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Research article

Monitoring GPS-collared moose by ground versus drone approaches: efficiency and disturbance effects

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Efficient wildlife management requires precise monitoring methods, for example to estimate population density, reproductive success, and survival. Here, we compared the efficiency of drone (equipped with a RGB camera) and ground approaches to detect and observe GPS-collared female moose *Alces alces* and their calves. We also quantified how drone (n = 42) and ground (n = 41) approaches affected moose behavior and space use (n = 24 individuals). The average time used for drone approaches was 17 min compared to 97 min for ground approaches, with drone detection probability being higher (95% of adult female moose and 88% of moose calves) compared to ground approaches (78% of adult females and 82% of calves). Drone detection success increased at lower drone altitudes (50–70 m). Adult female moose left the site in 35% of drone approaches (with > 40% of those moose becoming disturbed once the drone hovered < 50 m above ground) compared to 56% of ground approaches. We failed to find short-term effects (3 h after approaches) of drone approaches on moose space use, but moose moved > fourfold greater distances and used larger areas after ground approaches (compared to before the approaches had started). Similarly, longer-term (24 h before and after approaches) space use did not differ between drone approaches compared to days without known disturbance, but moose moved comparatively greater distances during days of ground approaches. In conclusion, we could show that drone approaches were highly efficient to detect adult moose and their calves in the boreal forest, being faster and less disturbing than ground approaches, making them a useful tool to monitor and study wildlife.

Keywords: *Alces alces*, behavior, GPS, Norway, unmanned aerial vehicle, wildlife

Introduction

Efficient management and conservation of wildlife populations requires accurate population monitoring. For hunted species, harvest records constitute the most accessible long-term data for monitoring relative population abundances and changes. However,

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these data can be biased due to varying hunting effort and type (Pettorelli et al. 2007, Imperio et al. 2010, Eriksen et al. 2018), and do not provide fine-scale information, for example regarding space use and behavior. Thus, several other methods are used to monitor wildlife populations, including camera traps (Rowland et al. 2020, Moll et al. 2022), aerial surveys (using aircrafts or satellites) (Peters et al. 2014, Schleper 2020), acoustic monitoring (Blumstein et al. 2011), spotlight counts (Corlatti et al. 2016), and E-DNA sampling (Nichols et al. 2012, Pawlowski et al. 2018).

In addition, marking and tracking individual animals, for example using GPS tags (Severud et al. 2015, Mayer et al. 2022), can provide valuable information regarding detailed movement and behavior, especially for species that are hard to observe (Rutz and Hays 2009). However, knowledge about reproduction and juvenile survival often still requires direct animal observations, such as by using ultra-light motorized aircrafts or unmanned aircraft systems, hereafter 'drones' (Stander et al. 2021). In general, drones are increasingly used to monitor and study wildlife due to technological advancements, making them affordable and user-friendly (Linchant et al. 2015, Schroeder et al. 2020, Iwamoto et al. 2022). Thus, they have a large potential to non-invasively monitor reproductive success in wildlife. Considering their increasing use not only by researchers, but also managers, photographers, and recreationists, it is important to understand their effects on animal behavior and movement (Mulero-Pázmány et al. 2017, Bennitt et al. 2019).

Generally, monitoring can be a direct or indirect stressor for animals that can trigger anti-predator behaviors, such as flight responses or altered time allocation (Frid and Dill 2002). Consequently, more frequent anti-predator responses to invasive monitoring methods can lead to increased energy expenditure and reduced time for foraging and resting, resulting in short- and long-term negative effects such as reduced survival and weight gain (Naylor et al. 2009, Northrup et al. 2014, Gaynor et al. 2018, Mortensen and Rosell 2020, Mayer et al. 2021). Disturbance effects might be especially important during the reproductive season and for individuals with dependent offspring. For example, female ungulates with offspring were more vigilant than females without offspring when approached by humans on foot (Stankowich 2008). Factors such as habitat type, group size, and disturbance type can also affect individual responses to disturbance (Jayakody et al. 2008, Mayer et al. 2019).

Moose *Alces alces* are a good example of a species that requires precise population monitoring. They occur in boreal forests across northern Eurasia and North America, and have large economic and cultural value as an important game species (Lavsund et al. 2003, Milner et al. 2005). In Norway, approximately 35 000 moose are harvested annually, generating a total economic value of ~ EUR107 million (Pedersen et al. 2020). However, moose can cause damage to forest stands, especially during winter when they browse on young pine trees (Hjeljord 2003, Sand et al. 2019). Young pine trees may be damaged to a degree that afflicts future timber production by slowing tree growth and lowering timber quality (Bergqvist et al. 2001, Wallgren et al. 2013). Consequently, the management of the Scandinavian moose population involves balancing the conflicting interests of maintaining a highly productive moose population while ensuring a sustainable density that supports timber production (Wam et al. 2005, Ezebilo et al. 2012).

The regulation of the moose population by harvest to adapt to forestry goals requires data on the moose population density. Current moose monitoring in Scandinavia relies on relative indices derived from hunter harvest and observations. Additionally, some moose management areas perform track counts along roads or aerial counts from helicopter during winter, and in Sweden fecal pellet counts are performed by hunters in spring to assess relative winter densities and distribution (Rönnegård et al. 2008). However, indirect measures (pellet counts, hunting statistics) entail inherent uncertainties (Ueno et al. 2014), and cannot estimate calf survival, which is an important factor to estimate recruitment. This is of special interest in areas with large carnivores that often specialize on neonate ungulates as prey in summer (Swenson et al. 2007, Sand et al. 2008). A more precise and adaptive management can be facilitated by monitoring specific individuals. Ground approaches of radio-collared moose cows have been successfully used for detecting and monitoring calves (Bergman et al. 2020, Fremstad 2021), but their potential disturbance has not been evaluated to date.

In this study, we evaluated a new method to monitor GPS-collared moose using a drone (McMahon et al. 2021). We investigated the detectability of calves and the behavioral responses of moose during drone approaches compared to ground approaches. We predicted that 1) the drone will be at least as effective at detecting calves as ground approaches, 2) the drone will be more efficient, measured in time used for each approach, and 3) moose will have a weaker behavioral response to drone approaches (flee less often and over shorter distances) compared to ground approaches.

Material and methods

Study area, moose captures, and GPS collaring

The study was conducted in southern Scandinavia, in the border region between Innlandet county in Norway and Dalarna and Värmland counties in Sweden (Fig. 1). All drone approaches were conducted on the Norwegian side due to border restrictions at that time, whereas ground approaches were conducted in both countries (because we had field personnel in both countries). The study area is dominated by boreal coniferous forest consisting of Norway spruce *Picea abies* and Scots pine *Pinus sylvestris* interspersed by bogs, lakes, and deciduous trees consisting mainly of birch (*Betula pendula* and *B. pubescens*), aspen *Populus tremula*, willow (*Salix* spp.), alder (*Alnus incana* and *A. glutinosa*), and rowan *Sorbus aucuparia*. There is a large network of gravel roads used for forestry, making the area easily accessible (Zimmermann et al. 2014). The climate is cold, with snow cover for 3–6 months

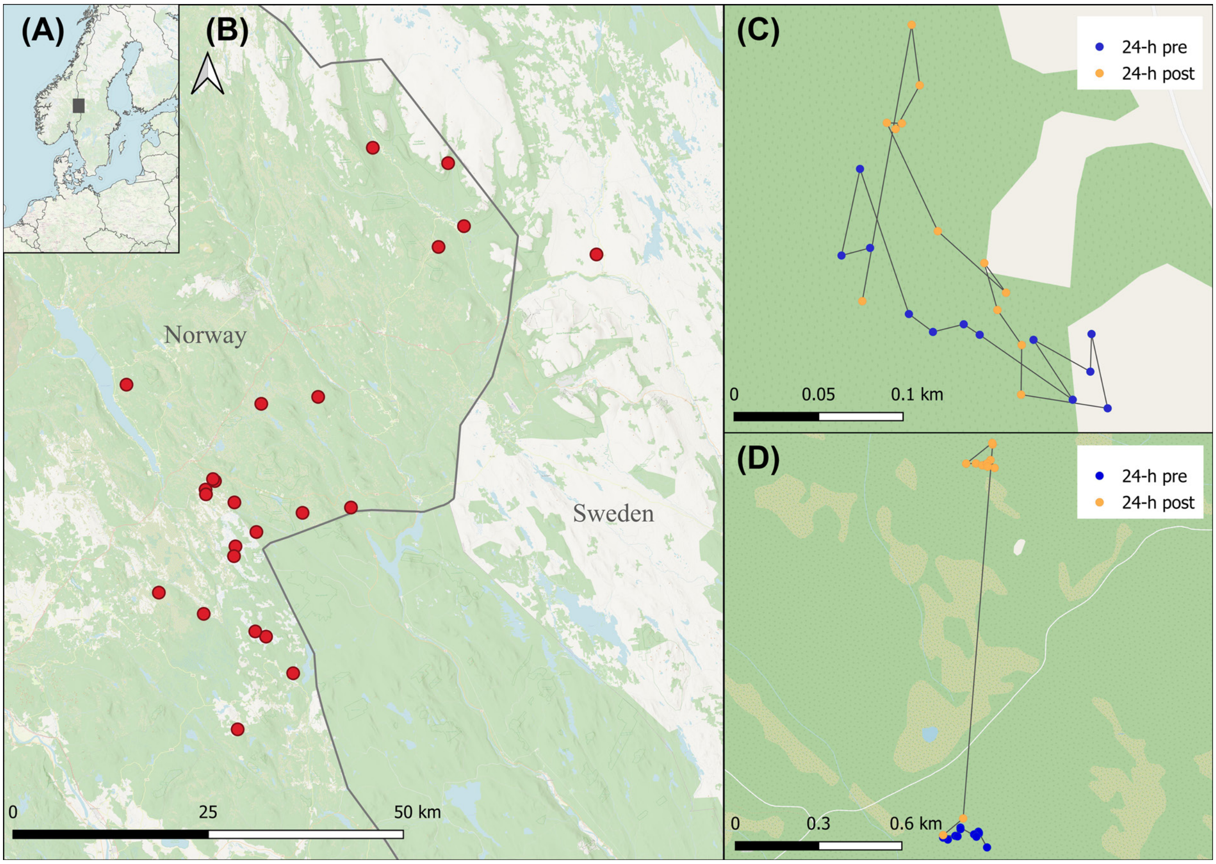

Figure 1. The location of our study area (grey rectangle; A), the centroid locations of the 24 GPS-collared female moose (red dots) (B), and GPS points 24 h before (blue dots) and after (orange dots) an approach was conducted, illustrated for a drone approach (C) and a ground approach (D). GPS positions (dots) were recorded every 2 h. Lines represent the schematic movement path of moose (C–D). Basemap sources: Open street map (https://tile.openstreetmap.org) and ESRI Topo Map (http://services.arcgisonline.com/ArcGIS/rest/services/Elevation/World_Hillshade/MapServer/tile).

per year (mainly from November to April) during cold and dry winters (Zimmermann et al. 2015, Milleret et al. 2017). Winter moose densities range between 1 and 3 per km^2 (Zimmermann et al. 2015). Generally, from November moose start to migrate to areas with less snow, often valley bottoms and forested lowlands (Gundersen et al. 2004). From April to May, they migrate back again to summer habitats at higher altitudes (Gundersen 2003, Zimmermann unpubl.). All four large carnivore species of Norway (wolf *Canis lupus*, brown bear *Ursus arctos*, wolverine *Gulo gulo*, and lynx *Lynx lynx*) are present in the area.

Moose were darted from a helicopter with a CO_2-powered dart gun and equipped with a GPS collar (Vectronic Aerospace, either VERTEX PLUS with GSM-link, or SURVEY with Iridium-link). The immobilization and handling procedure is described in detail elsewhere (Evans et al. 2012, Lian et al. 2014, Græsli et al. 2020b). GPS collars were programmed to take one position every hour (VERTEX PLUS) or every two hours (SURVEY) throughout the day. On days with drone or ground approaches, all except five GPS collars were programmed to take one position every 10 min between 08:00 and 18:00 local time. The five exceptions were individuals equipped with VERTEX PLUS collars with built-in cameras. These collars were not re-programmed, to save battery capacity. The positions from the GPS collars were sent to a server and shown in a web application with a map at www.dyreposisjoner.no. The web application also supports SMS notifications and lets the field team get the latest GPS positions to pinpoint the moose location.

Approaches

We attempted 44 drone approaches and 48 ground approaches on 24 individuals between May and December 2021, and obtained GPS data from 40 drone approaches and 41 ground approaches (Table 1). Individual moose were on average (± SD) approached 1.8 ± 0.7 times on ground (range: 1–4 times) and 1.8 ± 0.7 with a drone (range: 1–3 times). In two more drone approaches, we managed to observe the behavioral response of the moose cows from the drone but did not receive GPS positions. The remaining attempts were unsuccessful due to missing GPS data while in the field due to poor GSM coverage (six approaches), poor weather conditions (two approaches), and a bear predation event (one approach). Calf presence was defined when at least one approach detected at least one calf (two females were observed with twins). Ground

Table 1. Overview of the analyses conducted to evaluate disturbance effects of drone versus ground approaches on adult female moose.

Analysis Response variable	Predictor variables	Sample size
(1) Probability of a moose cow being flushed		
Flushed (yes/no)	Treatment (approach type) + tree cover density + distance to closest road + calf presence	40 drone approaches and 41 ground approaches of 24 individuals
(2) Shorter-term disturbance (3 h before and after approach started)		
Step length (distance moved between 10-min GPS fixes)	Treatment + period + time of day + tree cover density + distance to closest road + calf presence + treatment × period	31 drone approaches and 18 ground approaches (1603 GPS positions of 19 individuals)
Hourly range use (95% KDI)	Treatment + period + calf presence + treatment × period	
(3) Longer-term disturbance (24 h before and after approach started)		
Step length (distance moved between 2-h GPS fixes)	Treatment + period + (time of day^2) + tree cover density + distance to closest road + calf presence + treatment × period	40 drone approaches, 41 ground approaches, and 57 control days (3081 GPS positions of 23 individuals)
Daily range use (95% KDI)	Treatment + period + calf presence + treatment × period	

and drone field teams did not inform each other regarding calf presence to avoid biases in data collection. To get an estimate of baseline space use, we used GPS data from the same time of day two days before an approach was conducted, without any known disturbance (based on two-hourly positions). To compare calf detection success, we used a paired study design. That is, for comparisons of calf detection, we only used cases where the same individual was monitored using both a drone and a ground approach within one week (n = 44 approaches). To minimize the risk of calf mortality between approaches, we minimized the number of days between drone and ground approaches but left a minimum of one day between approaches to allow females to return to their baseline behavior after the potential disturbance. We randomized the order of drone and ground approaches.

For drone approaches, the drone ('DJI Mavic 2 Enterprise Dual' using a GPS+ GLONASS system with a ± 1.5 m horizontal and ± 0.5 m vertical accuracy range) was programmed to fly to the last known GPS position of the moose (flight speed was 6 m/s) at 100 m altitude while the operator stayed ≥ 500 m away (but within the visual line of sight). When the drone arrived at the last known position, the operator manually searched for the moose and – if it was detected – flew the drone over the exact location of the moose, where it hovered for 2 min while recording video, using a built-in RGB camera (1920 × 1080 resolution). If the moose did not flee from the site, the drone was progressively lowered to 70, 50, 30, and 20 m altitude with a 1-min hovering time for each altitude interval. At each altitude, we noted the presence of offspring and moose cow behavior. Behavior was classified into four categories: 1) lying, 2) standing still, 3) walking, which often included foraging, and 4) running. If the moose started running at any time during the approach, or when the drone had hovered for 1 min at 20-m altitude, the approach was completed; that is, the drone was flown back to 100 m altitude and returned to the original position. The speed for lowering or elevating the drone was set to 2 m/s. Drone operations were conducted by a licensed operator (open category A1/A3).

Ground approaches were conducted by a single person on foot to detect if female moose had calves. We approached the last known moose GPS position while using a VHF-receiver (RX98, Followit AB, Sweden) in case the moose had moved. All approaches were done with headwind and the track was recorded with a handheld GPS unit. We approached each moose close enough to determine the presence or absence of a calf/calves. We sneaked back downwind to minimize the risk of the female moose detecting us. We recorded the duration of approaches from the start (≥ 500 m from the last moose position) until the moose was detected or the approach stopped, using handheld GPS tracklogs for ground approaches and timestamps from drone videos.

Environmental variables

We obtained data regarding tree cover density in 2018 from the European Environment Agency (Tree Cover Density 2018; https://land.copernicus.eu/pan-european/high-resolution-layers/forests/tree-cover-density/status-maps/tree-cover-density-2018?tab=download), defined as the proportion of ground covered by trees. We evaluated these data with our drone footage from 100 m height. We classified habitat as 1) dense (80% tree cover), 2) intermediate (30–80% tree cover), or 3) open forest (< 30% tree cover). We merged dense and intermediate forest, because we only had two observations of dense forest, and then compared the tree cover density with our categorization (Supporting information). Using the same drone videos, we classified weather as sunny, cloudy, rainy, or foggy. We only conducted two approaches with (light) rain and three with light fog (> 100 m visibility). Finally, we downloaded vector data of roads (combined for forestry and main roads) from the open-source database OpenStreetMap (https://download.geofabrik.de/europe), excluding residential roads and paths (footpaths, hiking tracks, etc.).

Data preparation and analyses

We used the program R 4.2.3 (www.r-project.org) for data analyses. For all GPS positions, we estimated the distance to the closest road (in m) and extracted the tree cover density, using the R packages 'rgeos' and 'raster' (Hijmans et al. 2015, Bivand et al. 2018). Moreover, we estimated step length (Euclidean distance in m) between consecutive GPS positions (separately for 2-h and 10-min fix rate) and estimated daily and hourly area use using 95% kernel density isopleths (KDIs) using the reference bandwidth of the R package 'adehabitatHR' (Calenge 2006). Daily area use was estimated based on 2-h positions, only including approaches for which we had obtained at least 10 GPS positions during a 24-h period after the approach had started (leading to the exclusion of three approaches). Hourly area use (3 h before and after approaches; see below) was estimated based on 10-min positions, only including approaches for which we had obtained at least five GPS positions per hour.

Initially, we analyzed the probability of successful calf detections (response variable; 1 = calf detected versus 0 = calf not detected) for the paired approaches (described above) of moose cows for which at least one approach type had confirmed calf presence (n = 32 approaches), using GLMs with a binomial error distribution and a logit link. We included the approach type and tree cover density as predictor variables (we could not investigate seasonal differences as we only conducted two paired approaches during fall).

To analyze the potential disturbance approaches had on moose, we conducted three analyses at different spatio-temporal scales: 1) direct disturbance, analyzing the probability of a moose being flushed during an approach, 2) shorter-term disturbance effects on step length and area use comparing 3 h before and after the approach started, and 3) longer-term disturbance effects comparing step length and area use 24 h before and after the ground or drone approach started, or before and after a true control (no known disturbance). For analysis (1), we classified a moose as being flushed when we saw it moving away from the location it was detected during either the ground or drone approach. We used this behavioral response as a binomial response variable (0 = not flushed, 1 = flushed) in a generalized linear model (GLM) with a binomial error distribution and a logit link. We included the approach type (ground or drone), calf presence (yes/no), distance from the closest road, and tree cover density as independent variables. For analyses (2) and (3), we used step length (log-transformed to normalize residual distributions) as response variable in linear mixed effects models with a Gaussian error distribution of the R package 'lme4' (Bates et al. 2015). We included the time of the day, tree cover density, distance to the closest road, calf presence, approach type, period (before/after), and the two-way interaction of approach type × period as fixed effects, and moose ID and experiment ID as random intercept (Table 1, Supporting information). To avoid higher-order interactions, we additionally conducted an analysis only including the period after the approach had started, to test if flushed moose moved greater distances depending on approach type and calf presence. We included calf presence, tree cover density, distance to the closest road, approach type, flushing behavior (flushed or not flushed), and the two-way interactions of approach type × flushing behavior and calf presence × flushing behavior as fixed effects, and moose ID and experiment ID as random intercept (Supporting information). Moreover, we specifically tested if the closest distance of the ground personnel and drone, respectively, from the moose during approaches affected moose flushing behavior and distance moved. To do so we analyzed the proportion of flushed moose (for ground only) and the distance moved in the 1) 3-h period and 2) 24-h period after approaches had started (response variables in separate analyses for ground and drone approaches) and included the closest distance from the moose, calf presence, time of day, tree cover density, and distance to the closest road as predictor variables (Supporting information). Finally, we analyzed hourly and daily area use (log-transformed response variable to normalize residual distributions), including calf presence, approach type, period, and the two-way interaction of approach type × period as fixed effects and moose ID and experiment ID as random intercept (Table 1). We initially tested if the linear or quadratic function of distance to the closest road and time of day fitted better (based on Akaike's information criterion (AIC; Table 1). For the drone approaches only, we additionally analyzed the video recordings to quantify if moose behaviors changed during the drone approach at different hovering heights.

For all analyses, we conducted model selection by stepwise removing variables that reduced AIC corrected for small sample size (AICc) (Burnham et al. 2011) from the full model (described for each analysis above and presented in the supplementary material; see Results), using the R package 'MuMIn' (Barton 2016). There was no collinearity (Pearson's $r < 0.6$ and variance inflation factors < 3) between independent variables within the same model (Zuur et al. 2010). We scaled all numeric variables (mean = 0; SD = 1) to obtain comparable estimates. If ΔAICc was < 2 in two or more of the most parsimonious models, we performed model averaging of these candidate models (Bolker et al. 2009). Parameters that included zero within their 95% CI were considered uninformative (Arnold 2010). Model assumptions were verified by plotting residuals versus fitted values (Zuur and Ieno 2016) and performing dispersion and deviation tests, using the R package 'DHARMa' (Hartig 2021).

Results

Detecting moose

The time used for ground approaches was 3–244 min (mean ± SD: 97 ± 57 min for successful approaches and 66 ± 55 min for approaches where the moose was not detected) compared to 12 to 22 min (17 ± 2 min for successful approaches and 19 ± 4 min for unsuccessful approaches) for drone approaches. The drone detected adult female moose in 40 of 42 approaches (95%), while ground approaches detected adult females in 28 of 36 approaches (78%). One of the individuals not detected during a drone approach moved >1.5 km from the last transmitted GPS position for unknown reasons 20 min before the approach started. The average distance at which moose cows and their calves were detected during ground approaches was 90 ± 125 m (range: 7–511 m).

Out of 17 females with 'known' calves, the drone approaches detected calves of 15 females (88.2%) and ground approaches the calves of 14 females (82.4%). The probability of detecting a calf was best explained by the intercept-only model, and both the effect of approach type and tree cover density were uninformative in the full model. For drone approaches, the proportion of calves detected improved at lower hovering heights. We detected known calves in 72% of approaches at 100 m hovering height and in 92% at 70 and 50 m hovering height (n = 40 approaches). Calf detection improved further at lower hovering heights (96% at 30 m height and 100% at 20 m height), but moose cows walked and ran from the site at hovering heights ≤ 50 m more often than at greater hovering heights (Fig. 2).

Effects of drone and ground approaches on moose behavior and movement

Adult female moose were flushed (i.e. left the site) in 14 (35%) of 40 drone approaches, compared to 23 (56%) of 41 ground approaches. The probability of being flushed was greater during ground compared to drone approaches (Table 2, Supporting information). Distance to closest road was retained in the best models within ΔAICc < 2 but was uninformative (Table 2). Tree cover density and calf presence were not included in the best models. When analyzed for ground approaches only, proximity to the moose (in m) during approaches was included in the best model (Supporting information) but was uninformative (Estimate ± SE: 0.007 ± 0.006, 95% CI: −0.001; 0.026).

During drone approaches, 30 moose were lying (75%), seven were standing (17.5%), and three were walking (7.5%) when the drone hovered at 100 m height (Fig. 2). Of the 40 moose, none left the site at 100 m hovering height, one left the site at 70 m height (walking), three left at 50 m height (two running, one walking), two left at 30 m height (both walking), and eight left at 20 m height (one running, seven walking; Fig. 2). Of the 34 moose that were approached down to 20 m, 22 (65%) were still lying (Fig. 2).

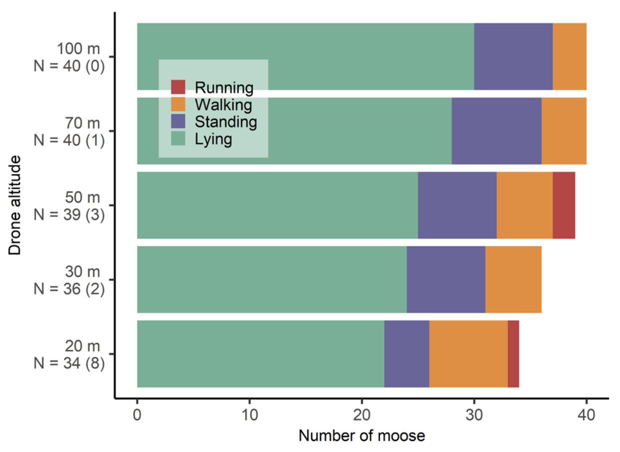

Figure 2. The number of moose showing different behaviors in relation to the approach altitude of the drone. The number of drone approaches conducted is shown for each altitude. The number of approaches stopped (when the moose fled) for each altitude is indicated in brackets.

Table 2. Effect size, SE and lower (LCI) and upper (UCI) 95% confidence intervals (presented on logit-scale) of explanatory variables for the probability of adult female moose being flushed during an approach by either a drone or a person on the ground. Drone approaches were used as reference level. We performed model averaging of best models (ΔAICc < 2) to estimate the effect size of each variable. Informative parameters are presented in bold (95% confidence intervals do not overlap with zero).

Parameter	Estimate	SE	LCI	UCI
Intercept	−0.62	0.33	−1.28	0.04
Approach type (ground)	**1.07**	**0.48**	**0.12**	**2.02**
Distance to closest road	0.15	0.24	−0.33	0.63

When analyzing shorter-term disturbance, the interaction of approach type and period indicated that moose step length was larger in the 3 h after ground approaches had started, but not when drone approaches were conducted (Fig. 3A, Table 3, Supporting information). Moreover, moose moved larger distances when they had a calf/calves (Table 3). Tree cover density, time of day, and distance to closest road were not included in the best models within ΔAICc < 2 (Supporting information). The additional analysis of the 3 h after the approach had started indicated that moose moved greater distances when being flushed (compared to not being flushed) during ground approaches, but not during drone approaches (Fig. 3B, Supporting information). During drone approaches, there was little difference in distance moved between moose that were flushed or not flushed (mean ± SD: 26 ± 65 m versus 17 ± 17 m per 10 min), whereas moose flushed during ground approaches moved > 4-fold greater distances compared to moose not flushed (111 ± 208 versus 24 ± 35 m per 10 min). Moose with calves moved greater distances than those without calves (Supporting information), but the interaction of calf presence × flushing behavior was not included in the best model. Proximity to the moose did not affect step length in the 3-h period after the approach had started for both ground and drone approaches (not included in the best model; Supporting information). The analysis of area use showed that moose used larger areas during and after ground approaches, but not during drone approaches (Fig. 3C). The effect of calf presence was uninformative for explaining the observed variation in area use before and after approaches (Table 3).

Step lengths of adult female moose 24 h before and after approaches were best explained by the time of day and distance to the closest road (Supporting information). Moose moved greater distances during nighttime, and when closer to roads (Table 4, Supporting information). Tree cover density, the presence of calves, approach type, period, and their two-way interaction were not included in the best model (Supporting information). The additional analysis of the 24 h after the approach had started indicated that moose with

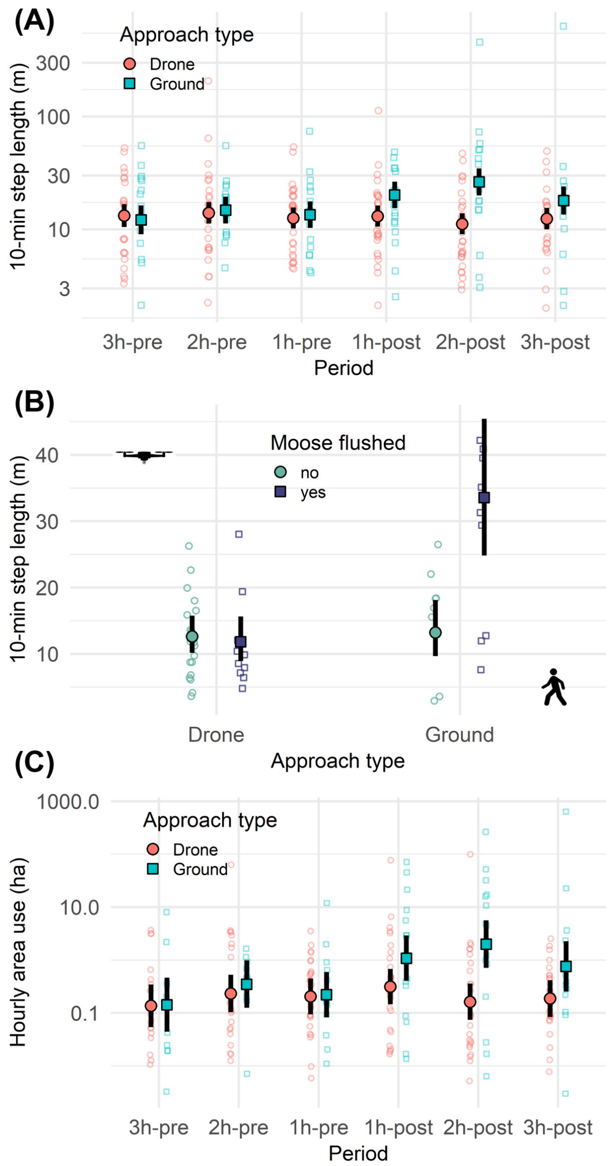

Figure 3. The predicted effect of (A) approach type on step length by adult female moose in the period 3 h before and after approaches had started; (B) interaction of flushing behavior and approach type on distance moved for the 3 h after the approach had started; (C) hourly area use by adult female moose 3 h before and after drone and ground approaches. Area use was estimated as 95% kernel density isopleths from 10-min GPS positions. Bars indicate 95% confidence intervals. Small symbols represent median values per experiment, treatment, and period estimated from raw data. Note that the y-axis in plot A and C is log-transformed.

calves moved greater distances when being flushed (compared to not being flushed), but not moose without calves (Fig. 4A, Supporting information). Approach type was included in the best model but was uninformative (Supporting information). Proximity to the moose did not affect step length in the 24-h period after the approach had started for both ground and drone approaches (not included in the best model; Supporting information). The analysis of area use 24 h before and after approaches was best explained by approach type, period, and the presence of calves (Supporting information). Moose used larger areas in the 24 h after approaches had started (Fig. 4B) and used smaller areas when having calves (Table 4). The effect of approach type was uninformative, although there was a trend that moose used larger areas on days with ground approaches (Fig. 4B, Table 4). The interaction of approach type and period was not included in the best model (Supporting information).

Discussion

Drone approaches were very useful in detecting GPS-collared female moose and their calves, similar to previous studies using drones to monitor wildlife (Hui et al. 2021, Stander et al. 2021, Iwamoto et al. 2022). Below, we discuss the implications of our findings regarding animal detectability and disturbance effects.

Efficiency of moose detection

Both drone and ground approaches were successful at detecting adult moose and their calves, but drones performed slightly better than ground approaches. Drone approaches detected 92% of known calves at 70 m hovering height. At lower drone altitudes (50–20 m) moose were increasingly disturbed, but calf detection success did not markedly improve. Thus, a hovering height of 70 m (or 100 m for adults) appears optimal to ensure moose detection while minimizing disturbance, similar to a study on eastern grey kangaroos *Macropus giganteus* (Brunton et al. 2019). Importantly, we did not have complete information regarding moose calf presence (determined if a calf was seen throughout the study), which might have led to an overestimation of calf detection success (as calves that were never observed were counted as true absences). Moreover, drone approaches were more time-efficient in detecting moose, taking only ca one-sixth of the time used for ground approaches.

Moose detection might have been facilitated by their large body size compared to smaller-bodied species. However, drones have also proven successful in detecting smaller animals, such as roe deer *Capreolus capreolus* fawns (Cukor et al. 2019) and bird nests (Stander et al. 2021). In addition to body size, other factors can influence detectability, including habitat structure, weather conditions, and image quality (Bonnin et al. 2018, Doull et al. 2021), though we failed to detect other factors affecting calf detection. Nevertheless, both drone and ground approaches could be negatively impacted by tree cover density (hindering visibility) and weather conditions. Drone operations, for instance, depend on suitable wind speed (Oleksyn et al. 2021), while ground approaches may be hindered by noisy walking caused by a snow crust. Moreover, in some habitat types, such as dense forest, the use of drones might not be applicable and could be replaced by other non-invasive methods, such as camera traps, to estimate cow–calf ratios.

Table 3. Effect size, SE, and lower (LCI) and upper (UCI) 95% confidence intervals of explanatory variables for (1) 10-min step length and (2) hourly area use by adult female moose. Drone approaches were used as baseline level. We performed model averaging of best models (ΔAICc < 2) to estimate the effect size of each variable. Informative parameters are presented in bold (95% confidence intervals do not overlap with zero).

	(1) 10-min step length				(2) Hourly area use			
Parameter	Estimate	SE	LCI	UCI	Estimate	SE	LCI	UCI
Intercept	**2.33**	**0.24**	**1.86**	**2.81**	−2.57	0.75	−4	−1.1
Approach type (ground)	0.18	0.22	−0.25	0.61	0.07	0.70	−1.3	1.44
Calf presence (yes)	**0.44**	**0.22**	**0.01**	**0.88**	1.04	0.65	−0.2	2.32
Period (2 h-pre)	0.06	0.11	−0.16	0.27	0.53	0.53	−0.5	1.57
Period (1 h-pre)	−0.05	0.11	−0.26	0.16	0.41	0.52	−0.6	1.43
Period (1 h-post)	−0.01	0.11	−0.22	0.20	0.83	0.51	−0.2	1.85
Period (2 h-post)	−0.17	0.11	−0.38	0.05	0.18	0.52	−0.9	1.2
Period (3 h-post)	−0.06	0.11	−0.28	0.15	0.31	0.53	−0.7	1.35
Period (2 h-pre) × Approach type (ground)	0.14	0.18	−0.22	0.50	0.36	0.87	−1.4	2.08
Period (1 h-pre) × Approach type (ground)	0.15	0.18	−0.20	0.51	0.02	0.85	−1.7	1.7
Period (1 h-post) × Approach type (ground)	**0.52**	**0.18**	**0.17**	**0.87**	1.19	0.85	−0.5	2.87
Period (2 h-post) × Approach type (ground)	**0.94**	**0.18**	**0.58**	**1.30**	**2.45**	**0.87**	**0.73**	**4.17**
Period (3 h-post) × Approach type (ground)	**0.46**	**0.19**	**0.08**	**0.83**	1.35	0.90	−0.4	3.11

Disturbance effects

Compared to ground approaches, drone approaches resulted in fewer instances of moose disturbance; and, when disturbance occurred, the affected moose fled shorter distances. Moose reacting less strongly to drone approaches could be attributed to the drone's resemblance to a large bird, as there are no avian predators of moose (although we note that it might be possible that moose associated drones with helicopters, which were used for captures). Conversely, humans (sometimes together with large carnivores) represent the primary cause of moose mortality in Scandinavia (Nilsen and Solberg 2006, Jonzén et al. 2013, Wikenros et al. 2020), which explains the > fourfold larger distance moved during and after being flushed by ground approaches compared to drone approaches. A previous study conducting ground approaches to detect calves reported similar behavioral responses of moose to those reported here (Johnsen 2013). Græsli et al. (2020a) investigated the effect of hunting dogs on moose behavior and found that moose moved on average 4.1 km longer on days when disturbed by baying dogs compared to the day after the disturbance, resulting in increased energy expenditure and resting time. This response was much stronger compared to our findings, which indicate little evidence of longer-term (24-h) disturbance effects, especially for drone approaches.

Overall, drone approaches were less disruptive than ground approaches for detecting calves, which are prone to predation (Swenson et al. 2007, Sand et al. 2008), suggesting that they are a good method for monitoring calves with minimal disturbance. A previous study showed that 18.4% of calves were left behind by their mother within 48 h post-capture for equipping calves with GPS or VHF collars (DelGiudice et al. 2015). Thus, disturbing moose during approaches might have serious consequences for calf survival. Similarly, disturbance of elk *Cervus canadensis* by ground approaches during the calving season decreased the calf–cow ratio (Phillips and Alldredge 2000).

The lack of behavioral change indicates that the drone did not disturb moose at higher altitudes (70–100 m). Similarly, drone monitoring at 100 m altitude of African elephants *Loxodonta africana* (Vermeulen et al. 2013) failed to detect evidence of disturbance by drones. However, we cannot exclude the possibility of responses that are difficult to detect with GPS-positioning only, such as changes in heart rate or physiological stress. For example, American black bears *Ursus*

Table 4. Effect size, SE, and lower (LCI) and upper (UCI) 95% confidence intervals of explanatory variables to explain the variation in (1) 24-h step length and (2) daily area use by adult female moose approached by a drone or a person on the ground. Control days (no approaches conducted) were used as baseline level. We performed model averaging of best models (ΔAICc < 2) to estimate the effect size of each variable. Informative parameters are presented in bold (95% confidence intervals do not overlap with zero).

	(1) 2-hourly step length				(2) Daily area use			
Parameter	Estimate	SE	LCI	UCI	Estimate	SE	LCI	UCI
Intercept	**4.89**	**0.08**	**4.73**	**5.06**	**4.38**	**0.35**	**3.68**	**5.07**
Approach type (drone)					−0.17	0.32	−0.81	0.47
Approach type (ground)					0.59	0.33	−0.06	1.23
Period (24-h post)					**0.34**	**0.17**	**0.01**	**0.67**
Calf presence (yes)					**−0.92**	**0.35**	**−1.62**	**−0.23**
Time of day	**−0.16**	**0.01**	**−0.18**	**−0.13**				
Time of day^2	**0.01**	**0.00**	**0.00**	**0.01**				
Distance to closest road	**−0.08**	**0.03**	**−0.14**	**−0.02**				

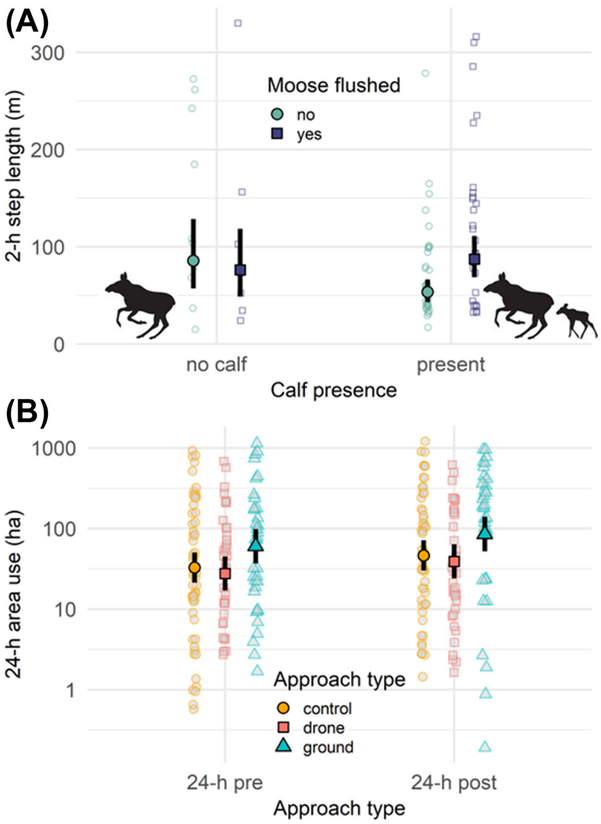

Figure 4. (A) Predicted effect of the interaction of flushing behavior and calf presence on distance moved for the 24 h after the approach had started. (B) Predicted (large symbols) daily area use by adult female moose for drone and ground approaches, and control days. Note that the interaction of period and approach type was not included in the best model. Area use was estimated as 95% kernel density isopleths from 2-h GPS positions. Bars indicate 95% confidence intervals. Small symbols represent median values for each experiment, treatment, and period estimated from raw data. Note that the y-axis in plot B is log-transformed.

americanus responded to drone flights with elevated heart rates but infrequent behavioral changes (Ditmer et al. 2015); and, in eastern grey kangaroos, drones elicited a vigilance response but kangaroos rarely fled from the drone if operated at an altitude > 60 m (Brunton et al. 2019).

Technological limitations

The drone used in this study has a digital zoom which helps the operator to crop the picture/video when flying. However, this function only works when recording in 1920 × 1080 resolution, resulting in suboptimal picture/video quality when flying at 70–100 m height. To improve this, we recommend using a camera that supports optical and digital zoom. Another shortcoming of using an optical camera only is that detectability might decline with increasing canopy cover (though we did not detect an effect of tree cover density in this study). Utilizing a thermal camera might reduce this issue, especially in favorable thermal conditions, such as colder weather (Cukor et al. 2019, McMahon et al. 2021). However, using a thermal camera during warmer temperatures can complicate the detection of animals, because the sun heats up large objects such as rocks, which can lead to false positive detections, especially when using software for automatic detection (Chrétien et al. 2016, Kays et al. 2019, Lethbridge et al. 2019). The drone used in this study had a thermal camera, but the resolution was not high enough to distinguish moose from large rocks heated by the sun. Larger drone models can carry better cameras, which might increase detection success at higher altitudes. However, larger drones, producing more noise, might be more disturbing to animals (Schad and Fischer 2022). Similarly, moose in other areas with differing hunting pressure, large carnivore communities and abundances, and human land use and activity, might react differently to ground approaches.

Conclusions and future perspectives

Our study demonstrates that drones are appropriate to monitor large mammals, while minimizing disturbance and increasing time efficiency compared to ground approaches. This might be especially relevant during periods when wildlife is vulnerable to disturbance, for example when a dependent offspring is present or during the winter months. Similarly, the use of drones likely provides benefits in areas difficult to access on ground, such as high mountain areas. Flight altitude under 70 m should be avoided to avoid disturbance. Apart from reduced disturbance of animals, drone approaches have the advantage that there is no risk of injury for field personnel by being charged by potentially dangerous study animals (we note that there was no incidence of a moose charging a person in this study). Flying beyond the visual line of sight and using improved camera systems could further improve the time efficiency of drone approaches, and the use of thermal cameras could improve detection success. Building on the current findings, future studies should investigate the feasibility of monitoring moose that are not GPS tagged (Corcoran et al. 2021), which would allow the estimation of population density over larger areas.

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Author contributions

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.cnp5hqccv (Mayer et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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