USING DISTANCE SAMPLING TO ESTIMATE MOOSE ABUNDANCE IN ISLE ROYALE NATIONAL PARK

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ABSTRACT: Efficiently and accurately estimating moose (*Alces alces*) abundance in geographically isolated ecosystems like Isle Royale National Park (IRNP), Michigan, USA, is important for planning management actions. To estimate the population size of moose in IRNP, we flew a Robinson R44 helicopter to apply distance sampling in February 2022. We surveyed the entirety of IRNP with 149 transects that were 500-m wide and 0.16–13.36 km long depending on island width. We observed 439 moose in 253 groups, and fitted eight competing distance sampling models using two distance key functions (half-normal and hazard-rate), each with four covariate models: a null model, a univariate model for canopy size, a univariate model for group size, and a model with both canopy and group size. We used a Horvitz-Thompson-like estimator with the best model to calculate moose abundance on IRNP with 90 and 95% confidence intervals. The top model included a hazard-rate key function and the group size covariate. The estimated moose population was 1039 (90% CI 835–1293, 95% CI 800–1349). To test how sampling effort affected our estimates of moose abundance, we systematically removed 1/3 or 2/3 of transects from the dataset and repeated the analyses. The estimated abundance was similar (each 95% CI contained all 3 point estimates) when using all, 2/3, or 1/3 of transects, with the most precise estimate derived from the full dataset. Our population estimate was within the historical range of moose population estimates in IRNP and similar to a concurrent Gasaway-type estimate. While our survey covered the entirety of IRNP, we found that reducing effort by 1/3 provided a similar abundance estimate and precision. We concluded that distance sampling is a reasonable and efficient method to estimate moose density in IRNP. Monitoring how moose abundance varies in response to predator restoration efforts and climate change will help inform long-term management and planning in IRNP.

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Accurately estimating the abundance and growth rate of wildlife populations is important for their management and conservation. Specifically, monitoring moose (*Alces alces*) populations is important due to their social and economic value (Timmermann and Rodgers 2005), sensitivity to climate change (Weiskopf et al. 2019), and the effects of their herbivory on forest succession and structure (McInnes et al. 1992). Despite logistical and financial challenges, monitoring moose populations in remote areas like Isle Royale National Park (IRNP) is as important as in more accessible mainland areas.

Managing ecosystem-level impacts of moose is particularly challenging in a population with limited emigration and sources of mortality. Moose arrived on Isle Royale sometime in the early 1900s, followed by wolves in the 1940s (Mech 1966). For much of the 20th century, moose populations fluctuated with biotic and abiotic factors, including predation which influenced their survival, recruitment, and population growth rate (McLaren and Peterson 1994). IRNP has consistently supported high moose densities, with the population reaching as many as 2400 (~4.5 moose/km^2) and as few as 500 individuals (~0.93 moose/km^2) (Hoy et al. 2023). Moose browsing has constrained tree recruitment and altered the prevalence of selected food sources on Isle Royle (McInnes et al. 1992). Their browsing influences the abundance and growth rate of palatable tree species (Sanders and Kirschbaum 2023); for example, the density of mountain ash declined while that of white spruce increased following the establishment of moose (Snyder and Janke 1976). After a decade (2008–2018) of declining wolf (*Canis lupus*) numbers and predation and increasing moose abundance, the National Park Service and its partners initiated a reintroduction program in 2018 (National Park Service 2018). During 2018–2019, 19 wolves were released to restore predation and help regulate the moose population (Romanski et al. 2020). Monitoring how moose abundance responds to the introduction of wolves is necessary to best guide resource management and planning in IRNP (National Park Service 2018). Future management options may include additional wolf releases or increasing the size and number of moose exclosures to protect sensitive plant communities.

Various methods are used to survey moose populations but cost, accuracy, and precision vary substantially depending on context (Rönnegård et al. 2008, Moll et al. 2022). In summer and fall when high canopy cover obscures moose during aerial counts, methods include pellet surveys (Härkönen and Heikkilä 1999), remote cameras (Pfeffer et al. 2018), and harvest surveys (Boyce et al. 2012). Aerial surveys are used most in winter when canopy cover is lowest and the high contrast between snow and moose facilitates animal observation (Timmermann 1993, Moll et al. 2022). However, moose tend to select for early successional or dense coniferous habitats in winter that reduce their visibility from the air (Montgomery et al. 2013), increasing the probability of undetectable animals in raw aerial counts. Failing to account for unobserved animals can lead to biased population estimates and incorrect conclusions about habitat use (Gu and Swihart 2003).

Imperfect detection is addressed differently across methodologies (Timmermann 1993, Moll et al. 2022). Some methods adjust raw counts post-hoc using detectability corrections derived from subsampling or expert opinion, such as the Gasaway method (Gasaway et al. 1986) and sightability models (Harris et al. 2015). These approaches can yield estimates sensitive to the correction factors used and assume no spatial or temporal variation in the detection process (Vander Wal et al. 2011).

In contrast, alternative methods incorporate imperfect detection directly into the survey and modeling process (Peters et al. 2014, Oyster et al. 2018). Examples include mark-recapture techniques (Wald and Nielson 2014, Oyster et al. 2018) and distance sampling (Dalton 1990, Peters et al. 2022). Mark-recapture methods may involve multiple observers or marking moose before the survey. Distance sampling entails observing unmarked animals from a fixed point or along a transect and measuring the distance from the point or transect to each animal. These distances are used to estimate a detection function, denoted as $g(x)$, which models changes in detection probability with distance from the observation point or transect.

Distance sampling also allows for the consideration of behavioral, habitat, and sampling factors that influence detectability (Dalton 1990). Distance sampling can provide reliable moose abundance estimates with less flight effort compared to post-hoc detectability correction methods (Peters et al. 2014). Like all estimation methods, distance sampling requires that certain survey assumptions are not violated. Key assumptions include 1) objects on the survey line are perfectly detected, 2) animals are detected at their initial locations, and 3) distance measurements are accurate.

While a promising method to survey moose in IRNP, distance sampling has not been attempted in this remote wilderness archipelago. Our objective was to assess if distance sampling produces moose abundance estimates that are biologically reasonable and meet managerial needs for precision.

STUDY AREA

IRNP is a wilderness archipelago in Lake Superior, USA, and also known as Minong or "the good place", the ancestral home and recognized as a Traditional Cultural Property of the Grand Portage Band of Lake Superior Chippewa. The main island supports most of the moose population and is 72-km long and 14-km wide (about 535 km^2). Separated 22 km from the nearest mainland (Ontario, Canada), IRNP hosts a unique subset of temperate and boreal flora (Sanders and Grochowski 2013). Elevations are 0–245 m above Lake Superior (180–425 m above sea level). Boreal forests of white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), and aspen (*Populus spp.*) are prevalent in lower elevation areas near Lake Superior and constitute about 75% of the park's terrestrial area (The Nature Conservancy 1999). Hardwood forests dominated by sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*) occur inland and at higher elevations, especially in the southwestern portion of the island (The Nature Conservancy 1999). Mean daily high temperatures are 21 °C in summer (June–August) and 3 °C in winter (December–February) (Environment Canada 2021). IRNP receives an average of 734 mm in annual precipitation. In 2022, snow depth ranged from 60 to 80 cm, with the snowpack density index (Ramsonde hardness value, Bader et al. 1939) increasing from 4 to 10 across the survey period (Hoy et al. 2022).

METHODS

We estimated moose population size using distance sampling (Dalton 1990, Oyster et al. 2018) during 14–17, 19, 23 February and 1 March 2022. Weather and logistics impeded continuous surveys, but we attempted to survey adjacent transects as quickly as possible. Moose may have crossed survey lines during the sampling window; however, we assume these movements are random and not in response to the survey itself or an underlying migration-like process. Thus, the influence of violating the closure assumption is negligible; i.e., we are as likely to double count a moose as to have a moose move from an unsurveyed transect to a surveyed transect. We generated 149 linear transects at 500-m intervals oriented NW to SE along the length of the park (Fig. 1); this bearing ran perpendicular to the length of Isle Royale. Survey transects had a total length of 1127 km, ranging from 0.16–13.36 km per transect.

We flew each transect in a Robinson R44 helicopter at 75 km/h, 150 m above the ground. The helicopter contained four observers including the pilot, and all observers looked for moose on the side of the helicopter they sat. When a moose was sighted by any observer, the pilot flew from the transect to the location of the observation.

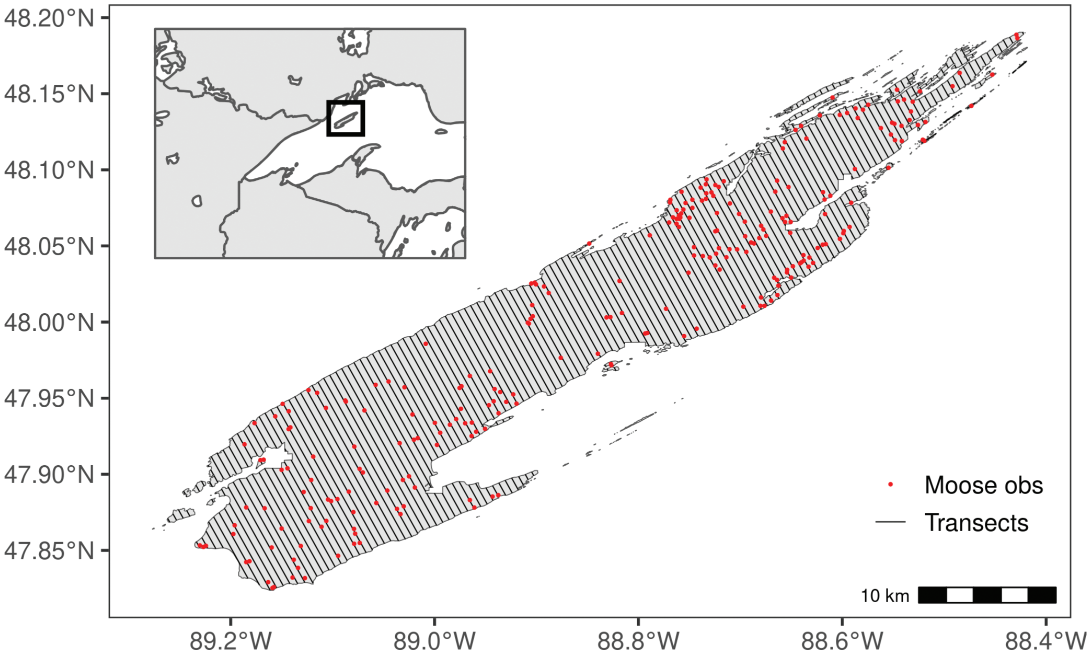

Fig. 1. Study area in Isle Royale National Park, Michigan, USA located in Lake Superior. Lines depict the 149 transects used to observe moose (red dots) and estimate abundance using distance sampling models.

For each observation, we recorded the observer(s), GPS location, and number and sex of moose. We also visually estimated and recorded the percentage canopy cover at the location of each moose sighting. After each observation, the helicopter returned to the original transect and continued the survey. Following the survey, we ensured the flight GPS track aligned with the pre-determined transect and calculated the straight-line distance from the transect to each moose observation.

We expected it would be difficult to detect moose directly below the helicopter (typical for aerial surveys; e.g., Oyster et al. 2018), so we left-truncated data 0–25 m from the transect line. We chose this distance based on expert opinion and the distribution of detection distances, which indicated a substantial decline in detections at distances <25 m. We right truncated the data at 250 m to avoid overlap with adjacent transects.

Perfect detection probability at the transect line (*g(0)*) is a key assumption of distance sampling, which is often tested using data from multiple observers and application of mark-recapture distance sampling (MRDS; Borchers et al. 1998). Though we had multiple observers, the data were not collected in a way that allowed for use of MRDS models due to non-independence between observers in the same helicopter. We expected that under the sampling conditions, detection probability at the transect would be close to but below 1. Thus, our approach should slightly underestimate abundance and density (Buckland et al. 1993).

We fit standard distance sampling models in program R version 4.3.1 (R Core Team 2023) using package Distance (Miller et al. 2016). We fit eight competing distance sampling models. Each model was a combination of a distance key function and a set of covariates. We compared two distance key functions: the half-normal and the hazard-rate. Distance key functions represent the shape of the distance – detection probability relationship, with detection probability expected to decline with increasing distance (Fig. 2A). The half-normal and hazard rate functions have similar shapes. The hazard-rate function requires estimating an additional parameter, but this allows for more flexibility in fitting the observed detection data (Miller et al., 2019). We combined each distance function with four covariate models: a null model, a univariate model for canopy size, a univariate model for group size, and a model with both canopy and group size. For null models, we allowed the Distance package to select an optimal number of additional cosine adjustment terms (Miller et al. 2019). We ranked candidate models using Akaike's Information Criterion (AIC) (Burnham and Anderson 2004) and assessed goodness-of-fit of each model using Cramér-von Mises tests (Miller et al. 2019). If the Cramér-von Mises test was non-significant ($p > 0.05$), we failed to reject the null hypothesis that the model fit the data. We considered models within 2 AIC units of the top model to have similar support, and, if there were competing models, we selected the model with the fewest covariates as the top model for further analysis.

We used a Horvitz-Thompson-like estimator with the top model to calculate moose abundance with 95% and 90% confidence intervals (Miller et al. 2019). Within the area covered by the aerial survey (C), we estimated the total abundance $\hat{N}_C$ as

$$\hat{N}_C = \sum_{i=1}^{n} \frac{s_i}{\hat{p}(\mathrm{z}_i)}$$

where s_i is one of n observed group sizes and $\hat{p}(z_i)$ is the corresponding detection probability with a vector of detection covariates z_i (Miller et al., 2019). In the (unrealistic) case where detection was perfect ($\hat{p} = 1$), then the estimated abundance

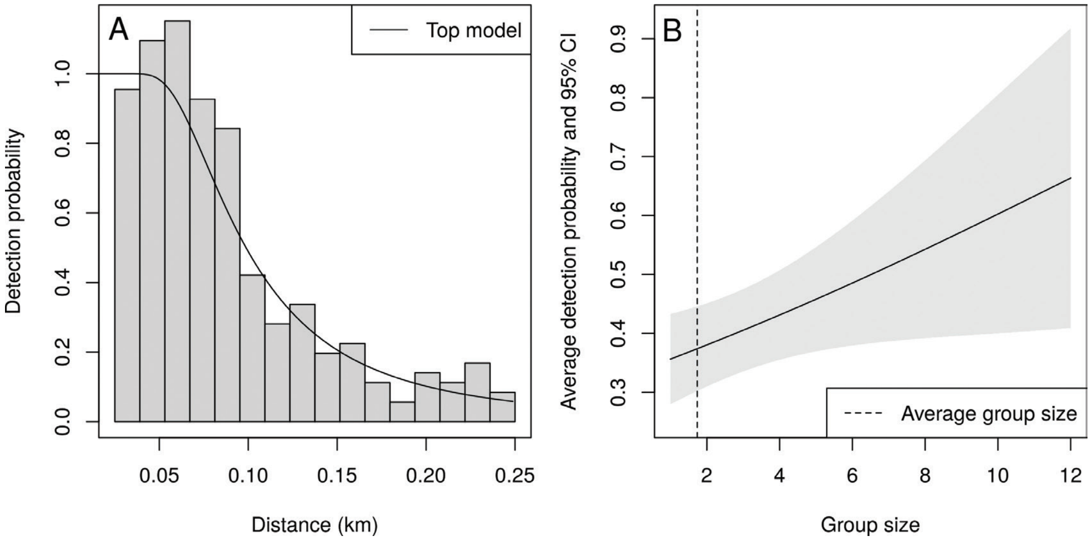

Fig. 2. Results from the top-ranked distance sampling model for moose in Isle Royale National Park, Michigan, USA, 2022. Panel A shows the fitted top-ranked detection model (black line) overlaid on the raw detection data (shaded bars). Panel B shows the relationship between group size and detection probability in the top-ranked model.

in the surveyed area would simply be the sum of the group sizes. When $\hat{p} < 1$, the observed group sizes are “weighted” upwards to account for undetected animals in the estimate of $\hat{N}_C$. Because the surveyed area C did not cover the entire Isle Royale study area, the estimate $\hat{N}_C$ was scaled up to get the total population size estimate $\hat{N}$:

$$\hat{N} = \frac{A}{a}\hat{N}_C$$

Here $A/_a$ is the ratio of the total study area to the surveyed area (Miller et al. 2019).

We calculated moose density by dividing the estimated abundance by the total area surveyed (535 km^2). We calculated a precision index (PI) of each estimate using the equation:

$$\frac{(u - \hat{p})}{\hat{p}}$$

where $\hat{p}$ is the model derived population abundance and u is the upper value of the 90% confidence interval. This precision metric is like a coefficient of variation with 0.25 as a benchmark for management decisions (Gasaway et al. 1986, Timmermann 1993, Peters et al. 2014). To test how sampling effort affected our estimates of moose abundance, we systematically removed one of every three transects (retaining 2/3 of the total transects) or two of every three transects (retaining 1/3 of the total transects) from the dataset, and repeated the analyses described above. If any of these abundance estimates fell within the 95% CI of the abundance estimate derived with the full dataset, we considered them statistically similar.

RESULTS

Total flight time was 18 h, and we included detections of 439 moose in 253 groups (mean group size = 1.74, range = 1–12) in our analysis after truncation. We left-truncated 21 moose in 17 groups, and right-truncated 11 moose in 6 groups. The top model included a hazard-rate key function and the group size covariate (Fig. 2, Table 1). Model goodness-of-fit was adequate based on a Cramér-von Mises test (CvM p-value = 0.70). Group size

Table 1. Distance sample model output used to estimate moose abundance, Isle Royale National Park, Michigan, USA, February – March 2022. Models had half-normal (HN) or hazard-rate (HR) key functions. Group size (group) and canopy cover (canopy) were covariates in some models. Null models included an optimized number of cosine adjustment terms (0–5). Models were ranked using Akaike’s Information Criterion (AIC). When multiple models had similar support (ΔAIC <2) we selected the model with the fewest covariates for further analysis, indicated with *. We used Cramer-von Mises tests (CvM) to check goodness-of-fit. A CvM *p*-value > 0.05 meant we failed to reject the null hypothesis that the model fit the data. Nest is the model estimates of the number of moose on Isle Royale.

Model	K	logLik	AIC	ΔAIC	Weight	CvM p	Nest
HR, canopy+size	4	467.38	-926.76	0.00	0.39	0.76	1036.11
HR, size*	3	466.23	-926.46	0.29	0.34	0.70	1038.78
HR, canopy	3	465.54	-925.08	1.68	0.17	0.79	1126.72
HR, null	2	464.04	-924.09	2.67	0.10	0.87	1140.97
HN, null	2	460.14	-916.28	10.48	0.00	0.27	1484.07
HN, size	2	459.02	-914.04	12.72	0.00	0.08	1074.87
HN, canopy+size	3	460.01	-914.02	12.74	0.00	0.09	1082.16
HN, canopy	2	457.75	-911.49	15.26	0.00	0.09	1160.41

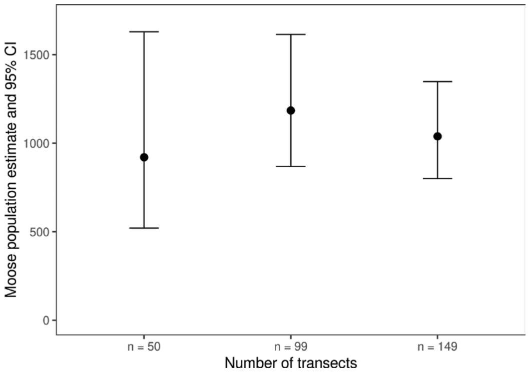

Fig. 3. Moose population estimates and 95% confidence intervals in Isle Royale National Park, Michigan, USA, 2022. Estimates are from the top models using three sample sizes of transects in each of the two years. The full dataset included 149 transects; we systematically removed 1/3 and 2/3 of the transects to yield sample sizes of 99 and 50 transects, respectively.

had a positive effect ($\beta = 0.17$, 95% CI 0.02–0.31) on average group detection probability (Fig. 2). Overall average group detection probability was 0.40 (95% CI 0.33–0.47). The top model yielded a total abundance estimate of 1039 moose (95% CI 800–1349, 90% CI 835–1293, PI = 0.24, Table 1) with a density of 1.94 moose/km^2 (95% CI 1.50–2.52, 90% CI 1.56–2.42). Other candidate models yielded similar abundance estimates (Table 1). The estimated abundance was similar (each 95% CI contained all 3 point estimates) when using all, 2/3, or 1/3 of transects, with the estimate derived from the full dataset the most precise ($PI_{Full} = 0.24$, $PI_{2/3} = 0.30$, $PI_{1/3} = 0.61$, Fig. 3).

DISCUSSION

Distance sampling produced a biologically reasonable and precise estimate of moose abundance on IRNP. Our results are within historic estimates of moose population size derived from block sampling on IRNP since 1991, which ranged from 500 to 1500 (Hoy et al. 2022). Our estimate using distance sampling was 23% less than the estimate using a Gasaway-type method 1346 (90% CI = 925–1842) conducted concurrently on IRNP (Hoy et al. 2022). Though confidence intervals of these two surveys overlapped point estimates of abundance, distance sampling had greater precision ($PI_{Distance} = 0.24$ vs $PI_{Gasaway} = 0.37$).

Cohort analysis conducted by Vucetich and Peterson (2004) indicates the moose population on Isle Royale has fluctuated over the last 60 years from 500 to 2400 animals with a long-term average of 1052 moose (SD = 482). Moose abundance on Isle Royale is influenced by predation forage availability, and abiotic factors (McLaren and Peterson 1994). Prior to the recent wolf restoration, the moose population had grown steadily from an estimated 510 individuals in 2010 to 2060 in 2019 (Hoy et al. 2019). In contrast, the moose population appears to have declined by ~20% annually after the restoration (Hoy et al. 2020, 2022, 2023). The recent decline in moose abundance is likely a result of increasing predation pressure, decreased forage availability, and increasing parasite burdens (i.e., winter tick [*Dermacentor albipictus*]).

Our population density estimate of 1.94 moose/km^2 is much higher compared to other populations in the Great Lakes region that declined sharply between 2005 and 2011 and subsequently stabilized (Timmerman and Rodgers 2017, Severud et al. 2022). Moose density in core range in the Upper Peninsula of Michigan was only 0.11 moose/km^2 in 2023 (T. Petroelje, Michigan Department of Natural Resources, pers. comm.) and ~ 0.20 moose/km^2 in core range in northeastern Minnesota in 2020 (Severud et al. 2022). The absence of human-caused mortality (Ballenberghe and Ballard 1994) and lack of meningeal worms (*Parelaphostrongylus* *tenuis*; Lankester 2010) may contribute to higher moose density in IRNP.

We observed high levels of grouping behavior, with some groups reaching 12 animals. Groups larger than 10 animals are rare in the southern limit of the moose range and tend to occur from October to December (Peek et al. 1974). Grouping behavior in moose may be associated with high population density, deep snow, location of palatable forage, and predation risk (Peek 1974, Molvar et al. 1994). While distance sampling can accommodate grouped animals, the high variance in group size we observed may increase uncertainty (Thomas et al. 2010). Nevertheless, distance sampling is likely more useful in accommodating grouping behavior than Gasaway-type estimators. Post-hoc sightability methods assume individual counts are independent and often rely on correction factors derived from previous surveys which do not account for process-driven variability in detectability. In addition, by systematically surveying the island, distance sampling is more likely to capture the variability of group sizes than the stratified blocks used for Gasaway-type estimators.

While distance sampling is a promising method to apply in IRNP, we could not perfectly meet its assumptions. Although we attempted to complete the survey as quickly as possible, weather and logistical delays forced our survey to extend over a two-week period, during which moose may have moved from their original transects. However, moose on Isle Royale move relatively short distances during the month of February (unpublished NPS data), and any such movements are likely in equilibrium – thus, violating the closure assumption likely did not substantially alter our results. Secondly, we could not validate if detection on the transect line was 1; if detection was <1, our estimates may be biased downwards.

Reducing sample effort from 149 to 99 transects did not have a strong effect on the moose abundance estimate but reduced precision. Including 2/3 of the transects resulted in a 25% reduction in precision ($PI_{Full} = 0.24$, $PI_{2/3} = 0.30$) and exceeded the suggested precision benchmark of 0.25 (Gasaway et al. 1986). However, our reduced effort estimate was more precise than the moose abundance estimate using the Gasaway-type approach conducted concurrently ($PI_{2/3} = 0.30$ vs $PI_{Gasaway} = 0.37$). Reducing survey effort to only 1/3 of the transects resulted in a large confidence interval that exceeded the suggested benchmark by 140%. Given this loss of precision, we suggest future surveys in INRP include at least 2/3 of the transects. It is important to recognize that our study system is unique in that our full data set of 149 transects covered nearly the entire area of IRNP, a level of effort and coverage likely unattainable in other systems.

Nevertheless, IRNP managers could reduce our effort by 1/3 and produce ecologically plausible and precise estimates of abundance. This reduction would require only 12 h of flight time (140 transects required 18 h) which can be accomplished in two days during February. This flight time is less than the 18–21 h (unpublished NPS data 2023) required to complete a Gasaway-type survey in IRNP without considering flight time between plots. Increasing the spacing between transects to 750 m could effectively reduce the number of transects by 1/3, ensure adequate coverage across the island, and maintain flight efficiency. Winter weather in IRNP is unpredictable and conditions appropriate for flying occur in limited time windows. Using distance sampling affords park managers greater flexibility in conducting surveys to fit weather and logistical constraints. We recommend distance sampling as a suitable method for estimating moose abundance on IRNP, as found elsewhere

(Peters et al. 2014, Oyster et al. 2018). Peek et al. (1974) found that moose in Minnesota had the smallest group size and lowest variance in February, thus we suggest that surveys be conducted in mid-to-late- February to reduce the variance associated with grouping behavior and increase moose detectability (Peterson and Page 1993).

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REFERENCES

Bader, H. P., R. Haefeli, E. Bucher, J. Neher, O. Eckel, and C. Thams. 1939. Der Schnee und seine Metamorphose. Beitraege zur Geologie der Schweiz, Geotechnische Serie, Hydrologie Lieferung 3. Kümmerly and Frey, Zürich, Germany.

Ballenberghe, V. V., and W. B. Ballard. 1994. Limitation and regulation of moose populations: the role of predation. Canadian Journal of Zoology 72: 2071–2077.

Borchers, D. L., W. Zucchini, and R. M. Fewster. 1998. Mark-recapture models for line transect surveys. Biometrics 1: 1207–1220.

Boyce, M. S., P. W. J. Baxter, and H. P. Possingham. 2012. Managing moose harvests by the seat of your pants. Theoretical Population Biology 82: 340–347.

Buckland, S. T., and D. A. Elston. 1993. Empirical models for the spatial distribution of wildlife. Journal of Applied Ecology 1: 478–495.

_____, D. R. Anderson, K. P. Burnham, and J. L. Laake. 1993. Distance Sampling: Estimating Abundance of Biological Populations. Chapman and Hall, London, England.

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociological Methods and Research 33: 261–304.

Burt, M. L., D. L. Borchers, K. J. Jenkins, and T. A. Marques. 2014. Using mark–recapture distance sampling methods on line transect surveys. Methods in Ecology and Evolution 5: 1180–1191.

Dale, V. H., L. A. Joyce, S. McNulty, R. P. Neilson, M. P. Ayres, M. D. Flannigan, and D. Simberloff. 2001. Climate change and forest disturbances: climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. BioScience 51: 723–734

Dalton, W. J. 1990. Moose density estimation with line transect survey. Alces 26: 129–141.

Environment Canada. 2021. Canadian Climate Normals 1971–2000, Thunder Bay A, Ontario. < http://www.cmc.ec.gc.ca/climate/normals/ONTT004.HTML> (accessed February 2023).

Gasaway, W. C., S. D. Dubois, D. J. Reed, and S. J. Harbo. 1986. Estimating moose population parameters from aerial surveys. Biological Papers of the University of Alaska 22: 1-99.

Gu, W., and R. K. Swihart. 2004. Absent or undetected? Effects of non-detection of species occurrence on wildlife–habitat models. Biological Conservation 116: 95–203.

Handler, S., M. J. Duveneck, L. Iverson, E. Peters, R. M. Scheller, K. R. Wythers, and C. Swanston. 2014. Michigan Forest Ecosystem Vulnerability Assessment and Synthesis: A Report from the Northwoods Climate Change Response Framework Project. General Technical Report NRS-129. USDA Forest Service, Northern Research Station, Newtown Square, Pennsylvania, USA.

Harris, R. B., M. Atamian, H. Ferguson, and I. Keren. 2015. Estimating moose abundance and trends in northeastern Washington state: index counts, sightability models, and reducing uncertainty. Alces 51: 57–69.

Härkönen, S., and R. Heikkilä. 1999. Use of pellet group counts in determining density and habitat use of moose *Alces alces* in Finland. Wildlife Biology 5: 233–239.

Kantar, L. E., and R. E. Cumberland. 2013. Using a double-count aerial survey to estimate moose abundance in Maine. Alces 49: 29–37.

Krefting, L. W. 1974. The Ecology of the Isle Royale Moose with Special Reference to the Habitat. Technical Bulletin 297. Minnesota Agricultural Experiment Station, University of Minnesota, Twin Cities, Minnesota, USA.

Lankester, M. W. 2010. Understanding the impact of meningeal worm, *Parelaphostrongylus tenuis*, on moose populations. Alces 46: 53–70.

McInnes, P. F., R. J. Naiman, J. Pastor, and Y. Cohen. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. Ecology 73: 2059–2075.

McLaren, B. E., and R. O. Peterson. 1994. Wolves, moose, and tree rings on Isle Royale. Science 266: 1555–1558.

Mech, L. D. 1966. The Wolves of Isle Royale. Fauna of the National Parks of the United States Fauna Series, U.S. Department of Interior, Washington, D. C., USA.

Miller, D. L., E. Rexstad, L. Thomas, L. Marshall, and J. L. Laake. 2016. Distance sampling in R. BioRxiv. <https://www.biorxiv.org/content/10.1101/063891v2.full063891> (accessed January 2024); (Journal of Statistical Software doi: 10.18637/jss.v089.i01).

Moll, R. J., M. K. P. Poisson, D. R. Heit, H. Jones, P. J. Pekins, and L. Kantar. 2022. A review of methods to estimate and monitor moose density and abundance. Alces 58: 31–49.

Molvar, E. M., and R. T. Bowyer. 1994. Costs and benefits of group living in a recently social ungulate: the Alaskan moose. Journal of Mammalogy 75: 621–630.

Montgomery, R. A., J. A. Vucetich, R. O. Peterson, G. J. Roloff, and K. F. Millenbah. 2013. The influence of winter severity, predation and senescence on moose habitat use. Journal of Animal Ecology 82: 301–309.

National Park Service. 2018. Isle Royale National Park Environmental Impact Statement to Address the Presence of Wolves. Isle Royale National Park, Houghton, Michigan, USA.

Oyster, J. H., I. N. Keren, S. J. K. Hansen, and R. B. Harris. 2018. Hierarchical mark-recapture distance sampling to estimate moose abundance. The Journal of Wildlife Management 82: 1668–1679.

Pastor, J., B. Dewey, R. J. Naiman, P. F. McInnes, and Y. Cohen. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. Ecology 74: 467–480.

Peek, J. M., R. E. LeResche, and D. R. Stevens. 1974. Dynamics of moose aggregations in Alaska, Minnesota, and Montana. Journal of Mammalogy 55: 126-137.

Peters, W., M. Hebblewhite, K. G. Smith, S. M. Webb, N. Webb, M. Russell, C. Stambaugh, and R. B. Anderson. 2014. Contrasting aerial moose population estimation methods and evaluating sightability in west-central Alberta, Canada. Wildlife Society Bulletin 38: 639–649.

Peterson, R. O., N. J. Thomas, J. M. Thurber, J. A. Vucetich, and T. A. Waite. 1998. Population limitation and the wolves of Isle Royale. Journal of Mammalogy 79: 828.

Pfeffer, S. E., R. Spitzer, A. M. Allen, T. R. Hofmeester, G. Ericsson, F. Widemo, N. J. Singh, and J. P. G. M. Cromsigt. 2018. Pictures or pellets? Comparing camera trapping and dung counts as methods for estimating population densities of ungulates. Remote Sensing in Ecology and Conservation 4: 173–183.

Romanski, M., E. K. Orning, K. Kellner, K. Brzeski, J. Hart, D. H. Lonsway, A. A. D. McLaren, A. A. D. Moore, B. Patterson, and L. Potvin. 2020. Wolves and the Isle Royale Environment: Restoring an Island Ecosystem, 2018–2020. National Park Service Report, Houghton, Michigan, USA.

Rönnegård, L., H. Sand, H. Andrén, J. Månsson, and A. Pehrson. 2008. Evaluation of four methods used to estimate population density of moose *Alces alces*. Wildlife Biology 14: 358–371.

Sanders, S., and J. Grochowski. 2013. The forests of Isle Royale National Park: can we preserve this pristine wilderness in the face of climate change? Natural Areas Journal 33: 66–77.

_____, and J. Kirschbaum. 2023. Woody species response to altered herbivore pressure at Isle Royale National Park. Ecosphere 14: 4623.

Severud, W. J., S. S. Berg, C. A. Ernst, G. D. DelGiudice, S. A. Moore, S. K. Windels, R. A. Moen, E. J. Isaac, and T. M. Wolf. 2022. Statistical population reconstruction of moose (*Alces alces*) in northeastern Minnesota using integrated population models. Plos one 17: 0270615.

Snyder, J. D., and R. A. Janke. 1976. Impact of moose browsing on boreal-type forests of Isle Royale National Park. American Midland Naturalist. 79-92.

The Nature Conservancy. 1999. USGS-NPS Vegetation Mapping Program Classification of the Vegetation of Isle Royale National Park. The Nature Conservancy Midwest Regional Office, Minneapolis, Minnesota, USA.

Thomas, L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. Bishop, T. A. Marques, and K. P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47: 5–14.

Timmermann, H. R. 1993. Use of aerial surveys for estimating and monitoring moose populations - a review. Alces 29: 35–46.

_____, and A. R. Rodgers. 2005. Moose: competing and complementary values. Alces 41: 85–120.

_____, and _____. 2017. The status and management of moose in North America-circa 2015. Alces 53: 1–22.

Tourville, J., M. Lindman, C. Weinstein, R. Schultze, and M. Noack. 2018. Moose Herbivory Monitoring Protocol for Isle Royale National Park. Natural Resource Report, National Park Service, Fort Collins, Colorado, USA.

Vucetich, J. A., and R. O. Peterson. 2004. The influence of top–down, bottom–up and abiotic factors on the moose (*Alces alces*) population of Isle Royale. Proceedings of the Royal Society of London. Series B: Biological Sciences 271: 183–189.

_____, and _____. 2009. Wolf and Moose Dynamics on Isle Royale. Pages 35–48 *In* A. P. Wydeven, T. R. Van Deelen, and E. J. Heske, editors. Recovery of Gray Wolves in the Great Lakes Region of the United States. Springer, New York, New York, USA.

Weiskopf, S. R., O. E. Ledee, and L. M. Thompson. 2019. Climate change effects on deer and moose in the Midwest. The Journal of Wildlife Management 83: 769–781.

Vander Wal, E., P. D. McLoughlin, and R. K. Brook. 2011. Spatial and temporal factors influencing sightability of elk. The Journal of Wildlife Management 75: 1521–1526.

Wald, E. J., and R. M. Nielson. 2014. Estimating moose abundance in linear subarctic habitats in low snow conditions with distance sampling and a kernel estimator. Alces 50: 133–158.