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Original article

Comparison of visual-based helicopter and fixed-wing forward-looking infrared surveys for counting white-tailed deer *Odocoileus virginianus*

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Aerial surveys using direct counts of animals are commonly used to estimate deer abundance. Forward-looking infrared (FLIR) technology is increasingly replacing traditional methods such as visual observation from helicopters. Our goals were to compare fixed-wing FLIR and visual, helicopter-based counts in terms of relative bias, influence of snow cover and cost. We surveyed five plots: four 41.4 km^2 plots with free-ranging white-tailed deer *Odocoileus virginianus* populations in Wisconsin and a 5.3 km^2 plot with a white-tailed deer population contained by a high fence in Michigan. We surveyed plots using both fixed-wing FLIR and helicopters, both with snow cover and without snow. None of the methods counted more deer than the other when snow was present. Helicopter counts were lower in the absence of snow, but lack of snow cover did not apparently affect FLIR. Group sizes of observed deer were similar regardless of survey method or season. We found that FLIR counts were generally precise (CV = 0.089) when two or three replicate surveys were conducted within a few hours. However, at the plot level, FLIR counts differed greatly between seasons, suggesting that detection rates vary over larger time scales. Fixed-wing FLIR was more costly than visual observers in helicopters and was more restrictive in terms of acceptable survey conditions. Further research is needed to understand what factors influence the detection of deer during FLIR surveys.

Key words: FLIR, forward-looking infrared, helicopters, Odocoileus virginianus, white-tailed deer, wildlife surveys

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Wildlife biologists commonly monitor large mammal abundance for management and research purposes. A wide variety of monitoring methods are used, including those based on hunter-harvest data (e.g. population reconstruction; Roseberry & Woolf 1991), direct counts of individuals (Loison et al. 2006, Belant & Seamans 2000, Jachmann 2002), indirect indices (e.g. browsing index and faecal pellet counts;

Morellet et al. 2007, Forsyth et al. 2007), and capture-mark-resight methods (Rice & Harder 1977, Skalski et al. 2005, Garel et al. 2010). The selection of a specific method depends on the monitoring goals, species characteristics (e.g. body size, habitats used, activity patterns and level of gregariousness), spatial scale of monitoring required (both extent and grain), and resources of the agencies responsible for monitoring. A primary challenge for wildlife biologists is to find a reliable method to monitor large mammals, given considerable budgetary, logistical and time constraints. Analytical and technological advancements may improve the ability of biologists to meet monitoring goals, but evaluation of these advancements should precede their wide adoption.

The discovery of chronic wasting disease (CWD) in white-tailed deer *Odocoileus virginianus* in Wisconsin, USA, in 2002 (Bartelt et al. 2003, Joly et al. 2006) led the Wisconsin Department of Natural Resources (WIDNR) to institute liberal harvest regulations and government sharpshooting programmes intended to dramatically reduce deer populations. Prior to the discovery of CWD, deer abundance at the scale of deer management units (DMUs $\approx$ 1,500 km^2) was monitored using hunter-harvest data and population reconstruction (Creed et al. 1984, Skalski et al. 2005). However, drastic changes in the harvest regime caused violations of the reconstruction method and alternative monitoring methods were required (Rolley 2009, Millspaugh et al. 2006). The WIDNR identified two monitoring needs: 1) deer abundance in DMUs affected by changes in harvest regulations and 2) fine-scale variation in deer abundance in the CWD-affected area. Fine-scale estimates of deer abundance were needed to identify areas for targeted deer reduction, to monitor deer population responses to harvesting and CWD at a finer scale than the DMU, and as a part of a research project designed to assess density-dependent transmission of CWD (Storm 2011). The WIDNR established quadrat surveys, using visual observers in helicopters, wherein a census of all deer was attempted for each quadrat (2.59 km^2). This allows for population estimates at both fine (quadrat) and large (DMU) scales. The advantage of this method, and similar aerial survey methods, is the relative simplicity and efficiency of surveying large areas (Stoll et al. 1991, Beasom et al. 1986, Jachmann 2002). A primary disadvantage (like all count-based methods) is that population estimates are negatively biased, because observers fail to detect some animals during surveys (Caughley 1974, Pollock & Kendall 1987). An implicit assumption of these surveys is that average detection rates are spatially and temporally stable.

Other survey methods that estimate detection rates exist, but these were considered impractical given the available resources and complexity of estimating detection rates for different spatial scales. For example, the need for immediate abundance information and the large area of interest ($>$ 20,000 km^2) precluded the development of capture-mark-resight methods. Aerial distance sampling was not considered practical because the assumption of complete detectability on the transect line is unlikely to be met in deciduous forest, which dominates much of the landscape.

While detection probabilities are likely influenced by numerous factors (e.g. observers, habitat and weather), snow cover is so influential that it is generally considered a prerequisite for conducting large-scale aerial-visual surveys of large mammals in forested habitats. Snow cover is critical because it provides a high visual contrast between the animal and their background. Even with adequate snow, white-tailed deer detection probabilities are $<$ 1.0 and can vary from 72% to 99% using visual observers in helicopters (Rice & Harder 1977, Ludwig 1981, Stoll et al. 1991, Beringer et al. 1998). In some regions, snow cover may be so ephemeral that it does not cover the ground for the length of time needed to complete aerial surveys.

An aerial survey technique that does not rely on snow cover would expand the timeframe and area over which aerial surveys can be effective. Detection of animals by forward-looking infrared (FLIR) technology relies on a thermal contrast between animals and their background, rather than visual contrast, and has been assumed to be unaffected by snow cover (O'Neil et al. 2005). Modern FLIR technology operates similarly to a video camera. Sensors detect infrared radiation, which is emitted by living organisms and the environment, but is invisible to humans. The signal is converted to a visual image and displayed on a screen (see Baldacci et al. 2005 for an overview of infrared radiation and FLIR technology). The potential for FLIR technology to be effective without snow cover, along with claims that FLIR surveys have higher detection probabilities, better safety and lower cost (O'Neil et al. 2005, Blackwell et al. 2006), has led some natural resource agencies to either purchase commercially available FLIR equipment or contract with companies specializing in FLIR applications for wildlife surveys (Bernatas 2006, Green 2006, Prange & Barber 2008).

Like any count-based method, FLIR surveys are subject to visibility bias which is rarely quantified because of the added expense and logistical difficulty. Among the studies reporting detection rates of aerial FLIR surveys for deer (Naugle et al. 1996, Haroldson et al. 2003, Potvin & Breton 2005), detection rates varied markedly between (31-89%), and within studies (Haroldson et al. 2003, Potvin & Breton 2005). Variability of detection rates and use of different equipment and survey protocols make it difficult for managers to apply these reported detection rates to their particular areas.

Other studies have focused on comparing aerial FLIR surveys with other more commonly used techniques (Naugle et al. 1996, Drake et al. 2005, Prange & Barber 2008). Naugle et al. (1996) found that aerial FLIR counts were higher than road-based spotlight counts, while Drake et al. (2005) found that aerial FLIR and roadside counts of a suburban deer population were similar. These comparisons are important because they address relative bias; however, precision also should be considered. An evaluation of precision is warranted because biased but precise counts might be used to monitor population changes provided visibility is relatively constant over time (Diefenbach 2005). The choice of a method to survey animal populations involves consideration not only of bias and precision, but also of cost, and cost comparisons are lacking in published literature (but see Garel et al. 2005).

The dependence of helicopter-based visual surveys on unpredictable snow cover motivated us to consider FLIR as a potential alternative to helicopter surveys to estimate small scale deer abundance (at $\approx$ 2.59 km^2) over an extensive area ($>$ 500 km^2). Our goal was to determine if FLIR provides less biased counts and a greater time window for conducting deer surveys than is possible with visual observation from helicopters. Our principle goals were to compare fixed-wing FLIR and helicopters in terms of 1) relative bias, 2) relative influence of snow cover and 3) cost. Additionally, we evaluated the precision of fixed-wing FLIR surveys.

Material and methods

Study area

We used study areas in Wisconsin (WI) and Michigan (MI), USA. In WI, we conducted surveys on four 12.9 × 3.2 km (41.4 km^2) survey plots, oriented east-west and located approximately 35 km west of Madison, WI. We oriented survey plots so that they aligned with 2 × 8 blocks of Public Land Survey System sections (each section = 2.6 km^2). Our WI study area was characterized by highly dissected deciduous forest patches (43%) on hillsides and hilltops with agricultural crops (30%) and grassy fields (14%) in small valleys. The northernmost plot (4) of our WI study area also included bottomlands of the Wisconsin River composed mostly of large, flat agricultural fields and deciduous floodplain forest. Small pine plantations are scattered throughout the study area. Our MI study area was the University of Michigan's Edwin S. George Reserve (ESGR), a research facility approximately 30 km northwest of Ann Arbor, MI, which is surrounded by a high fence. The ESGR study area is 5.3 km^2 and is composed of deciduous forest (60%) and oldfield (16%) in the uplands, and wooded swamps and shrubby wetlands (23%) in the lowlands (University of Michigan 2009).

Study design and data collection

We surveyed plots using both fixed-wing FLIR and helicopters with two observers during two seasons: 1) winter with $>$ 20 cm of snow cover on the ground (SNOW), and 2) early spring, when the ground was not covered by snow, but before leaves emerged (NO SNOW). All four WI plots were to be surveyed during the SNOW season, while (due to budgetary constraints) plots 1, 2 and 3 were to be surveyed during the NO SNOW season.

An ideal comparison of survey methods would involve replicated surveys of closed populations (i.e. no immigration, emigration, births or deaths) of meaningful size so that detection rates accounted for differences in counts. Although closed populations were not strictly possible in our WI study area, we designed our study to ameliorate the lack of population closure. Specifically, deer in our WI study area are non-migratory, have small home ranges ($<$ 2 km^2 for most deer; Skuldt 2005) relative to the size of our survey plots (41.4 km^2), and have high survival during winter and spring (T. Van Deelen, unpubl. data). Additionally, we attempted to minimize the time between FLIR and helicopter surveys. Therefore, we believe it was unlikely that large changes in deer abundance occurred between surveys during our study.

The ESGR is enclosed by a 3.0-4.3 m high deer-proof fence, which received routine (at least once per month) inspections as required by the state of MI. The integrity of the fence was not compromised at any time during our study, thus deer did not move into or out of the ESGR between survey seasons. The deer population was maintained well below biological carrying capacity through annual culling operations, which were completed prior to our surveys. A telemetry study conducted from 2006 to 2007 found high over-winter survival (Malcolm et al. 2010), and an intensive, systematic carcass survey conducted during 14-16 April, 2008, found no carcasses, thus mortality between survey seasons was probably negligible. Because of lack of mortality and movement in or out, we assumed that the deer population on the ESGR was closed during our study.

Vision Air Research (Boise, Idaho, USA) conducted the FLIR surveys using a PolyTech Kelvin 350 II infrared sensor (Sweden) mounted with a gimbal on a Cessna 206 fixed-wing aircraft. The sensor detected long-wave (8-12 μm) infrared radiation and had a thermal resolution of $< 1°C$. Each plot was surveyed comprehensively in transects 150 m apart at 300 m above ground level. The aircraft travelled at approximately 120 km/hour and in each plot, it took two hours to complete each replicate survey. A sensor-operator on board the aircraft viewed real-time images on a screen and panned the sensor side-to-side along each transect. When the operator detected a potential deer, based on thermal contrast, the aircraft would circle around the deer to confirm the sighting. The imagery was recorded on video tape, which was reviewed by the FLIR contractor to confirm deer detections, georeference groups of deer, and count the number of deer. There was overlap in the field-of-view of adjacent transects, and the FLIR contractor used their judgment to remove what they believed to be duplicate sightings of deer groups. The results were used to produce GIS shapefiles that contained the locations and sizes of observed deer groups. The FLIR crew was instructed to conduct two replicate surveys/plot in the WI study area and three replicates for the ESGR study area during each survey season. Replicates were separated by approximately two hours needed for landing to refuel and rest. FLIR surveys were conducted opportunistically, as weather allowed, and they were therefore not restricted to any particular time of day.

WIDNR observers and private contractor pilots conducted helicopter surveys in the WI study area using survey methods previously established for monitoring deer populations in WI. The survey crews comprehensively searched plots one section at a time using either a Schweizer 333 or Bell 47 helicopter at 48-56 km/hour and ca 30 m above ground level. We were not able to replicate helicopter counts in the WI study area due to budgetary constraints.

The Huron-Clinton (MI) Metropolitan Authority (Metroparks) conducted helicopter surveys of the ESGR deer population. Metroparks used a Robinson R-44 helicopter and surveyed at ca 30 m above ground level at between 65 and 72 km/hour. Surveys were conducted from late morning to early afternoon. The entire ESGR was surveyed twice during each survey.

Helicopter survey crews consisted of a pilot and two observers, working as a team. Survey crews used a systematic search pattern of tightly spaced transects. Pilots maintained altitude via altimeter and visual assessment of height above tree tops. Surveys were conducted during mid-day to avoid shadows which may reduce the ability of the crew to detect deer. Deer often flushed and ran short distances but sometimes remained bedded or standing. Observers carefully recorded group size and direction of moving deer to avoid double counting.

Data analyses

We calculated density (deer counted/km^2) for each survey and mean, standard deviation (SD) and coefficient of variation (CV) of deer densities for each season and plot with replicate surveys. Although our surveys estimated deer abundance, we used densities rather than counts to facilitate comparison between ESGR and WI study area plots. To determine if densities differed with respect to the survey method (FLIR vs helicopter) or season (SNOW vs NO SNOW), we fitted a linear mixed model where the response variable was the deer density for each survey (plot and replicate), and survey method, season and the interaction were fixed effects. We used survey plot as a random effect to account for the lack of independence of observations of the same plot. We fitted the model using restricted maximum likelihood in program R (R Development Core Team 2009), package 'nlme' (Pinheiro et al. 2008).

To facilitate a more detailed evaluation of the relative bias of fixed-wing FLIR and helicopters, we calculated count ratios for each plot surveyed, by dividing the FLIR count by the corresponding helicopter count for the same plot and season. To evaluate the influence of snow on each survey method, we similarly calculated the ratio of the

SNOW count to the NO SNOW count for each plot. We used mean counts when we had replicates.

We determined whether the size of observed deer groups differed between survey methods or survey periods. Group size influences detection rate in large mammals (Samuel et al. 1987), thus we reasoned that relative biases in the survey methods and periods might be reflected in differences in the group size of detected deer. Our group-size data had a multilevel structure (i.e. groups observed during the same replicate survey) within each plot. Normally, one could account for this structure by including 'replicate' nested within 'plot' as an additional random-effect term in the mixed model. In our case, however, some plots had only one survey for a given method and season, thus we had insufficient data to estimate this variance component. Therefore, for FLIR surveys with replicated counts we only used the group-size observations from the first replicate in the group-size analysis to avoid potential dependence between the replicates. We fitted a linear mixed model using the log of observed group size as the dependent variable, survey method and season as fixed effects, an interaction term and plot as a random effect. We used restricted maximum likelihood in program R (R Development Core Team 2009), package 'nlme' (Pinheiro et al. 2008) to fit the model.

Results

Precipitation prevented FLIR surveys on three days and low ceiling (clouds < 300 m above ground level) prevented FLIR surveys on seven days. One additional day was lost when the aircraft became covered in ice during a storm. Due to problems in conducting FLIR surveys, we obtained the following FLIR surveys for evaluation: in the WI study area, four plots with two replicate surveys each during the SNOW season, one plot with two replicates and two plots with one replicate each during the NO SNOW season, and in the ESGR, two replicates during the SNOW season and three during the NO SNOW season (Table 1).

The SNOW season helicopter surveys of WI plots occurred during 24-26 January 2008, and FLIR surveys occurred on 27 January, 31 January, 5 February and 7 February 2008. During the NO SNOW season, WI plots were surveyed by helicopter on 7 April, 8 April and 9 April 2008 and by FLIR on 5 April, 6 April and 7 April 2008. The helicopter surveys of the ESGR during the SNOW season were conducted on 11 February and 3 March 2008, and FLIR surveys took place on the overnight period of 11-12 February 2008. The ESGR was surveyed for the NO SNOW season by helicopter on 17 April and 23 April and by FLIR on 3 April 2008.

Table 1. Number of plots and replicates per plot surveyed for white-tailed deer during each survey season, by each survey method in Wisconsin (plots 1-4) and Michigan (ESGR) during 2008. Number of replicates in parentheses.

	Survey method	
Survey season	FLIR	Helicopter
Snow	Plot 1 (2)	Plot 1 (1)
	Plot 2 (2)	Plot 2 (1)
	Plot 3 (2)	Plot 3 (1)
	Plot 4 (2)	Plot 4 (1)
	ESGR (2)	ESGR (2)
No snow	Plot 1 (2)	Plot 1 (1)
	Plot 2 (1)	Plot 2 (1)
	Plot 3 (1)	Plot 3 (1)
	ESGR (3)	ESGR (2)

The mean CV for the FLIR surveys was 0.089 (Table 2). The SNOW helicopter counts of the ESGR were identical, and the CV for the NO SNOW counts was 0.354 (see Table 2).

The main effects for season and method were not significant (β_{season} = -0.867, SE = 1.387, P = 0.539; β_{method} = -0.888, SE = 1.400, P = 0.533, respectively), but the interaction was significant ($\beta_{interaction}$ = -7.460, SE = 2.117, P = 0.002), indicating the mean deer density for helicopter surveys during NO SNOW was lower than the other method-season combinations, which were similar to each other. During SNOW, FLIR counted more deer than did helicopters on two WI plots (count ratios of 1.21 and 1.16) and at the ESGR (1.9), but fewer on two other WI plots (0.57 and 0.62). During NO SNOW, FLIR counts were between 3.32 and 11.63 times higher than helicopter counts on WI plots and were 3.88 times higher at the ESGR. Helicopter counts during SNOW were always higher than helicopter counts during NO SNOW (WI plots had ratios of 3.99, 4.65, and 16.13, and the ratio at the ESGR was 2.69). FLIR counts during SNOW were higher than FLIR counts during NO SNOW on two WI plots (1.57 and 1.60) and at the ESGR (1.31), but lower on one WI plot (0.69).

We used 1,666 observations of deer group size in our analysis. The overall mean group size was 3.16 (SE = 0.07). Neither the main effects nor the

Table 2. Raw and mean white-tailed deer counts, densities (deer/km^2 in brackets) and associated coefficients of variation (CV) using forward-looking infrared (FLIR) and visual observers from helicopters (Helicopter), during SNOW- and NO SNOW-season surveys in Wisconsin (plots 1-4) and Michigan (ESGR) during 2008.

		FLIR					Helicopter			
Season	Area	Replicate 1	Replicate 2	Replicate 3	Mean	CV	Replicate 1	Replicate 2	Mean	CV
Snow	Plot 1	450 (10.86)	389 (9.39)	-	419.5 (10.12)	0.103	731 (17.64)	-	-	-
	Plot 2	730 (17.62)	651 (15.71)	-	690.5 (16.66)	0.081	572 (13.80)	-	-	-
	Plot 3	333 (8.04)	263 (6.35)	-	298 (7.19)	0.166	258 (6.23)	-	-	-
	Plot 4	184 (4.44)	148 (3.57)	-	166 (4.01)	0.153	268 (6.47)	-	-	-
	ESGR	81 (15.43)	82 (15.62)	-	81.5 (15.52)	0.009	43 (8.19)	43 (8.19)	43 (8.19)	0
No snow	Plot 1	584 (14.09)	632 (15.25)	-	608 (14.67)	0.056	183 (4.42)	-	-	-
	Plot 2	441 (10.64)		-	-	-	123 (2.97)	-	-	-
	Plot 3	186 (4.49)		-	-	-	16 (0.39)	-	-	-
	Plot 4	-	-	-	-	-	-	-	-	-
	ESGR	61 (11.62)	66 (12.57)	59 (11.24)	62 (11.81)	0.058	20 (3.81)	12 (2.29)	16 (3.05)	0.4

interaction were statistically significant (all $P > 0.20$), indicating that the group size of deer observed during our surveys did not differ between survey methods or seasons.

We converted study costs to dollars/km^2 of survey to facilitate comparison between FLIR and helicopter survey methods. In the WI study area, surveying using privately contracted helicopters and WIDNR observers cost US\$57.67/km^2. The total cost of the FLIR surveys was US\$66,364 or US\$126.90/km^2.

Discussion

Variation in FLIR surveys in our study was similar to that reported by Naugle et al. (1996) and Diefenbach (2005), but much lower than that reported by Haroldson et al. (2003). Haroldson et al. (2003) estimated detection rates, and variation in their study was attributed to high variation in detection rates. The most comparable study to ours was Diefenbach's (2005), who used the same contractor to survey deer in a deciduous forest and obtained a CV of 0.084 based on four replicate surveys conducted on two consecutive nights. Our very limited assessment of precision of helicopter counts suggested that they may be more precise when snow covers the ground than when the ground is snow-free. Published precision estimates of helicopter counts are lacking, but Beringer et al. (1998) concluded, based on consistent detection rates, that helicopter counts of deer over snow were relatively precise.

Despite claims to the contrary (O'Neil et al. 2005, Blackwell et al. 2006), we found that detection of deer using FLIR was not consistently higher than visual observation from helicopters over snow. FLIR surveys counted between 16% and 90% more deer than did helicopter observers on three plots, while for two plots, helicopter observers counted 61% and 75% more deer than FLIR. This inconsistency suggested that the detection rates of one or both of the methods were variable. When snow was absent, FLIR counts were always higher than helicopter counts, indicating FLIR provides less biased estimates of deer abundance under these conditions than helicopters. Our results illustrate that helicopter counts in our study area are more effective with snow cover and were always > 2.5 times higher than counts without snow. This was expected because without snow on the ground, there is little visual contrast between deer and environmental surroundings.

An assumed advantage of FLIR is that the animal detection rate is relatively insensitive to environmental conditions, and thus surveys can be conducted over longer time periods and with less variation than observers in helicopters (O'Neil et al. 2005). This claim would seem to be supported by the non-significant season effect; however, the substantial seasonal variation within plots indicates considerable seasonal variation in FLIR detection rates. The between-season counts at the ESGR differed by 31%, which we believe can be attributed almost entirely to differences in the detection rate of FLIR. The between-season counts on the WI plots differed by 45%, 57% and 60%; however, differences on the WI plots may be due, in part, to the lack of population closure. Based on our study design and deer behaviour, we believe the between-season differences in counts was larger than would be expected due to lack of closure, suggesting that FLIR detection rates varied between seasons and/or from other factors that were not evaluated in our study.

Variable detection rates could reflect a dependence of FLIR on environmental factors. FLIR depends on the thermal contrast between the animal and its background, and is influenced by numerous physical features (e.g. bare ground, rocks and standing water; Dunn et al. 2002, Tappe et al. 2003, Bernatas & Nelson 2004, Potvin & Breton 2005) and atmospheric factors (e.g. air temperature, humidity and cloud cover; Graves et al. 1972, Moen 1974, Garner et al. 1995, Amstrup et al. 2004, Baldacci et al. 2005). Haroldson et al. (2003) found that thermal contrast between deer and their environment varied greatly even when weather conditions were relatively stable, indicating that factors affecting FLIR detection rates are poorly understood. Although these factors have been demonstrated to influence FLIR detection of animals, no study has estimated their quantitative relationship with detection rates of white-tailed deer. We found higher FLIR counts during SNOW on three of four plots, and while the role of snow cover remains unclear, it does not appear to have an overwhelming influence on FLIR detection, as it does on helicopter detection. Although high detection rates are possible with FLIR, inconsistency between seasons in our study and those reported in the literature indicates that detection may be inconsistent.

If detection probability of FLIR varies over time because of environmental conditions, then replicate surveys conducted within hours (our study) or perhaps days (Diefenbach 2005) could yield similar counts because survey conditions are likely to be similar. This would explain the high precision of our sequential FLIR surveys, but larger differences between seasonal (SNOW and NO SNOW) FLIR surveys. FLIR surveys that do not account for variable detection through time (e.g. seasons or years) could lead one to believe that the population had changed when in fact the true change in the population remains unknown. For example, at the ESGR, the mean FLIR count for the SNOW season was 81.5, while the mean count for the NO SNOW season was 62. Even though our sample size was small (two replicates for the SNOW season and three for the NO SNOW season), the difference was significant because the counts were precise and the difference in the means was relatively large ($> 30\%$) despite little if any change in deer population between seasons (see above). We caution that population estimates over time and space could be confounded with changes in detection probability. Thus, 'apparent' changes could occur because replicated FLIR estimates have such high precision that small differences in counts may be statistically significant. The high precision of FLIR in our study may be due, in part, to the short time between replicates, if deer moved little between replicates and the survey crew remembered where they previously sighted deer.

Group size has been related to the probability of detection of ungulates during aerial surveys (Samuel et al. 1987, Udevitz et al. 2006, Rice et al. 2009). We cannot directly address this relationship because we did not know the size of unobserved groups. However, we found no differences in mean group size, suggesting that group size was not an important predictor of detection probability in our surveys and that deer aggregation did not differ between SNOW and NO SNOW seasons. Of the observed groups in our study, 88% had ≤ 5 individuals and 52% had ≤ 2 individuals, thus small groups of deer were readily detected. These small groups are the norm for white-tailed deer, which are less gregarious than most other cervids, especially in landscapes dominated by forest (Hirth 1977).

Acceptable weather conditions for FLIR surveys were more restrictive than helicopter surveys. FLIR surveys in our study could not be conducted when the cloud ceiling was < 300 m above ground level, while helicopter surveys can be conducted as long as there is no precipitation and winds are not extreme. On one occasion, helicopter surveys were conducted when low ceiling prevented FLIR surveys. Daniels (2006) reported similar difficulty in finding suitable weather to conduct FLIR surveys of red deer *Cervus elaphus* in Scotland and concluded that FLIR surveys were infeasible in some areas.

Privately-contracted FLIR surveys were twice as expensive as surveys using WIDNR observers with privately contracted helicopters and pilots. Helicopter costs included WIDNR personnel support, pilot and helicopter rental. FLIR costs include surveying, imagery review and GIS file construction, daily support of FLIR survey personnel and additional daily support when inclement weather prevented surveying, and ferrying to and from the study area. Ferrying and support costs due to inclement weather comprised 15.8% and 13.3% of our total costs, respectively. These costs are situation-specific, thus the extent to which our costs represent other FLIR surveys is contingent on ferrying distances and weather encountered during surveying. While the costs of privately-contracted FLIR surveys were substantially greater than helicopter surveys, they do not require the dedication of staff time, which may be at a premium.

Some natural resource agencies have adopted FLIR for large-mammal surveys, under the assumption that FLIR does not have the deficiencies of traditional survey methods. We found that FLIR was not necessarily superior to helicopter surveys when snow cover was adequate. No count-based method, regardless of technological sophistication, is immune to imperfect detection of animals. In most cases, the relationship between the count and the true abundance is unknown, and these counts may have limited value, especially if that relationship is highly variable (Anderson 2001). These counts may be counterproductive, as they give a false impression of deer abundance and population trend. Although it may be challenging to identify and quantify the factors influencing detection rates, our results suggest that this research is necessary before FLIR (or any other count-based survey method) can be considered a reliable means of monitoring deer in forested landscapes. We urge caution in the use of raw counts for population monitoring and suggest that they be interpreted in conjunction with other information (e.g. hunter harvest, vegetation impacts and animal performance; Morellet et al. 2007).

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