvous site) in 2003–2005 despite disturbance at this site during each of these years. It is likely that adequate habitats for den and rendezvous sites are plentiful in the Algonquin ecosystem (Norris et al. 2002), and thus reuse of sites following significant disturbance may reflect some advantage offered by those particular sites despite disturbance having occurred there (Fuller 1989). Tradition may also play an important role in homesite reuse (see Frame et al. 2007); however, this has not been studied and requires further investigation.

Most researchers have actively avoided disturbing den and rendezvous sites for research purposes because of the perceived detrimental effects to wolf behaviour and survival (Mech 1977). This study demonstrates that wolves do respond to anthropogenic disturbance at homesites by relocating homesites; however, we did not detect long-term effects on subsequent wolf behaviour such as avoidance of disturbed homesites in subsequent years. We observed elevated pup mortality following capture and handling, though the degree that disturbance contributed to these deaths was probably low. Additionally, the level of mortality we documented did not exceed natural levels that occurred during the study period, and was similar to capture myopathy rates reported in other studies. This resilience to disturbance, and our documentation of effective techniques for radio-tagging young pups (e.g., Crawshaw et al. 2007), demonstrate that wolf pup demography can be studied directly without causing negative impacts on wolf behaviour or mortality that exceed acceptable standards.

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