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# ESTIMATING TIGER (*PANTHERA TIGRIS*) PREY DENSITY USING CAMERA TRAPS AND FECAL ACCUMULATION RATES

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ABSTRACT

The conservation of tiger populations requires the preservation of their prey. Assessing prey populations is therefore important, but challenges arise due to the elusive nature of many prey species. We used two indirect methods to estimate the density of sika deer (*Cervus nippon*), an elusive tiger prey species, in the Sikhote-Alin Biosphere Reserve in the Russian Far East. The fecal accumulation rate (FAR) is widely used and provides estimates of ungulate density based on the accumulation of fecal pellet groups in previously cleared plots. More recently, the random encounter model (REM) was developed to estimate population density from the rates of contact between study animals and camera traps. Its use is controversial because of questions on how to define an encounter, estimate daily travel distance, and adjust for herds.

The goal of this project was to compare density estimates from the two techniques and assess whether and when REM could replace FAR in such surveys. Detectability of the study animals was similar for both methods, but the FAR technique yielded a much higher density estimate, 13.97 ± 2.74 standard error (SE) sika deer $km^{-2}$ than did the REM method 4.91± 1.76 (SE) sika deer $km^{-2}$, which was closer to expectation based on previous studies. Both methods required estimates from outside studies: of defecation rates for FAR and of average travel distances for REM. REM also required an assumption on group sizes which were likely underestimated in the camera images. Our analysis suggests theoretical considerations and practical adjustments that must be made to both methods when estimating population density. We also propose integrating the two techniques by using the camera traps over cleared plots to estimate defecation rates

directly from the study population. Overcoming challenges like these is vital to designing effective conservation plans for tigers and their prey.

# DEDICATION

To Skooner- with all my love and so much appreciation.

ACKNOWLEDGMENTS

I have learned so much throughout this process, but the biggest lesson was given to me before I set foot in the field. I owe my gratitude to Dr. Kathryn McFadden who told me to "MacGuyver through every day" as she handed me a bag of batteries. Her words became my mantra and remind me still that when challenges arise, the best course of action is to look around, gather my resources, and create a solution.

The most valuable resources for this project were all of the people whose advice, expertise, and support I relied on. I cannot thank my family and friends enough for their support as I followed a dream. I am indebted to all of my instructors and the Biological Sciences Department of Clemson University for refining me as a scientist. Thank you, Christie Sampson and Vratika Chaudhary for being uplifting labmates and excellent adventure partners. This work would not have been possible without Dr. Dale Miquelle, The Wildlife Conservation Society in Russia, and the tireless researchers, managers, and staff of the Sikhote-Alin Biosphere Reserve. I would like to thank my committee members, Dr. Patrick Gerard and Dr. David Jachowski for their honest input and for being available to advise me even in the last minute. Most of all, I would like to thank Dr. David Tonkyn for his patient leadership. A lot of things can go awry in any project; it is something special when a large portion of a Russian village is attributing the first absence of snow in over a century to the presence of an American master's student. David guided me through this and so many trials while always reminding me that this journey should be enjoyed. My work is better for his input and I am better for knowing him.

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# CHAPTER ONE

# INTRODUCTION

Effective management of predators such as tigers requires knowledge about the density of their prey (Chapron *et al.* 2008; Marques *et al.* 2001). However, tiger prey species, which are typically ungulates, can be almost impossible to census directly because they are elusive, occupy closed forests, lack identifying marks or vocalizations, have large home ranges, and often travel in groups. Ungulate populations may also be fragmented due to hunting/poaching or habitat loss and degradation (Carroll & Miquelle 2006). As a consequence, researchers typically estimate ungulate densities indirectly, from signs that the animals leave such as tracks, hair snags, vocalizations, and scat (Buckland *et al.* 2001). Sometimes these signs can be used in mark-recapture-like studies, where the researchers revisit a study site and measure the proportion of signs not previously detected (Carbone *et al*. 2001; Karanth & Nichols 1998). DNA from hair and scat can been used to identify individuals in single or mark-recapture-like surveys, for density estimation, or to estimate genetic diversity in the population which can yield another estimate of density. Unfortunately, many of these methods are not practical for forest ungulates such as deer in remote regions such as the Russian Far East, home of the endangered Amur tiger *Panthera tigris altaica* (Temminck 1844). There, researchers and managers must rely on indirect methods that can be applied over large areas and that do not require individual identifications or laboratory analyses of DNA in order to estimate prey densities.

Fecal pellet group (FPG) methods are popular for estimating ungulate density because they do not require DNA analysis or individual recognition. The fecal accumulation rate (FAR) technique is a common FPG application when pellet groups decay slowly relative to the study period (Campbell, Swanson, & Sales 2004). The FAR technique estimates density *D* by dividing the number of pellet

groups *P* that accumulate over time *t* in a previously cleared plot of area *A*, divided by the defecation rate per individual *r* (Equation1).

$$D = \frac{P}{trA} \qquad Eqn. 1$$

The FAR technique is popular because it is simple to apply and understand, can be used in large, remote areas, and does not require identifying individuals or counting their numbers in herds (Horino and Nomiya 2008). However, it does require an estimate of defecation rate, and ideally this should be from the study population itself since defecation rates can vary with age, gender, food source, elevation, and other factors (Horino and Nomiya 2008; Koike *et al.* 2013). In the case of elusive animals in remote areas such as the Russian Far East, this may not be possible to obtain, so defecation rates must be estimated in other studies or on captive animals. This may bias the estimate of population density *D*, in unknown ways.

An alternative way to estimate population density is to survey for tracks in the winter snow, and plug the resulting observations into a formula assuming random encounters with the survey transects while accounting for daily travel distance. The Formozov-Malyshev-Pereleshin formula estimates density from winter track count data and has been tested in the Russian Far East (Stephens *et al.* 2006). We planned to use this method but due to atypical weather with light snowfall on only five days during the study, we were unable to gather track data.

Motion sensing cameras, or camera traps, are now widely available (McCallum 2013), and Rowcliffe *et al*. (2008) developed and tested the random encounter model (REM) between arrays of such traps and animals, to provide a new, indirect estimate of density (Equation 2).

$$D = \frac{y}{t}\,\frac{\Pi}{vr(2+\theta)} \qquad Eqn.2$$

Here, the estimated density, *D*, is equal to the trapping rate or number of encounters *y* per unit time, *t*, and wedge-shaped area of the camera's detection zone, $\frac{r(2+\theta)}{\pi}$, where *r* is the radius and $\theta$ is the angle of view, all divided by the average daily travel distance, *v*. Note that when animals move in herds, this equation estimates the number of groups, $D_g$, based on an encounter rate with groups, $y_g/t$, and it must be multiplied by an estimate of group size, G, to give the density of individual animals D. This modified REM for herd animals has been described in concept (Rowcliffe, Field, Turvey & Carbone 2008) and applied to Grevy's zebras in East African savannah, where herds can be censused in full (Zero *et al.* 2013).

The REM has compared favorably in field studies with other, more established methods (e.g., track counts, mark-recapture, etc.) and with populations of known density (Rowcliffe, Field, Turvey & Carbone 2008; Zero *et al.* 2013). However, its use remains controversial because of difficulties in its application. Like most other sampling methods, it assumes that animals move freely across the landscape and are not restricted to particular trails or areas, and that they become neither "trap-happy" nor "trap-shy". However, it also assumes that animals are not recorded multiple times and, when in groups, that the group sizes are constant and known (Foster & Harmsen 2012; Hutchinson & Waser 2007).

We applied the FAR and the REM techniques in the Sikhote-Alin Biosphere Reserve (SABR), a stronghold for the Amur tiger *P. tigris altaica* (Temminck 1844), in the Russian Far East. Our goals were to estimate prey density but also to compare the strengths and weaknesses of the two methods for

this task. There are six ungulate species that tigers typically consume in the SABR: red deer *Cervus elaphus* (Linnaeus 1758), roe deer *Capreolus capreolus* (Linnaeus 1758), sika deer *Cervus nippon* (Temminck 1838), musk deer *Mochus moschiferus* (Linnaeus 1758), and wild pig *Sus scrofa* (Linnaeus 1758) (Hebblewhite *et al.* 2014). Of these, sika deer have been observed the most frequently, and our surveys were designed with their biology in mind.

Sika deer are elusive herd animals that typically travel in larger groups than roe deer or red deer, with whom they are believed to compete and potentially exclude (Stephens *et al.* 2006; Feldhamer and Armstrong 1993). While sika deer are considered pests in many areas including the eastern United States and Great Britain (Feldhamer and Armstrong 1993; Ratcliffe 2008) they are protected in the SABR and efforts are being made to reduce the threat of poaching habitat loss and degradation.

In this paper, we estimate the density of sika deer by both REM and FAR techniques, compare the results, and conclude with a discussion of the strengths and weaknesses of each when used on an elusive ungulate population. We also include recommendations for managers and researchers that are considering employing one or both of these methods.

# CHAPTER TWO

# MATERIALS AND METHODS

## *Study Area*

This study was conducted from January to March 2014 in the Sikhote-Alin Biosphere Reserve (SABR), Primorsky Krai, in the southeastern Russian Federation. The SABR is 406,177 hectares, was established in 1935, and has been maintained primarily to protect habitat of the Amur tiger. This area has an unusual mix of broadleaf and temperate forests that lie between taiga (boreal) and sub-tropical forests. Mongolian oak *Quercus mongolica* (Fisch.), Korean pine *Pinus koraiensis* (Siebold & Zucc.), needle fir *Abies holophylla* (Maxim.) and several species of birch *Betula* and larch *Larix* are the characteristic large trees (Hebblewhite *et al*. 2014). The SABR is included in the World Heritage Forest Programme due to its unique and diverse species composition. Along with the Amur tiger, the SABR provides protected habitat for several other threatened carnivores, including brown bear *Ursus arctos* (Linnaeus 1758), Himalayan black bear *Ursus thibetanus* (Cuvier 1823), Eurasian lynx *Lynx lynx* (Linnaeus 1758), and Blakiston's fish owl *Bubo blakistoni* (Seebohm 1884). The distribution and population dynamics of prey animals in the SABR are poorly understood. A growing concern that poaching of prey may be harming tigers in this region has created an immediate need to better understand prey population density and dynamics (Goodrich *et al.* 2010; Miquelle et al. 2010).

We conducted camera trap and scat surveys in the approximately 30 $km^2$ basin of Blogadatna Lake, in the southern portion of the SABR. This basin lies between Plastun Road and the Sea of Japan, from which it is separated by a small isthmus (Figure 1). We chose this area based on its accessibility and the confirmed presence of tigers. We selected survey sites in the lake basin that were less than 100 m in altitude to reduce variability in vegetation and invertebrate populations which might affect

defecation rate and pellet decay (Koike *et al.* 2013). We selected survey sites that would ensure full coverage of the area based on the lower 95% confidence interval limits of daily travel distance for sika, roe, and red deer estimated in the SABR by Stephens *et al.* (2006). This study used radio collars and snow tracks to estimate daily movement of the three deer species. The lower limit of the 95% CI for sika deer daily movement was 1.50 km/day; 1.25 km/day for red deer; 0.79 km/day for roe deer.

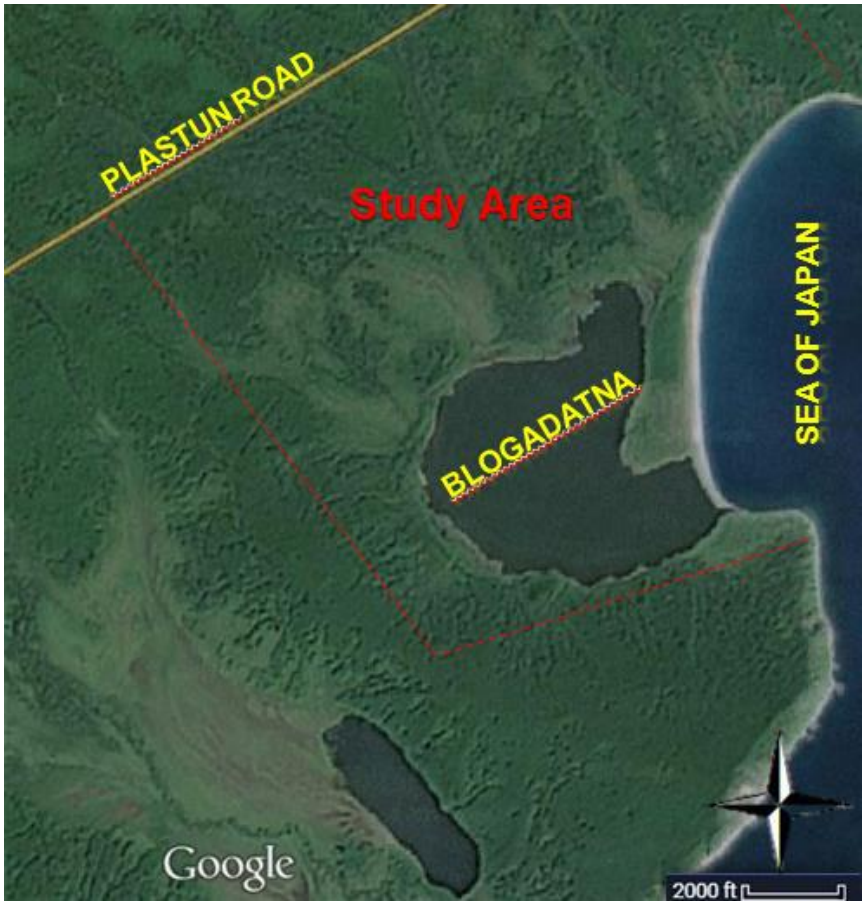


Figure 1. Map of the study area with outer boundaries marked by red dashes and Plastun Road. Surveys covered the Blogadatna Lake basin in the Sikhote-Alin Biosphere Reserve in Primorsky Krai, Russia. Map data © 2015 Google.

*Fecal Pellet Group Survey*

We conducted surveys along 11 transects running perpendicularly to Plastun Road into the Blogadatna Lake Basin. We used a random number generator from 1-500 to select the distance, in meters, along the road to place the first transect. The remaining transects were established on the same azimuth every 500 m. Any areas without trees, including the lake itself and wetland sites were considered unsuitable for survey plots. If our plot layout included an unsuitable site, we relocated the plot to the nearest suitable point on that transect. If a suitable plot site was not located within 250 m of the pre-determined site, that plot was removed from the planned transect and the 500 m spacing of plots was resumed. We placed a total of 63 circular plots, each with a radius of 5m (Figure 2).

In each plot, we identified and recorded a standing count of ungulate scat in and then cleared the plot of scat so that it could serve as an accumulation plot. Scat was counted for sika deer, roe deer, red deer, and wild pig. Scat was identified as being left by a particular species based on size, shape, color, and any nearby tracks (Chame 2003, Yamashiro *et* al. 2013). We returned to the plots on average 34 days later to check for the accumulation of new pellet groups, but recorded the precise number of days for each plot. We defined a pellet group as having 6 or more individual pellets that were less than 10 cm from another pellet, in order to limit the uncertainty that could arise from counting individual pellets or “walking defecations” (Horino and Nomiya 2008). We used a defecation rate of 25.8 pellet groups per sika deer per day from a previous winter study in a similar habitat (Horino and Nomiya 2008).


Figure 2. Location of fecal accumulation plots in Blogadatna Lake basin in the Sikhote-Alin Biosphere Reserve, Primorsky Krai, Russia. Each circle indicates one plot.

*Camera Placement, Settings, and Parameters*

The camera trap sites were set along six transects, 1 km apart, that ran parallel to but not directly over the scat plot transects. We used a random number generator from 1-500 to select the distance, in meters, that the first transect would begin along Plastun Road, and then where the first camera would be located on each transect. We used the same criteria for selecting appropriate camera trap sites as in selecting fecal accumulation plots. If a suitable camera trap site was not found within 500 m of the planned site, that camera was removed from the planned transect and the next camera was placed 1 km from the pre-determined site.

We moved the cameras twice, for a total of three trapping periods and 18 transects. Each time the cameras were moved 300 m to the northeast, keeping transects perpendicular to the road and the same method to assign the position of the first camera on each transect. There were a total of 57 camera placements, with 20 cameras each in the first and second arrays, and 17 cameras in the third array, due to a reduced number of suitable sites. Cameras were monitored regularly for battery power, memory, and function. Care was taken to visit camera sites less than once per week in order to minimize the disturbance of survey areas.


Figure 3. Location of camera trap sites in Blogadatna Lake basin in the Sikhote-Alin Biosphere Reserve, Primorsky Krai, Russia. Camera sites were set up in three arrays.

We used 21 cameras. One was taken out of the study early on due to malfunction. Eight were Cuddeback® Attack IR five mega pixel cameras (Cuddeback Digital, Wisconsin, USA). These use passive infrared heat and motion detectors to detect animals with a 0.25 second trigger speed and 18.29 meter (60 foot) flash range. They were set to take a single photograph in response to each trigger, but no more than one photograph every five seconds. The remaining 13 cameras were 3.1 megapixel Reconyx® HC600 Hyperfire IR cameras (Reconyx Inc., Wisconsin, USA). They also use passive infrared heat and motion detection to trigger a photograph within 0.21 seconds and were set to take two additional photos at one second intervals for every trigger. Both camera types attach the date, time, and approximate temperature to each photograph and store the information on SD cards.

We randomly selected a camera type for each camera placement then calculated a detection zone using the method described in Rowcliffe *et al.* (2008). This method requires each camera to be set in "test" mode and then watch for a flashing light as a team member moves in front of the camera to determine the triangular area in which a photo may be triggered by the motion sensors. The furthest straight-line distance, $r$, and the angle of the zone of detection, $\theta$, were recorded for each camera placement. We performed a least square means analysis to test for any differences in the detection zones that might be based on camera type.

*Photographic Data Analysis*

We recorded the number of individuals of each ungulate species in each photograph, and the total number of encounters for each camera placement. Encounters were defined as any photograph or series of photographs that were triggered at least five minutes apart. If photographs were separated by less than five minutes, we assumed that the ungulates recorded were part of the same group.

Each series of three photographs from the Reconyx® cameras was treated as one "trigger set" and referred to as one photograph. If the photographs in a series of three showed different numbers of individuals, the largest number of individuals in a single photograph was used for all calculations as the minimum estimate of the number of individuals present.

We used a previously published estimate of mean daily travel distance to estimate sika deer density from the camera trapping rate (*v*, Equation 2) (Stephens *et al.* 2006). This mean, of 2.78 km/day was from a small sample size (n=10), so we also used the 95% confidence interval limits (1.50 km/day, 4.06 km/day) to obtain upper and lower estimates on the density. We calculated the dimensions of the camera detection zone, $r$ and $\theta$, and the encounter rate, $y/t$, for each camera placement. To calculate the density of individuals, we multiplied the group density ($D$, Equation 2) for each camera placement by the median of the maximum deer visible for all encounters.

We performed a confidence interval test to determine whether the sika deer density estimates by the FAR and REM methods were significantly different. Here, a confidence interval is constructed for the difference between the two means, $\mu_1$ and $\mu_2$. If the confidence interval includes the null hypothesis value for the difference, then the null cannot be rejected. We chose to test a 95% confidence interval and zero as our null value. All statistical analyses were completed using JMP statistical software (JMP Pro v. 11, SAS, North Carolina, USA).

# CHAPTER THREE

## RESULTS

The 62 fecal accumulation plots were cleared over nine days. Sika deer pellet groups were found in 55 of the plots, and were then removed. On revisiting the plots, an average of 34 days later, I found sika deer pellets in 29 plots (Figure 3), roe deer pellets in 17, red deer in three, and wild pig scat in seven.

Using the defecation rate of 25.8 pellet groups per day for sika deer (Horino and Nomiya 2008)), we calculated (Equation 1) a mean density of 13.97 ± 2.74 SE sika deer $km^{-2}$.

The 57 camera traps were in place an average of 19.4 days each, for a total of 1108 trapping days. They yielded a total of 795 photographs from 102 encounters with an average of 3.16 individuals per photograph. For all camera placements, the average number of photographs per day was 0.56 ± 0.315 SE. The majority of encounters (91.2%) were with sika deer. Only seven encounters resulted in photographs of red deer, roe deer, or boar. Due to the small numbers of encounters with ungulates other than sika deer, our analysis is for sika deer only.

The REM relies on the angle, θ, of the detection zone for each camera. We analyzed possible differences in camera type and placement. In a least square means test with $\alpha$=.05, we found that the mean θ was significantly affected by camera type ($p < .001$). The mean θ for the Cuddeback® cameras was 0.279 ± .026 SE radians and the mean θ for the Reconyx® cameras was .604 ± .019 SE radians.

Using the mean estimate of daily travel distance of 2.78 km/day (Stephens *et al.* 2006), and an estimated median group size of two deer, we calculated a mean density of 4.91 ± 1.76 SE sika deer $km^{-2}$. Using the lower CI limit for daily travel distance, we calculated a mean density of 9.1 ± 3.26 SE. sika

deer $km^{-2}$. Using the upper CI limit for daily travel distance, we calculated a mean density of 3.4 ± 1.20 SE sika deer $km^{-2}$.

In a confidence interval test, the difference of the means was 9.06 sika deer $km^{-2}$ and had a pooled standard deviation of 18.23.

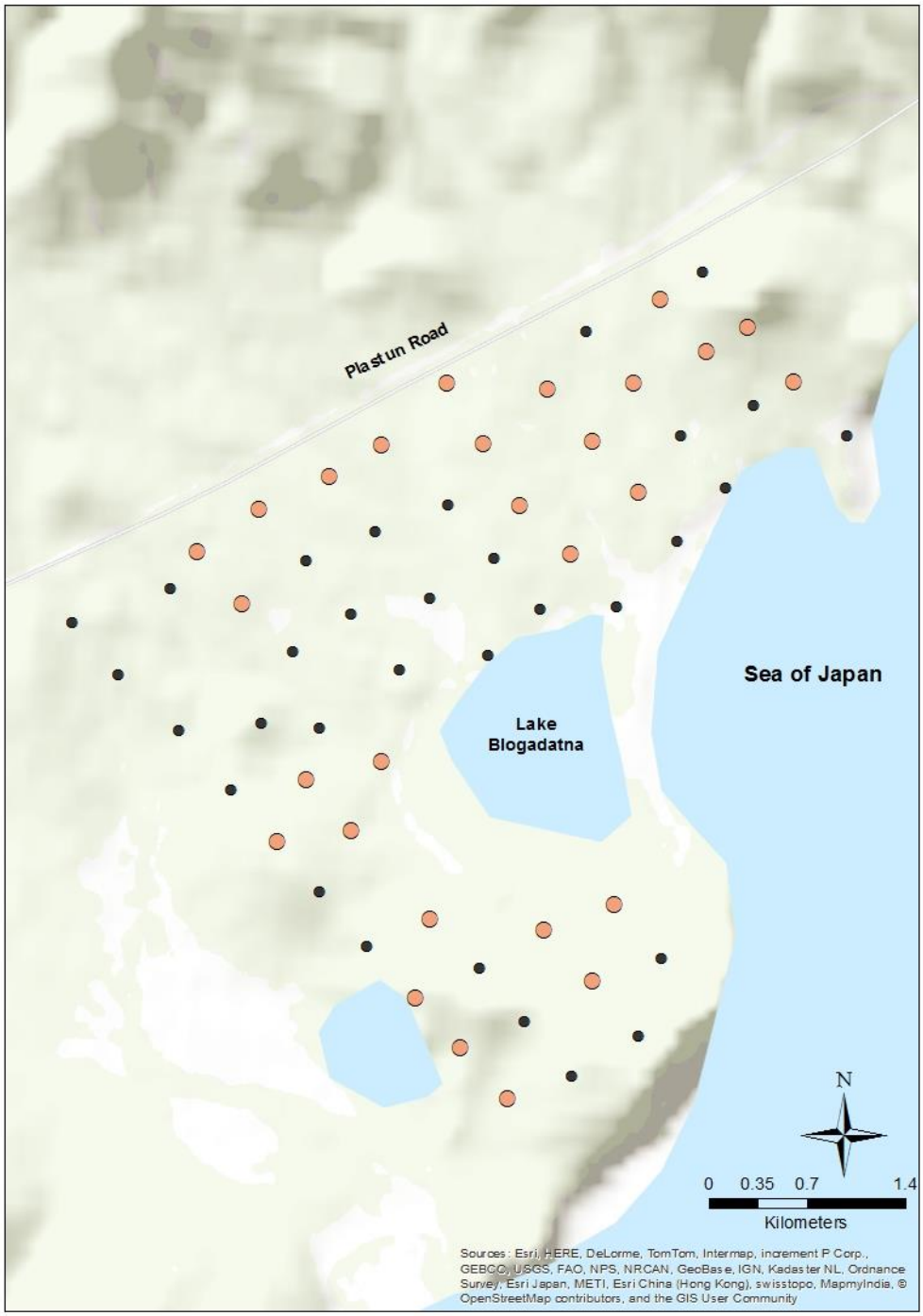


Figure 4. Locations of scat plots where pellet groups were present after the accumulation period are shown in orange. Locations of scat plots where pellet groups were not present after the accumulation period are shown in black.

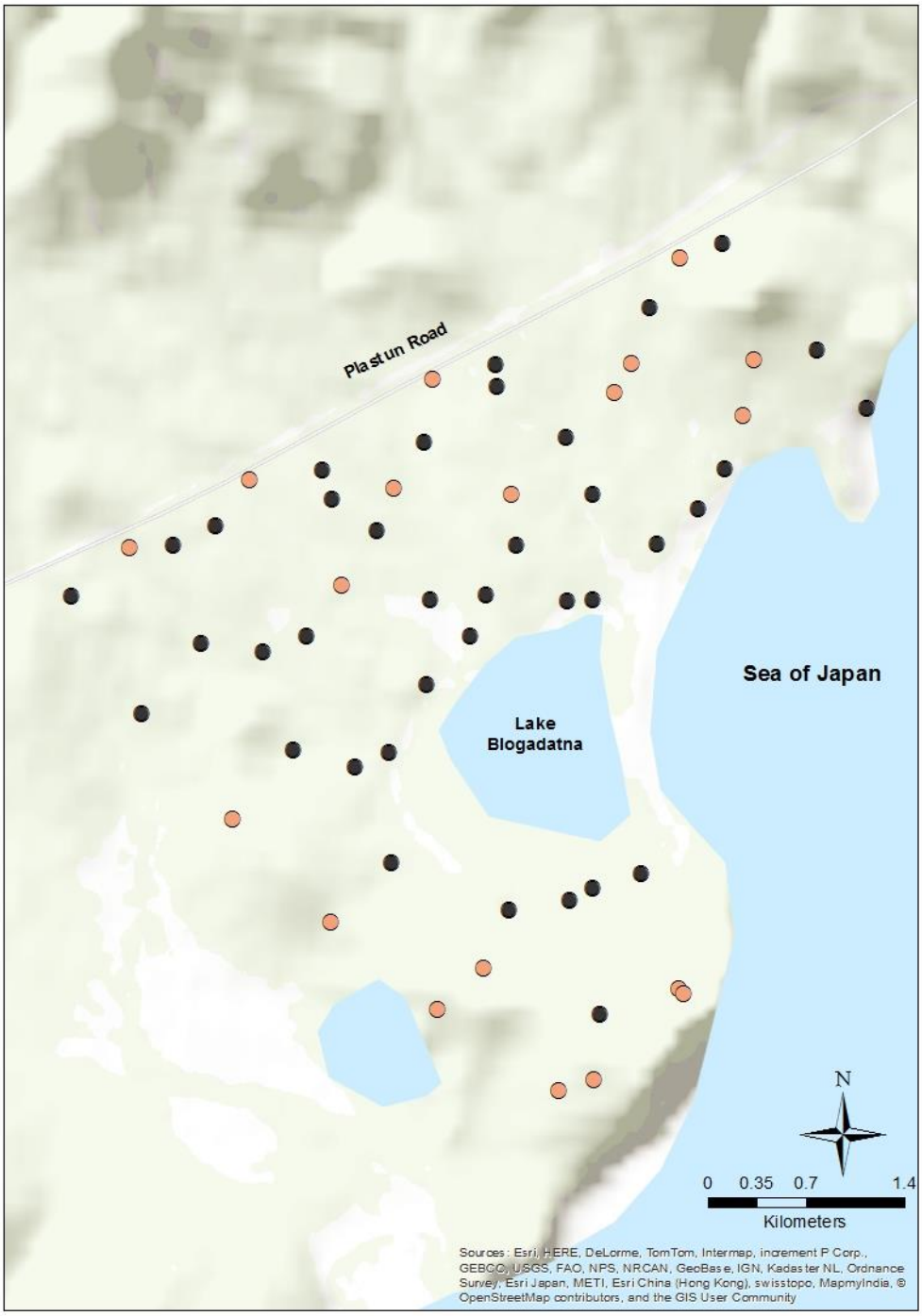


Figure 5. Locations of camera traps that detected sika deer are shown in orange. Locations of camera traps that did not detect ungulates are shown in black.

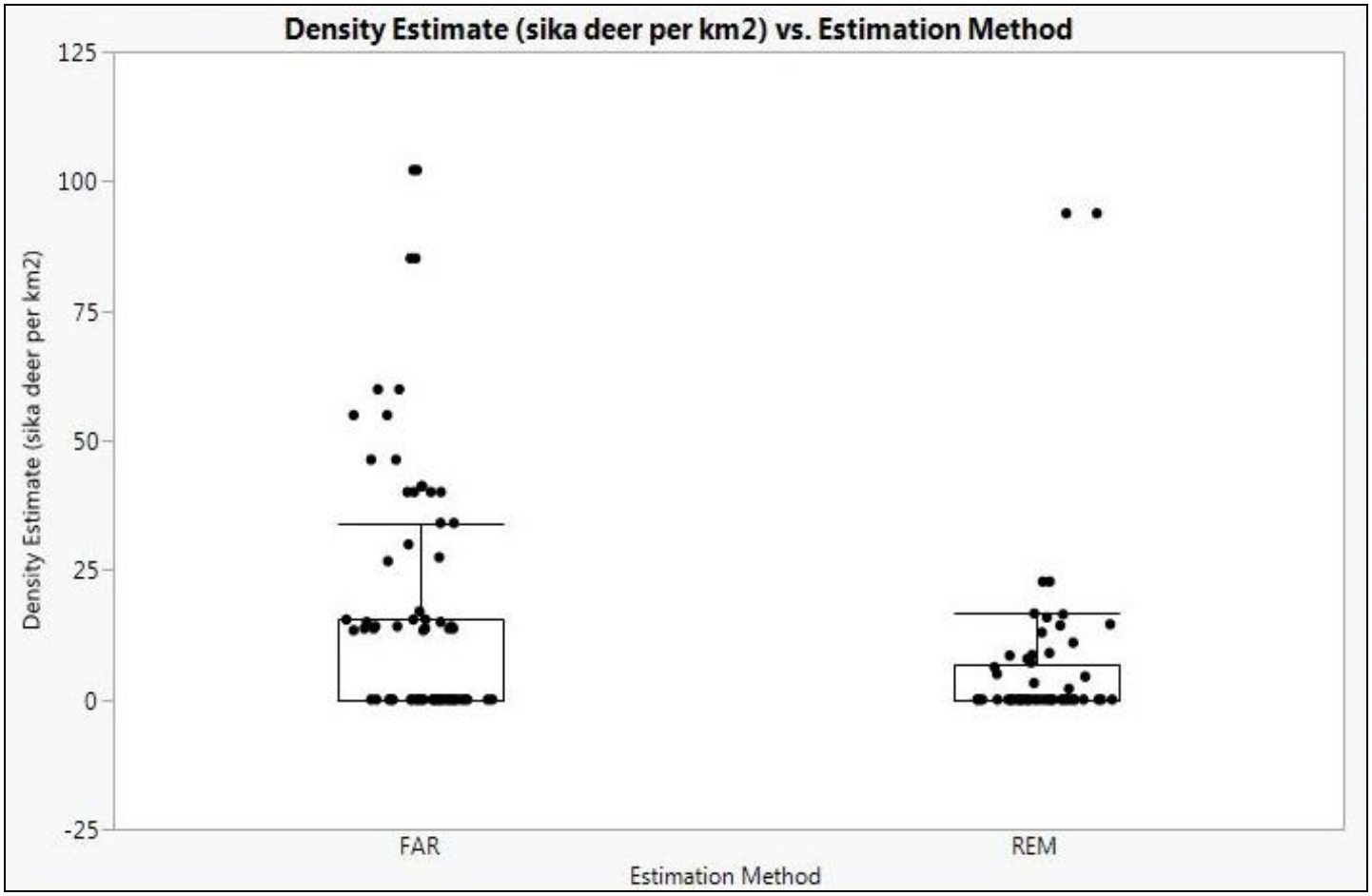


Figure 6. Outlier box plots for the FAR (mean 13.97 deer/ $km^2$) and the REM (mean 4.91 deer/ $km^2$) population density estimates. FAR points represent a density estimate from each accumulation plot. REM points represent a density estimate from each camera trap site. The upper and lower boundaries of the box mark the 3rd and 1st quartiles, respectively.

# CHAPTER FOUR

# DISCUSSION

The two methods for estimating sika deer density in the Blogadatna Lake basin yielded estimates of 4.91 (REM) and 13.97 (FAR) sika deer $km^{-2}$ The confidence interval of their difference [2.53 - 24.65 deer $km^{-2}$] does not cross zero, indicating that this difference is statistically significant. A previous study estimated slightly less than 1 sika deer/ $km^2$ in the SABR using the Formozov-Malyshev-Pereleshin formula and showed a trend of increasing population density over the previous decade (Stephens *et al.* 2006). Based on field observations and this earlier study, the results from using the REM are closer to predicted. The striking difference between the two estimates warrants consideration of the underlying assumptions of each and whether violating these assumptions contributed to this difference.

The FAR method for estimating population density is simple to use and based on well-established principles. Since it is a measure of animal activity, it does not require individual identification and is insensitive to whether study animals are elusive and/or travel in groups. It does assume that the plots provide a representative sample of the animals' activity. This is usually interpreted to mean that the plots are distributed randomly across the study area and that the animals also move across the landscape and defecate at random (i.e., no preferred use of trails or latrines). The SABR forest is relatively open and the sika deer move readily across the landscape, so our randomized distribution of plots should satisfy this assumption. The amounts of pellet groups observed in the plots were positively skewed in both the standing and accumulated crops. The number of standing pellet groups in each plot had a sample skewness value of 2.81. The number of accumulated pellet groups in

each plot had a sample skewness value of 1.81. The positive skews indicate that sika deer in this area do not use latrines and are likely defecating while foraging or bedding down.

Another set of assumptions surround the accurate identification and counting of pellet groups. Specifically, FAR assumes that all pellet groups deposited in an accumulation plot will be censused (i.e., have not decayed or been concealed) and that individual pellet groups can be distinguished from one another. We identified and defined pellet groups based on recommendations from previous studies (Chame 2003; Horino and Nomiya 2008; Koda *et al.* 2011; Koike *et al.* 2013). Defining pellet group size is difficult and arguments have been made for counting individual pellets (Horino and Nomiya 2008), but heavy leaf litter and time constraints made counting individual pellets impractical for our study. We observed little decay in pellet groups left outside of the accumulation plots and attribute this to limited precipitation (mean < 0.025 cm) and cold temperatures (mean = -2$^{o}$C).

Many of the underlying assumptions of FAR are easily satisfied, a consideration that has likely contributed to its wide use in estimating population density. However, the estimate of population density that the FAR yields is inversely related to the defecation rate per animal, which varies with place and time according to diet, age, and other variables (Horino and Nomiya 2008). Therefore, the proper use of this method is dependent on having an accurate estimate of defecation rate for the time, area, and population of interest. As we have noted, this is not easy to obtain for sika deer in the Russian Far East or, presumably, for many other forest animals. This problem can be solved by finding an alternative way to estimate defecation rates in the study population, or by adopting a different census method altogether.

We propose that camera traps can provide a solution for direct estimation of defecation rates in a study population. They can be positioned over cleared fecal accumulation plots, and data from camera

images linked to actual defecation rates. The camera images would provide number of "deer minutes" *d* that deer are in the plots, equal to the unit of time a group of deer is in front of the camera (based on a series of photographs). By collecting data on the number of pellet groups *p* produced while any number of individuals *i* is in front of the camera, we can relate deer minutes to defecation rate *r* per individual (Equation 3).

$$r = i - \qquad \textit{Eqn. 3}$$

We began testing this method late in the study period, but the camera traps were not in place long enough to reliably estimate defecation rate. Using a series of test photographs, we established a zone of sight for each camera placement. These triangular plots were marked and cleared of all scat. We checked the plots for fecal accumulation before each camera was moved. To our knowledge this is an entirely new method that could reduce uncertainty in the widely used FPG methods. If viable, this method could increase the use of FPG methods for estimating density of elusive animals for which defecation rates are difficult to measure.

The recent widespread adoption of camera traps in wildlife biology has provided a completely different way to estimate prey density (Rowcliffe *et al*. 2008). This has similar advantages to FAR in that it can used on elusive animals that lack individual marks. However, the estimate of population density that it yields is inversely dependent on the mean travel distance per day, which can also vary with place and time and therefore should be measured on the study population. If this is not possible, then outside estimates must be used, introducing uncertainty in the resulting estimate. Also, REM can be problematic when used with animals that travel in herds. To use this method with herd animals requires that encounters are clearly defined, that group size is constant and known, and that the detection zone of each camera placement can actually record the entire group. If not, it will

underestimate both group size and total density, and by the same factor. We estimated group size by the maximum number of animals visible in an encounter (from one or a series of photographs). The median value in this case was also the mode for all encounters. We believe that estimating group size based on the field of view of each camera may yield more reliable group size and density estimates because the field of view is similar to and closely associated with the detection zone of each camera, which is used in REM density calculations.

Using camera traps and the REM to estimate population density requires an estimate of group size in order to estimate the density of individuals, as opposed to groups (Rowcliffe *et al.* 2008). Applying the REM to herd animals by multiplying the density for each encounter by an independent estimate of herd size potentially introduces bias. If an independent estimate of herd size is larger than the number of animals that physically fit or are typically present in the area surveyed by each camera trap, then applying that estimate to each encounter will result in an overestimate of population density. An independent estimate of group size may also introduce uncertainty if herd size is highly variable. Group size may change depending on the presence of snow, predators, and other factors. Group size is typically higher for ungulates during times of restricted movement, breeding, or migration (Hojnowski *et al*. 2012). Our study was conducted in a period where movement was not restricted by snow depth and a season when mating activity does not typically take place (Geist 1998).

Future studies may use the REM to estimate variability in group size and establish correlating or causing factors in order to predict bias when a REM is applied. The requirement of a randomized survey reduces the REM's utility in areas where animal movement is restricted by dense forest or severely fragmented habitat. When estimating tiger prey specifically, many habitats include dense brush that cannot be accessed by humans or prey animals and movement is restricted to trails (O'Brien,

Kinnaird, & Wibisono 2003). Likewise, when study species show high variability in habitat use, the REM may not be preferable. We believe the REM method is a potential solution for estimating population density when indirect methods are required. However, the REM will require additional rigorous testing in a variety of habitats and species in order to reliably estimate the density of elusive herd animals.

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