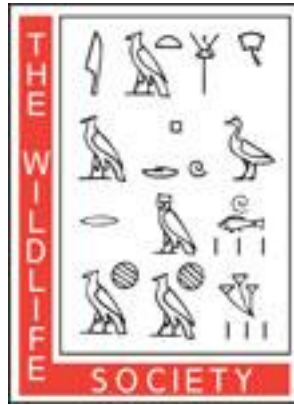


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## Estimating Wolf Densities in Forested Areas Using Network Sampling of Tracks in Snow

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# Estimating wolf densities in forested areas using network sampling of tracks in snow

*Brent R. Patterson, Norman W. S. Quinn, Earl F. Becker,  
and Derek B. Meier*

**Abstract** Few reliable methods exist for estimating population size of large terrestrial carnivores. This is particularly true in forested areas where sightability is low and when radiocollared individuals are unavailable in the target population. We used stratified network sampling to sample wolf (*Canis lycaon*) tracks in the snow to estimate density in western Algonquin Park, Ontario in February 2002. We partitioned our 3,425-km<sup>2</sup> study area into 137 5 × 5-km sample units (SU) and stratified SUs as having a high ( $n=61$ ) or low ( $n=76$ ) probability of containing detectable wolf tracks based on the relative amount of watercourses and conifer cover within each block. We used a Bell 206B helicopter to survey 28 high (46%) and 17 low (22%) SUs. When fresh tracks were found in a block, we followed the tracks forward to the wolves themselves and then backward until the tracks were no longer considered “fresh.” We observed 17 “fresh” track networks within 45 SUs. The average pack size in the area we surveyed was  $4.2 \pm 0.4$  (SE). These observations resulted in an estimate of  $87 \pm 11.4$  (90% CI) wolves in the study area, for a density of  $2.5 \pm 0.3$  wolves/100 km<sup>2</sup>. We detected no violations of the assumptions of this survey design and obtained a similar density estimate (2.3 wolves/100 km<sup>2</sup>) in 2003 using location data from 24 radiocollared wolves in 10 packs from an area that overlapped our 2002 survey area. The sampling unit probability estimator (SUPE) provides an objective, accurate, and repeatable means of estimating wolf density with an associated measure of precision. However, tracking wolves in forested cover was time-consuming, so costs will be considerably higher per unit area in forested areas relative to the more open cover types where this technique was originally developed.

**Key words** aerial survey, Algonquin Park, *Canis lupus*, density estimation, Ontario, population estimation, probability sampling, radiotelemetry, track surveys, wolves

Few reliable methods exist for estimating population size of large terrestrial carnivores (Crête and Messier 1987, Fuller and Snow 1988, Becker 1991, Ballard et al. 1995, Miller et al. 1997, Becker et al. 1998). This is particularly true for forested areas where sightability is low and when radiocollared individuals are unavailable in the target population.

Although radiotelemetry might remain the best technique for estimating wolf density associated with intensive, relatively small study areas, it is expensive and may not be logistically or socially feasible in all areas (Crête and Messier 1987, Fuller and Sampson 1988). These difficulties notwithstanding, estimating population size remains cen-

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tral to the conservation of wolves (*Canis lupus*, *C. lycaon*, *C. rufus*) and other large carnivores. Becker et al. (1998) presented a novel method of estimating gray wolf density and statistical confidence intervals over large areas based on stratified network sampling of wolf tracks in snow. Population size and statistical confidence intervals were calculated based on the probability of observing track networks in snow. This method, called the sampling unit probability estimator (SUPE), makes the following assumptions: 1) all animals of interest move during the study, 2) their tracks are readily recognizable from survey aircraft, 3) tracks are continuous, 4) wolf movements are independent of the sampling process, 5) tracks made within and outside the sampling window (pre- and post-snowfall) can be distinguished, 6) "fresh" tracks in searched sample units (SU) are not missed, 7) tracks can be followed forward and backward to determine all SUs containing those tracks, 8) group size is correctly enumerated. Because most study areas will require several days to survey, an additional assumption is that no animals were double-counted by moving among SUs on subsequent days. Using concurrently collected radiotelemetry data on 9 wolf packs in their study area, Becker et al. (1998) did not detect any violations of these assumptions. Although promising, there are no published reports of the application of this method for estimating density of a large carnivore species in a densely forested habitat.

At 7,571 km<sup>2</sup>, Algonquin Provincial Park in south-central Ontario represents the largest protected

area for the eastern timber wolf (*C. lycaon*, Wilson et al. 2000, 2003). Amid concern that wolves may be declining in Algonquin Park (Theberge 1998, Vucetich and Paquet 2000), we used the SUPE to estimate wolf abundance in the park in February 2002. We then compared this estimate with an independent estimate obtained for the same general area in winter 2003 using "traditional" methods based on radiotelemetry (e.g., Fuller and Snow 1988).

## Study area

Algonquin Provincial Park (45°N, 78°W) encompassed 7,571 km<sup>2</sup> on the southern edge of the Canadian Shield and ranged in elevation from 180–380 m in the east side up to 580 m in the west (Figure 1). Data were collected primarily in the western portion of the park. The average January temperature was –12°C, and temperatures approaching –40°C were common (Environment Canada 1993). Mean annual precipitation ranged from 66–86 cm, with more snowfall in the western portion of the park (Environment Canada 1993). Algonquin Park consisted of 2 forests that were sharply delineated: the eastern third consisted of white pine (*Pinus strobus*), red pine (*P. resinosa*), and jack pine (*P. banksiana*) stands on well-drained sandy outwash and rolling to flat terrain (Strickland 1993). The park's west side consisted primarily of tolerant hardwood forests composed of sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), and eastern hemlock (*Tsuga canadensis*), on a glacial till over poorly drained, rugged terrain. Commercial logging occurred in approximately 75% of the park, and an extensive network of logging roads covered much of it. No other large carnivore species were present in the study area during winter. Although coyotes (*C. latrans*) lived immediately south of the park (Sears 1999), they were rarely found within it. For example, of the 92 canids (*Canis* sp.) live-trapped for research purposes from August 2002 to February 2004, only one appeared to be a coyote (B. R. Patterson, Ontario Ministry of Natural Resources, unpublished data). This animal was radiocollared but was never relocated in the park. Medium-sized carnivores that leave tracks in the area in winter included fishers (*Martes pennanti*), red foxes (*Vulpes vulpes*), and river otters (*Lutra canadensis*).



The tracks left by this pair of wolves were followed for about 10 km before the wolves were finally sighted on a lake during the February 2002 sampling unit probability estimator (SUPE) survey used to wolf abundance in Algonquin Park, Ontario.



Figure 1. Stratified network-sample design used to estimate wolf numbers in a 3,425-km<sup>2</sup> study area in Algonquin Park, Ontario, Canada during a February 2002 survey. Also shown are the wolf-track segments identified during this survey and the 2,335-km<sup>2</sup> area used to estimate wolf density with radiotelemetry in winter 2003.

## Methods

### SUPE survey

We considered as study area a 3,425-km<sup>2</sup> area in the park's western section (Figure 1); it was divided into 137 5 × 5-km sample units. We stratified the study area a priori by assigning each SU a high or low probability of housing fresh wolf tracks. This designation was based on the number of watercourses and the relative amount of hemlock cover (selected for by moose [*Alces alces*] in Algonquin; Forbes and Theberge 1993) within each SU. Our study area contained 61 high and 76 low SUs. We began flying on 6 Feb 2002 and attempted to sample 30 (50%) SUs in the high strata and 19 (25%) SUs in the low strata. Similar effort was put into searching all sampled SUs.

We initiated the survey approximately 24 hours after a 5-cm snowfall on top of a good snow base

(50–60 cm). We surveyed each SU using a Bell 206B Jet-ranger helicopter with a 4-person crew, including the pilot. We searched all major watercourses and road or trail networks within each SU for the presence of fresh wolf tracks (Figure 2; fresh = since most recent snowfall or windstorm; Becker et al. 1998). Other animals in our study area that left tracks that potentially could have been confused with those of wolves were foxes, otters, fishers, white-tailed deer (*Odocoileus virginianus*), and moose. If the identity of the species that left a track segment was uncertain, we landed the helicopter to examine tracks more closely. We also looked for presence of ungulate carcasses and ravens (*Corvus corax*) or other scavengers as an indicator that a wolf kill-site might be within an SU. In blocks with heavy conifer cover, we carefully examined all sloughs and meadows for tracks and also searched open areas and possible travel routes in unsampled

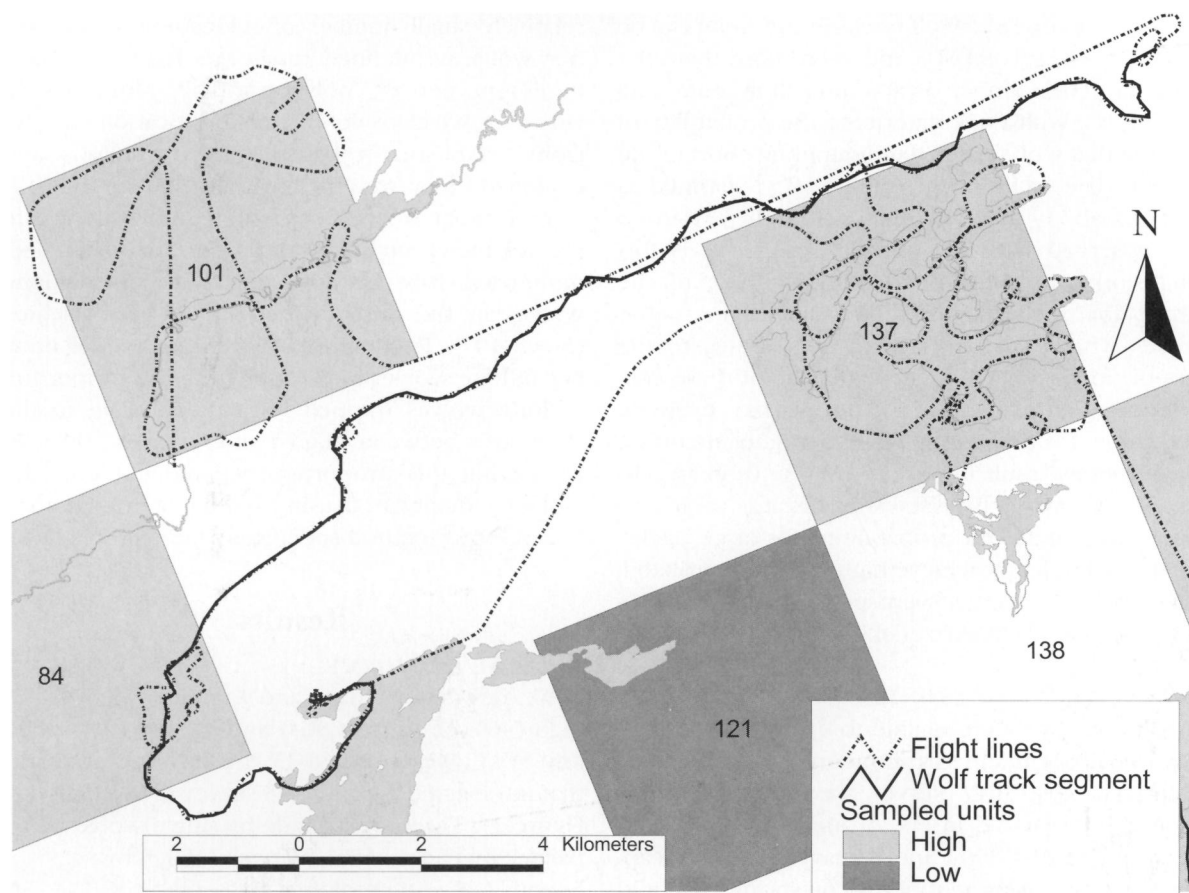


Figure 2. Flight lines indicate pattern used to search sample units 101 (containing small amount of watercourses) and 137 (containing large amount of shoreline) during a wolf-track survey conducted in Algonquin Park, Ontario, Canada in February 2002.

adjacent SUs in an attempt to detect any tracks entering or leaving the sampled SUs. Excluding time spent tracking wolves, it required 23–60 minutes to adequately search each SU depending on the forest overstory, presence of tracks of nontarget species, and lighting conditions. In some cases we were able to increase sampling efficiency by collectively searching adjacent SUs.

When we found fresh tracks, we followed them forward to the wolves and then backward until the tracks were no longer considered “fresh.” This was assumed to be the point beyond which we would have disregarded the tracks if we first discovered them at that location. Generally, this occurred at a bedding or large windswept area. In cases where we could not actually see the wolves, we followed them forward until we were confident we knew their location and their trail did not cross into any additional SUs. In these cases, pack size was enumerated by observing areas where the pack split

into individual trails or by counting the number of beds in a resting area. If a good count could not be obtained from the air in this manner, we landed to examine the tracks more closely. We attempted to reduce the possibility of counting the same group more than once by initiating our survey in the south end of the study area and progressively radiating outward toward the north end. In doing so, we surveyed SUs in close proximity to each other within a relatively short period of time to reduce the possibility of counting the same group of wolves multiple times in different parts of the study area.

We obtained population and variance estimates using standard probability sampling techniques applied to the appropriate wolf observations within the respective SUs as per Becker et al. (1998). Probability network sampling is different from other sampling schemes in that the object of interest, tracks of a wolf or pack of wolves, is not

restricted to one SU. Wolf tracks in the snow can be contained in several SUs and even more than one stratum. The number of SUs in each stratum containing the wolf track determine the probability of finding that wolf for the fixed sampling effort of the survey. The inclusion probability,  $P_u$ , is defined as the probability that fresh tracks from the  $u^{\text{th}}$  group are observed with the sample design. It is this inclusion probability divided by the size of the group that made the respective tracks that determines what each observation contributes to the population estimate. Indeed, the sum of these contributions constitutes the population estimate (equation 1; Becker et al. 1998). Higher inclusion probabilities result in a more precise estimate. To obtain reasonably precise estimates, it is critical to have large inclusion probabilities for large packs. Stratification helps achieve high inclusion probabilities. All calculations were performed using program SUPEPOP (Becker et al. 1998).

### *Telemetry-based estimate*

Although we were unable to estimate wolf density via radiotelemetry concurrently with our February 2002 SUPE survey, we radiocollared 46 wolves  $\geq 1$  year old in and around our study area between August 2002 and January 2003. We captured wolves using number 3 coil-spring foot-hold traps or a handheld netgun fired from a helicopter and physically restrained them with a snare-pole. We immobilized wolves with an intramuscular injection of Telazol (A. H. Robins, Richmond, Va.) at a dosage of ca. 7 mg/kg of estimated body mass. Each wolf was fitted with a VHF radiocollar (Holohil Systems Ltd., Woodlawn, Ont., and Lotek Engineering Inc., Newmarket, Ont.) weighing approximately 400 g. Wolf capture and handling procedures were approved by the Ontario Ministry of Natural Resources' animal care committee (permit no. 02-75).

We located wolves primarily from the air and occasionally from the ground using standard methods of triangulation (White and Garrott 1990). We delineated a census area that contained the territories of 24 animals living in 10 adjacent packs and the area in between these packs. Although not identical to our 2002 SUPE survey area, the 2 areas overlapped considerably (Figure 1). We defined a territory as the composite area of seasonal home ranges used by members of each pack. We pooled locations from all marked members of a pack to estimate territory sizes and boundaries. Given the

relatively small number of relocations ( $n = 24\text{--}43$  per wolf), we defined territories based on 100% minimum convex polygon (MCP; Mohr 1947). However, we considered isolated locations  $> 5$  km from established territories as excursions and excluded them from the analyses (Messier 1985).

We estimated wolf density in winter 2003 within the telemetry census area as the summed maximum pack sizes plus the estimated number of lone wolves in the area, divided by the census area (Mech 1973, Fuller 1989). We estimated the number of lone wolves in the area from the proportion of lone wolves trapped for radiocollaring in the study area between August and October 2002. In calculating this proportion, we did not consider wolves radiocollared using helicopter netgunning because this method specifically targeted packs.

## Results

### *2002 SUPE survey*

We flew on 11 days and sampled 45 SUs—28 high (46% of all high SUs) and 17 low (22% of all low SUs). We observed 17 “fresh” track networks that intersected  $\geq 1$  of the 45 surveyed SUs (Table 1; Figure 1). Three were made by single wolves, 2 by pairs, 2 by packs of 3, 3 by packs of 4, 5 by packs of 5, and 2 by packs of 6 wolves (Table 1). These observations resulted in an estimate of 87 wolves in the 3,425-km<sup>2</sup> study area ( $2.5 \pm 0.5$  [90% CI] wolves/100 km<sup>2</sup>). We did not consider the single wolves to be “packs” or territory holders (e.g., Messier 1985, Ballard et al. 1987), and, excluding solitary wolves, the average pack size in the area we surveyed was  $4.2 \pm 0.4$  (SE),  $n = 14$ . We estimated there were approximately 16 packs (90% CI = 12–21) and 4 solitary wolves (90% CI = 3–5) within the study area at the time of the survey.

### *2003 telemetry-based estimate*

We aerially located collared wolves from each pack in the 2,338-km<sup>2</sup> census area 24–43 times during January–April 2003. Although all territories were not adequately defined, Figure 1 suggested that it was unlikely any undetected packs lived entirely inside the census area. The 10 packs with radiocollared wolves within the census area contained 42 members, producing a density estimate of 1.8 resident wolves/100 km<sup>2</sup>. Based on a ratio of 4 lone to 13 pack-living wolves trapped in our study area from August–October 2002, we estimated there were also 10 solitary wolves living in the cen-

Table 1. Observed wolf pack size ( $y_u$ ), number of sample units containing tracks ( $m$ ), inclusion probability ( $p_u$ ), contribution to the population estimate ( $y_u/p_u$ ), and contribution to the variance [ $V(T_{yu})$ ], by pack, for a February 2002 wolf survey in Algonquin Provincial Park, Ontario, Canada.

| Group ID | $y_u$          | No. SUs containing tracks |                  | $p_u$ | $y_u/p_u$ | $V(T_{yu})$ |
|----------|----------------|---------------------------|------------------|-------|-----------|-------------|
|          |                | $m_{\text{high}}$         | $m_{\text{low}}$ |       |           |             |
| 1        | 5              | 2                         | 2                | 0.83  | 6.05      | 5.59        |
| 2        | 1              | 1                         | 1                | 0.58  | 1.72      | 1.48        |
| 3        | 4 <sup>a</sup> | 2                         | 0                | 0.71  | 5.62      | 6.75        |
| 4        | 6              | 3                         | 2                | 0.91  | 6.60      | 2.55        |
| 5        | 3              | 0                         | 2                | 0.40  | 7.51      | 30.3        |
| 6        | 4              | 1                         | 0                | 0.46  | 8.71      | 36.6        |
| 7        | 1              | 3                         | 0                | 0.85  | 1.18      | 0.0         |
| 8        | 2              | 1                         | 1                | 0.58  | 3.45      | 3.06        |
| 9        | 4              | 2                         | 1                | 0.78  | 5.16      | 3.99        |
| 10       | 5              | 4                         | 0                | 0.92  | 5.43      | 1.26        |
| 11       | 2              | 2                         | 2                | 0.83  | 2.42      | 0.20        |
| 12       | 5              | 2                         | 0                | 0.71  | 7.03      | 11.4        |
| 13       | 6              | 4                         | 1                | 0.94  | 6.39      | 1.44        |
| 14       | 5              | 0                         | 4                | 0.65  | 7.75      | 18.2        |
| 15       | 5              | 4                         | 4                | 0.97  | 5.14      | 0.25        |
| 16       | 1              | 1                         | 0                | 0.46  | 2.18      | 1.17        |
| 17       | 3              | 0                         | 4                | 0.65  | 4.65      | 5.53        |

<sup>a</sup> The actual pack size was 6 but as only 2/3 of the fresh track segment left by this group was in our study area we reduced the effective pack size by 1/3 (inclusion rule, see methods).

sus area. The ratio of solitary wolves in our trapped sample was similar to that observed during the 2002 SUPE survey (3 singles vs. 14 packs; Table 1). The pooled density of solitary and pack wolves in the surveyed area was 2.3 wolves/100 km<sup>2</sup>.

## Discussion

### *Suitability of SUPE for estimating wolf densities in forested areas*

The SUPE provided an objective, repeatable means of estimating wolf density with an associated measure of precision. Additionally, the SUPE alleviated the problem of dealing with the proportion of lone wolves used in telemetry-based density estimates (Fuller and Snow 1988, Ballard et al. 1995). However, a number of statistical assumptions (listed in the introduction) must be considered when assessing the likelihood that SUPE will provide an unbiased density estimate for a given area (Becker 1991, Becker et al. 1998). Key assumptions that could have compromised our population estimate were 1) *All animals of interest move during the*

*study.* Wolves generally move between 7–25 km/day during winter (Mech 1970, Kolenosky 1972, Jedrzejewski et al. 2001). During our survey we observed that even wolves at or near fresh deer or moose carcasses had moved >1 km in the previous day (Figure 1), thus satisfying this condition. 2) *Tracks are continuous.* Although this condition usually was met, we occasionally lost tracks in thick conifer cover. When this occurred, we searched the perimeter of the habitat patch until we found the track again or determined the wolves had not exited the patch. Thus, even though we occasionally missed segments of the entire track network left by wolves, we clearly established a 1-to-1 correspondence between all track segments and the animals that made them. Becker (1991) demonstrated that an unbiased estimate could still be made provided that such a 1-to-1 correspondence could be demonstrated. 3) *“Fresh” tracks in searched SUs are not missed.* Becker et al. (1998) used the locations of radiocollared wolves in their survey area to confirm that this assumption was met. There were no radiocollared wolves in our survey area during the time of the SUPE survey, so we can not say with certainty that we did not miss the tracks of any wolves in our sampled SUs. However, we never observed a wolf track (either opportunistically or in searching a new SU) that was subsequently tracked back to an SU that had been previously searched without detecting the track in question. Also, population estimates based on radiotelemetry during 1988–1992 (Forbes and Theberge 1995, 1996), 2003 (this paper), and 2004 (B. R. Patterson, unpublished data) suggest that wolf densities in our study area have been relatively stable since the late 1980s. The correspondence between the population estimate generated by SUPE in 2002 and the aforementioned telemetry-based estimates suggests that few if any track segments were missed during our survey.

Because most study areas will require several days to survey, an additional assumption is that no animals were double-counted by moving among SUs on subsequent days. We attempted to survey SUs in close proximity to each other within a relatively short time to reduce the possibility of counting the same wolf pack multiple times in different parts of our study area. Additionally, although there were no radiocollared wolves in our study area during the SUPE survey to help assess this assumption, we did carefully investigate the origin of any track segments within 10 km of a previously enumerated track segment.

Although track segments 10, 11, and 13 were all located in relatively close proximity (Figure 1), we were confident that they were made by 3 different groups of wolves. We tracked wolves responsible for segments 10 (5 wolves—not observed but confined to a small but dense conifer stand) and 11 (2 wolves - observed) within a few hours of each other. Although all 7 of these wolves may have belonged to the same pack, they were traveling separately on the day we tracked them. The next day we tracked group 13 a few km to the northeast. Although this pack (6 wolves observed on a deer kill) was in close proximity to group 10, there were no tracks joining their respective track segments.

**Efficiency of stratification.** We used stratification to help achieve high inclusion probabilities (Table 1). Our stratification was based on 1) the relative amount of trails and watercourses in each SU, which influenced our ability to easily see wolf tracks, and 2) the relative amount of hemlock cover, which was related to prey (moose and deer) density (Forbes and Theberge 1993). Unlike traditional random-block aerial surveys, overall effectiveness of the stratification can not be assessed by the coefficient of variation of the strata estimates because the calculations are summed over observations and not strata. However, Becker et al. (1998; equation 5) presented a method to determine the contribution of each observation to the population variance. This tool can be used to determine the effectiveness of the stratification and indicate stratification refinements for future surveys. The inclusion probabilities for our observations were positively associated with group size ( $r_s = 0.57$ ,  $P = 0.016$ ; Table 1), indicating optimal sampling effort as a result of a good stratification. For example, if we knew which SUs contained the large packs, we would pick those over ones with no wolves or containing single wolves. Specifically, if there were a covariate correlated with pack size that was known for every SU, we would have used this information to assign probabilities to each SU and obtain the optimal sample design (Cochran 1977, Sarndal et al. 1992). Not having this information, we stratified using available information. A strong correlation between pack size and the inclusion probabilities suggested that our stratification was effective.

Because each pack was enumerated on only a single occasion, pack-size estimates represent minimums. Although eastern wolves tend to form cohesive packs (Messier 1985, Fuller 1989, Forbes and Theberge 1995), individuals do temporarily disasso-

ciate from the pack, particularly during the breeding season (Messier 1985, Cook et al. 1999). This, coupled with the possibility that we underestimated the size of  $\geq 1$  groups by enumerating pack size based on tracks in snow alone, suggested that we likely underestimated the true size of some packs during the 2002 SUPE survey. Nonetheless, mean pack size estimated during the 2002 SUPE survey was the same as that estimated with telemetry for 10 packs living within roughly the same area during 2003 ( $4.2 \pm 0.5$ ).

### *Wolf population trends in Algonquin Park*

Densities of both deer and wolves were high in Algonquin Park during the late 1950s and early 1960s (Pimlott et al. 1969) but declined dramatically in the early 1970s (Voigt et al. 1976). Whereas the park used to contain several prominent deer wintering areas (N.W.S. Quinn, unpublished data), most white-tailed deer now migrate each winter to yards located outside the park boundary (Swanson 1993, Forbes and Theberge 1995). In response to this annual exodus of deer, many wolf packs in the eastern section of the park undertake several excursions of up to 10–60 km to areas containing high numbers of deer outside the park (Forbes and Theberge 1995, 1996; Cook et al. 1999; Pisapio 1999). Many of these wolves are trapped or shot while outside the park in winter (Forbes and Theberge 1995, Theberge 1998, Pisapio 1999). Theberge (1998) and Vucetich and Paquet (2000) have suggested that both pack size and densities of



Brent Patterson poses with an adult male wolf captured and radiocollared in the Algonquin Park, Ontario in August 2002.

wolves declined in eastern Algonquin Park from 1988–1999. In response to these concerns, a 30-month moratorium on hunting and trapping of wolves within 10 km of the park boundary was introduced in December 2001.

In winter 2003, 5 of 6 packs monitored in eastern Algonquin made repeated forays to deer yards outside the park (B. R. Patterson, unpublished data). In contrast, only 1 of 10 packs in our census area (western Algonquin) made excursions outside of their territory (and the park) during this time. This suggests that fewer wolves from western Algonquin may be exposed to exploitation by humans in areas outside the park during winter. Using 2 independent methods, we estimated density of wolves in western Algonquin at 2.5 and 2.3 wolves/100 km<sup>2</sup> in winters 2002 and 2003, respectively. These estimates were similar to those made by Forbes and Theberge (1995, 1996) in Algonquin using radiotelemetry in winters 1987–1992. Thus, although wolf densities in eastern Algonquin may have declined during the 1990s (Vucetich and Paquet 2000), our results suggest little difference in wolf density in western Algonquin between the late 1980s and 2002–2003.

## Management implications

The dynamic nature of weather, wolf movements, pack sizes, and location (including resting on kills) presents a worst-case scenario for a population estimator. Although several authors have expressed confidence that all wolves present in their telemetry census areas were enumerated (e.g., Mech 1977, Fuller 1989, Hayes and Harestad 2000), it remains difficult to statistically quantify the uncertainty surrounding telemetry-based population estimates. In our case, a relatively low number of relocations meant that some territories in our telemetry census area were not fully defined. Because we used the total area approach (e.g., including interstices between territories, Messier 1985), the only issue is that underestimation of the size of territories around the perimeter of the census area might result in our density estimate being biased high (i.e. the denominator of the density estimate was biased low). However, tracks of uncollared packs were observed in areas immediately surrounding our census area, suggesting there was little room for expansion along the outer edges of the territories in our census area.

Given the correspondence between our SUPE

and telemetry-based population estimates, and that we seemed to meet the statistical assumptions of the SUPE, we believe the SUPE can provide useful, relatively accurate, and precise estimates of wolf density in forested areas. The SUPE will be particularly useful when radiocollared wolves are unavailable for use in population estimation. However, owing to greater forest cover throughout much of our study area, the average length of time to complete each SU using a rotary-wing aircraft ( $\bar{x}$  = 46 minutes/SU including time to follow track segments; range 23–132 minutes,  $n$  = 45) was considerably greater than that required to survey even larger (41-km<sup>2</sup>) SUs from a fixed-wing aircraft in Alaska (12–33 minutes/plot; Becker et al. 1998). We originally had thought that each SU could be effectively searched in less than half the time it actually took. Although we generally became more efficient as the survey progressed, we are uncertain as to how much quicker we could effectively search forested SUs regardless of the amount of experience gained. A helicopter will probably be required for inexperienced observers to continuously follow wolf tracks in heavily forested areas. However, professional wolf trackers in both the Yukon and Alaska have demonstrated the ability to efficiently follow wolf tracks through dense cover using small fixed-wing aircraft (E. F. Becker, personal observation). Using such trackers should increase the size of the area that could be surveyed for a given amount of money. Given that Becker et al. (1998) surveyed an area almost 10 times the size of our present study area, SUPE has potential for estimating wolf densities over larger forested areas than the one we surveyed.

Our 2002 SUPE survey cost about \$40K (Canadian, excluding staff time). The cost of deploying radiocollars and tracking wolves within our telemetry census area (2,338 km<sup>2</sup>) during winter 2003 was approximately 25% higher (about \$50K). Because other ecological objectives can be pursued simultaneously with radiocollared wolves in a given study area, we cannot recommend the SUPE survey on a cost-savings basis alone. Nonetheless, the SUPE provides an objective, seemingly accurate, and repeatable means of estimating wolf density with an associated measure of precision. The SUPE can be employed in forested areas and may be particularly useful in areas where a traditional density estimate via radiotelemetry is logistically or socially unfeasible.

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