ASSESSING THE CONTRIBUTION OF HARVEST MORTALITY TO OVERALL MORTALITY RATES OF GRAY AND FOX SQUIRRELS ON PUBLIC LANDS IN MINNESOTA

Ryan G. Tebo and John H. Giudice

SUMMARY OF FINDINGS

Squirrel hunting is a popular activity in Minnesota, but hunter perceptions of squirrel decline on publicly-owned land near the Twin Cities Metropolitan Area of Minnesota (hereafter, metro) has led interested user groups to voice concern over squirrel populations in recent years. To explore these concerns, we conducted a study to compare squirrel mortality rates on a site with heavy hunting pressure (Whitewater Wildlife Management Area (WWMA) to a paired non-hunted site (Whitewater State Park (WSP) in southeastern Minnesota. From 1 July 2015 – 18 September 2015 and 2 May 2016 – 16 September 2016, we trapped and radiocollared 107 gray and fox squirrels (*Sciurus carolinensis* and *S. niger*, respectively) on WWMA and 101 gray squirrels on WSP. Using survival data from the first year of the study, we failed to find evidence that survival probabilities differed between sites during most of the monitoring period (1 July 2015 – 12 April 2016). The estimated survival probability for late summer (1 July 2015 – 18 September 2015) on both sites was 0.916 (85% CI: 0.871-0.946) and for the late fall through early spring monitoring interval (1 November 2015 – 12 April 2016) was 0.835 (85% CI: 0.752-0.892). However, during the first 6 weeks of the 2015 hunting season, 13 squirrels were harvested on WWMA and the survival probability was estimated to be 0.529 (85% CI: 0.398-0.645). Conversely, survival probability was estimated to be 0.955 (85% CI: 0.929-0.971) on WSP during the same time period. We again saw a high number of squirrels harvested during the first 6 weeks of the 2016 hunting season (10), but harvests were also recorded as late as 21 February 2017. Estimates of survival from the first year of the study may show a positive bias due to the high proportion of animals with unknown fates (e.g. missing animals, unrecoverable collars in mortality mode). Monitoring of squirrels radiocollared in 2016 has recently come to an end and with the addition of the second year of data we intend to construct more sophisticated survival models that reflect likely variation in survival probabilities over space, time, and individual covariates.

INTRODUCTION

Small game hunting is a popular recreational activity in Minnesota with approximately 292,000 hunters buying licenses each year since the late 1990s (Dexter 2009, Dexter 2014). Nearly 15% of small game hunters pursue gray and fox squirrels with an estimated take of 5.1 gray and 3.9 fox squirrels per hunter (Dexter 2009, Dexter 2014). The combined gray and fox squirrel harvest and the number of squirrel hunters has each declined by 13.8% since the late 1990s; however, the combined take per hunter has declined by only 3.3% during this same time (Dexter 2009, Dexter 2014). In an effort to better understand barriers to hunter participation, the Minnesota Department of Natural Resources (MNDNR) conducted a survey of squirrel hunters (Dunbar 2009). More hunters in the metro responded that they believed squirrel populations were declining (51%) as compared to other hunters statewide (19%). Metro hunters also indicated that they had limited access to private land and heavy hunting pressure existed on publicly-owned land (Dunbar 2009).

Many factors cause squirrel populations to fluctuate naturally (e.g., mast abundance, population density, disease outbreaks; see Barkalow et al. 1970, Nixon et al. 1974, Nixon et al. 1975, Healy and Welsh 1992, Descamps et al. 2009, Vander Haegen et al. 2013), and population dynamics are determined by reproduction, immigration, emigration, and mortality. Although squirrels are considered a game species where hunting mortality is often assumed to be compensatory to natural mortality, previous research suggests hunting mortality can be additive to non-hunting mortality in exploited squirrel populations (Herkert et al. 1992). If so, wildlife managers can alter hunting regulations to adjust the contribution of hunting mortality to overall mortality rates.

The number of gray and fox squirrels harvested during fall hunting season is correlated with pre-hunt densities and the amount of effort expended by hunters early in the hunting season (Nixon et al. 1975). A study in Virginia found the rate of population turnover, the annual mortality rate, and the rate of juvenile recruitment was higher in hunted squirrel populations (Mosby 1969). In an Ohio study, approximately 50% of the harvest was comprised of squirrels born the previous spring and summer and there was no difference observed in the harvest sex ratio for young-of-the-year or adult squirrels (Nixon et al. 1975). Annual mortality rates were 70-80% for young-of-the-year squirrels and nearly 80% for adult squirrels, with hunting accounting for nearly 60% of the annual mortality across all age classes (Nixon et al. 1975). The researchers concluded that the population could not sustain itself with this level of mortality and that squirrels were likely immigrating from surrounding habitats (Nixon et al. 1975). In Illinois, the annual mortality rate for fox squirrels was 79% on a hunted site and 44% and 45% on non-hunted sites, while mortality rates outside of the hunting season were not significantly different (Herkert et al. 1992). Reproductive intensities did not differ between the sites and the researchers also concluded that the hunted population was being sustained by immigration (Herkert et al. 1992). In a prior Minnesota study, researchers found an annual survival rate of 27% for gray squirrels on a hunted site with 74% of all mortalities attributed to hunting (Longley 1963). The annual survival rate was 48% the following year when the site was not hunted (Longley 1963). Reproductive rates were 2.4 young per litter regardless of the prior year's squirrel hunt status (Longley 1963).

The MNDNR Section of Wildlife has considered changes to the squirrel season structure in the metro based on the aforementioned survey results. However, because a paucity of information exists with respect to the impacts that the current hunting regulations have on squirrel population growth rates, no changes have been made to date. This study intends to assess the contribution of harvest mortality to overall mortality rates of gray and fox squirrels on public lands in Minnesota. Prior to initiating this expanded research project, we completed a pilot study to evaluate squirrel trapping, handling, and tracking methods (see Curtis and Davros 2014).

OBJECTIVE

1. Assess mortality rates of radiocollared squirrels across multiple seasons (fall/early hunting season, winter/late hunting season, spring, and summer) on heavily-hunted public land and nearby non-hunted land.

STUDY AREA

Our study was conducted in southeastern Minnesota during 2015-2017. Within the study area, we chose 2 sites in close proximity to achieve a paired design of 1 treatment (i.e., hunted) and 1 control (i.e., non-hunted) site. Whitewater Wildlife Management Area, which receives pressure from squirrel hunters, was the treatment site. Whitewater State Park is not open to hunting and was used as the control site.

METHODS

Trapping

We trapped gray and fox squirrels during July-September 2015 and May-September 2016. We used wire box traps (48 x 15 x 15 cm; 2.5 x 1 cm mesh) baited with sunflower seeds, dried corn, peanut butter, and/or black walnuts. Using the MNDNR Forest Inventory layer (where available) or the MNDNR Landcover layer, we selected oak habitat within our sites in ArcGIS 10.2 (ESRI, Redlands, California, USA). In oak habitat areas where terrain allowed, we created a grid of points 25 m apart and placed traps at these points. In areas with challenging terrain or insufficient contiguous oak habitat, traps were selectively placed at locations that researchers deemed to be likely squirrel-use areas. We checked traps at least twice per day (i.e., late morning and late evening) to reduce the amount of time squirrels remained in the traps. We closed traps during inclement weather. We also removed traps before the weekends, thereby allowing us to clean and repair traps before changing sites, reducing the risk of theft, and reducing disturbance to WSP and WWMA visitors during peak visitation days.

Upon capture, we identified the sex of each squirrel and determined the reproductive status of females. We weighed squirrels in the trap to the nearest 10 g using a digital hanging scale. We used a modified handling cone to restrain squirrels, which allowed us to handle and radiocollar without sedation (Koprowski 2002). Handling cones were constructed of denim with hook and loop straps to help secure the squirrel and a zipper opening to allow access to the head and neck during collar attachment. Once in the handling cone, a removable plastic funnel was attached around the squirrel's neck to protect handlers from bites during collaring (McCleery et al. 2007). We only collared squirrels weighing ≥300 g in an effort to keep the transmitter weight below 3% of the animal's body mass. Squirrels received a 7-g, 10-g, or 13-g VHF necklace-style radiocollar (models M1525 and M1535, Advanced Telemetry Systems, Isanti, MN) depending on the weight of each individual squirrel. Each transmitter was equipped with an integrated mortality sensor that changed the pulse rate of the signal if an animal did not move for 12 h. Expected battery life was 362 days for the 13-g collar and 302 days for the 7- and 10-g collars. Upon completion of the handling procedure, all squirrels were immediately released. All non-target captures were released immediately. No specimens were collected.

Tracking

Following capture, radiocollared squirrels were monitored for mortality weekly using a vehicle-mounted non-directional radiotelemetry antenna system. Beginning on the first day of the squirrel hunting season (19 September 2015 or 17 September 2016), squirrels were monitored twice weekly until the end of October. Squirrels were then monitored once weekly until the end of December, and once biweekly until 1 March. When a radiocollar transmitted a mortality signal, we used homing techniques in an attempt to recover the collar and determine the cause of mortality. Squirrels remaining on the air beyond 1 March continued to be monitored biweekly until death or battery failure.

Data Analysis

Mortality is a continuous time process, but in this study we observed it discretely and incompletely (interval-censored and truncated monitoring data with staggered entry, missing animals, unknown fates, and uneven monitoring intervals). This data-collection design shares many similarities with nest-survival studies (Heisey et al. 2007). Therefore, we used a logistic-exposure modeling approach (Shaffer 2004) with interval- or right-censoring of animals with unknown fates (Bunck et al. 1995) to conduct an exploratory analysis of the survival process using monitoring data from squirrels captured during the 2015 trapping season. We used the glm function in the R programming language (R Core Team 2016) with a user-defined link function (https://rpubs.com/bbolker/logregexp) to estimate daily survival rates (DSR) as a function of site, study time (relative to 01 July 2015) or time groups (seasons), and individual covariates (e.g., sex, body mass, collar weight, capture location [x,y], distance from capture location to public roads). For the exploratory analysis, we did not attempt to model competing risks (harvest vs. natural mortality) and instead focused on estimating overall survival probabilities on the 2 study sites. However, for analysis purposes, we treated data from the WWMA during the first 6 weeks of the hunting season (19 Sep 2015 – 31 Oct 2015) separately because all observed harvest mortalities in 2015 occurred during this period. Thus, we used 2 datasets for survival estimation: 1) WWMA data from the first 6 weeks of the hunting season, and 2) all remaining data from both sites (which generally described the natural mortality process). We used Akaike's Information Criterion (AIC) to select among competing models, including a null model with constant daily survival. For inference, we used the most parsimonious model (fewest model parameters) that was within 2 AIC units of the best-approximating model (lowest AIC value).

An important assumption in this type of analysis is that censoring is independent of fate. Overall, 41% of our study animals had some form of censoring that reflected unknown fates (either interval status or final fate). Further, there were 4 times as many "missing" animals on WWMA (vs. WSP) that disappeared during the hunting season. Thus, we were concerned that censoring might not be independent of fate, which can lead to positively biased estimates of survival. We used a replicated imputation algorithm with simulated survival parameters (informed by the data) to construct complete histories for each animal with missing data or unknown fates. We used this procedure to construct 300 replicate monitoring datasets, which we fit to the models selected above (based on the observed data) to produce estimates of daily survival probabilities. We used the estimates from the imputation datasets as our point estimate and the conditional variance formula to compute the variance in the daily survival rate. We then extrapolated both imputed and observed daily survival rates to obtain annual survival probabilities, which we used to quantify potential biases due to censoring. We did not attempt to vary the simulated survival parameters (other than allowing the survival process to vary as a function of binomial variation); thus, differences between imputed and observed annual survival probabilities do not include uncertainty in the simulated survival parameters. We have included the information gleaned from the first monitoring year's exploratory analysis and are currently working on more sophisticated methods to analyze the full monitoring dataset. However, this approach was sufficient to inform our exploratory analysis and provide guidance on analysis options for the full monitoring dataset (years 2015-2017).

RESULTS AND DISCUSSION

Trapping and Monitoring

We successfully captured 132 squirrels (119 gray, 13 fox) during the 2015 and 2016 trapping seasons on WWMA, 107 of which received radiocollars. In an effort to distribute captures throughout WWMA, trapping locations were spread out across the unit (Figure 1). Fifty-one males and 56 females were collared. Based on their lactation status, 21 female squirrels that received collars (38%) showed evidence of prior reproductive activity. Weights of collared squirrels on WWMA ranged from 410-920 g ($\bar{x}$ = 655 g).

One hundred twenty-four squirrels (123 gray, 1 fox) were captured on WSP during the 2015 and 2016 trapping seasons, 101 of which received radiocollars. Trapping locations were spread out across the interior of WSP (Figure 2). Fifty males and 51 females were collared. Of 49 radiocollared females checked for reproductive status, 22 (45%) showed signs of prior reproductive activity. Weights of collared squirrels on WSP ranged from 370-840 g ($\bar{x}$ = 649 g).

From 1 July – late August 2015, trapping success was very low on both sites; only 10 squirrels had been captured on each site (3,564 trap checks; 0.56% capture rate). However, following this period of low capture success, we switched to fresh-picked walnuts as our bait type. In the remaining 3 weeks of the 2015 trapping season following the bait change, 46 and 39 squirrels were captured on WWMA and WSP, respectively (1,181 trap checks; 7.2% capture rate). Thereafter, we used fresh walnuts as the predominant bait-type when they were available. The preference for walnuts may have been due in part to a seasonal behavior change, where caching food became the ultimate goal of squirrels once trees began producing the year's walnut crop. Overall capture rates for WWMA and WSP for the duration of the study were 1.99% (6,629 trap checks) and 5.02% (2,470 trap checks), respectively. Two squirrels on WWMA and 4 squirrels on WSP originally captured in 2015 were recaptured during the 2016 trapping season and fitted with new radiocollars.

Twenty-nine (27.88%) squirrels were harvested by hunters on WWMA (Figure 3). In addition, 9 (8.65%) animals were lost to natural mortality events, 9 (8.65%) squirrels dropped their collars, 13 (12.50%) collars were unrecoverable (e.g., in a tree or inaccessible), 1 (0.96%) collar was recovered but fate could not be determined, 19 (18.27%) squirrels went missing due to unknown reasons, and 24 (23.07%) squirrels went missing due to presumed collar battery failure (Figure 3). On WSP, 21 (20.79%) squirrels were lost to natural mortality events, 15 (14.85%) squirrels dropped their collars, 20 (19.80%) collars were unrecoverable, 8 (7.92%) squirrels went missing due to unknown reasons, and 37 (36.63%) squirrels went missing due to presumed collar battery failure (Figure 3). We censored 3 of the 107 radiocollared squirrels on WWMA from the survival study due to capture complications.

Of squirrels captured in 2015, all known harvest mortalities (13; 100%) occurred within the first 6 weeks of the hunting season (Figure 4). The last observed harvest mortality was 27 October 2015. In 2016, however, 10 of 15 (67%) known harvests occurred during the first 6 weeks of the hunting season. The latest harvest mortality recorded was 21 February 2017. In addition, 8 of 12 (67%) squirrels that went missing for reasons not deemed to be collar battery failure went missing during the first 6 weeks of the hunting season in 2015. Four of 7 (57%) missing squirrels did so during the first 6 weeks of the 2016 hunting season. Although it cannot be confirmed, we believe it is very likely some, if not most, of these squirrels were harvested.

Despite efforts to inform and encourage hunters to report harvests of radiocollared squirrels, only 4 of the 29 (14%) known harvests were reported. Signs placed throughout WWMA and at popular parking areas asked hunters to report the harvest of any radiocollared squirrels. Additionally, squirrels captured in 2016 each received a unique numbered ear tag that included a call back telephone number. However, most radiocollars from harvested squirrels were found cut off in the presumed location of harvest, or in parking lots. Other squirrels were found deceased with noticeable gunshot wounds, but were left in the woods or unrecovered by hunters.

The majority (85.29%) of unrecoverable collars were in trees. Whether these squirrels died or dropped their collars is unknown; however, we believe that a majority of these losses are due to dropped collars. We base this assumption on numerous examples where collars fluctuated between mortality and normal signal, an indication that the collars were still subject to movement in the tree cavities the collars were presumed to be in. On another occasion, a collar was emitting a mortality signal until researchers reached the tree; at that point the collar switched out of mortality mode and an uncollared squirrel exited a cavity in the tree. Finally, one collar that had been unrecoverable in a tree for months was found on the ground by researchers in late March, with clear signs that the zip-tie attachment had been chewed through.

Survival Analysis

Our analysis of the first year of survival data failed to present strong evidence that the log odds of survival varied as a function of site (excluding the first 6 weeks of the hunting season on WWMA), time, season (again, excluding the first 6 weeks of the hunting season on WWMA), or the individual covariates we examined for squirrels captured during the first year of the study. Thus, we used constant-survival models (null models) to make inferences on the survival process, at least for our exploratory analysis. We acknowledge that constant daily survival is unlikely to be true, especially over long periods of time, but given the paucity of monitoring data for some seasons (late summer on both sites and winter-spring on WWMA) and concern about the amount of censoring in our data, it was a reasonable starting point for the exploratory analysis. With the second year of survival data, we anticipate being able to construct more sophisticated survival models that reflect likely variation in survival probabilities over space, time, and individual covariates (e.g., age, sex, distance). For example, we found weak signals that suggested the log odds of harvest decreased with distance from capture site to public roads (i.e., access points for hunters) on WWMA (Figure 5), and the log odds of survival in WSP and WWMA (excluding the first 6 weeks of hunting season) was lower during late summer compared to fall, winter, and early spring (Figure 6). The latter might reflect dispersal and greater vulnerability of juvenile squirrels to natural mortality events, but we lacked a sufficient sample size during this time period (due to trapping challenges) to precisely estimate the effect on survival probabilities.

The estimated daily survival rate (DSR) on WWMA during the first 6 weeks of the 2015 hunting season was 0.985 (85% CI: 0.978-0.990). Conversely, the estimated DSR for WWMA during other times of the year and in WSP was 0.999 (85% CI: 0.998-0.999). Extrapolating the DSRs to seasonal time intervals resulted in an estimated survival probability of 0.529 (85% CI: 0.398-0.645) for WWMA during the first 6 weeks of the hunting season, compared to 0.955 (85% CI: 0.929-0.971) for WSP during the same time period (Figure 7). The estimated survival probability for late summer (1 July 2015 – 18 Sep 2015) on both sites was 0.916 (85% CI: 0.871-0.946) and for the late fall through early spring monitoring interval (1 Nov 2015 – 12 Apr 2016) was 0.835 (85% CI: 0.752-0.892).

Not surprisingly, our imputation analysis suggested that censoring was not independent of fate and, thus, survival estimates based on the censored data were positively biased for both sites (Figure 8). The degree of bias should be interpreted cautiously because it was based on one set of survival parameters (assumptions). Nevertheless, it suggests that censoring by itself may not be sufficient to generate accurate estimates of survival given the limitations of our data (e.g., the presence of many animals with unknown fates and the likely lack of independence between censoring and fate). One potential solution is to use a Bayesian integrated survival analysis where the probability of relocation and survival for animals with unknown fates is estimated via a mark-resight approach (Walsh et al. 2015). We are exploring this option for analyzing the full monitoring dataset (years 2015-2017). Despite the potential bias in survival estimates caused by unknown fates, it is still clear that squirrels subjected to hunting pressure have much lower survival rates during the first 6 weeks of the season.

The survival estimates derived from this study will improve our understanding of the extent to which hunter harvest affects overall mortality rates in gray and fox squirrels. Our results will be used by MNDNR’s Section of Wildlife to determine if adjustments to squirrel harvest regulations are warranted or if further research on squirrel populations and their habitat is needed.

ACKNOWLEDGMENTS

We would like to thank the employees at Whitewater State Park and Whitewater Wildlife Management Area, especially Brent Anderson, Colin Wright, and Don Nelson for their continued support. We appreciate the tolerance and curiosity of the Park and WMA visitors. We would like to thank Tonya Klinkner for handling all of our travel arrangements and project equipment purchases. Finally, we thank our technicians Natalie Schmidt, Sean Gibbs, Eric Anstedt, Alicia Freeman, Kelly Deweese, Brandon Berndt, Quinlan Eatwell, Andy Nelson, Calypso Gagorik, and Gwen Jutz for their assistance during the 2015 and 2016 field seasons. This study was funded by MNDNR and through the Federal Aid in Wildlife Restoration Act.

LITERATURE CITED

Barkalow, F.S., R.B. Hamilton, and R.F. Soots, Jr. 1970. The vital statistics of an unexploited gray squirrel population. Journal of Wildlife Management 34:489-500.

Bunck, C.M., C-L. Chen, and K.H. Pollock. 1995. Robustness of survival estimates from radio-telemetry studies with uncertain relocation of individuals. Journal of Wildlife Management 59:790-794.

Curtis, R., and N. Davros. 2014. Pilot study to assess harvest mortality rates of gray and fox squirrels on public land in Minnesota. Pages 8-17 *in* L. Cornicelli, M. Carstensen, M. D. Grund, M. A. Larson, and J. S. Lawrence. Summaries of wildlife research findings 2014. Division of Fish and Wildlife, Minnesota Department of Natural Resources, St. Paul, Minnesota. 234 pp.

Descamps, S., S. Boutin, A.G. McAdam, D. Berteaux, and J.M. Gaillard. 2009. Survival costs of reproduction vary with age in North American red squirrels. Proceedings of the Royal Society 276:1129-1135.

Dexter, M. 2009. 2009 Small game hunter mail survey. Division of Fish and Wildlife, Minnesota Department of Natural Resources, St. Paul, Minnesota. 14 pp.

Dexter, M. 2014. 2013 Small game hunter mail survey. Division of Fish and Wildlife, Minnesota Department of Natural Resources, St. Paul, Minnesota. 11 pp.

Dunbar, E.J. 2009. Hunting, management, and ecology of gray and fox squirrels: a pilot study for squirrel management and hunting seasons for Minnesota. Minnesota Department of Natural Resources, Madelia, Minnesota, USA.

Healy, W.M., and C.J.E. Welsh. 1992. Evaluating line transects to monitor gray squirrel populations. Wildlife Society Bulletin 20:83-90.

Heisey, D. M., T. L. Shaffer, and G. C. White. 2007. The ABCs of nest survival: theory and application from a biostatistical perspective. Studies in Avian Biology 34:13-33.

Herkert, J.R., C.M. Nixon, and L.P. Hansen. 1992. Dynamics of exploited and unexploited fox squirrel (Sciurus niger) population in the midwestern United States. Pages 864-874 in Wildlife 2001: Populations, D. R. McCullough and R. H. Barrett, editors. Elsevier Applied Science, New York, USA.

Koprowski, J.L. 2002. Handling tree squirrels with a safe and efficient restraint. Wildlife Society Bulletin 30:101-103.

Longley, W.H. 1963. Minnesota gray and fox squirrels. American Midland Naturalist 69:82-98.

McCleery, R.A., R.R. Lopez, and N.J. Silvy. 2007. An improved method for handling squirrels and similar-size mammals. Wildlife Biology in Practice 3:39-42.

Mosby, H. S. 1969. The influence of hunting on the population dynamics of a woodlot gray squirrel population. Journal of Wildlife Management 33:59-73.

Nixon, C.M., R.W. Dohohoe, and T. Nash. 1974. Overharvest of fox squirrels from two woodlots in western Ohio. Journal of Wildlife Management 38:67-80.

Nixon, C.M., M.W. McClain, and R.W. Donohoe. 1975. Effects of hunting and mast crops on a squirrel population. Journal of Wildlife Management 39:1-25.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>. Accessed 29 June 2016.

Shaffer, T. L. 2004. A unified approach to analyzing nest success. Auk 121:526-540.

Vander Haegen, W.M., G.R. Orth, and M.J. Linders. 2013. Survival and causes of mortality in a northern population of western gray squirrels. Journal of Wildlife Management 77:1249-1257.

Walsh, D. P., V. J. Dreitz, and D. M. Heisey. 2015. Integrated survival analysis using an event-time approach in a Bayesian framework. Ecology and Evolution 5:769-780.

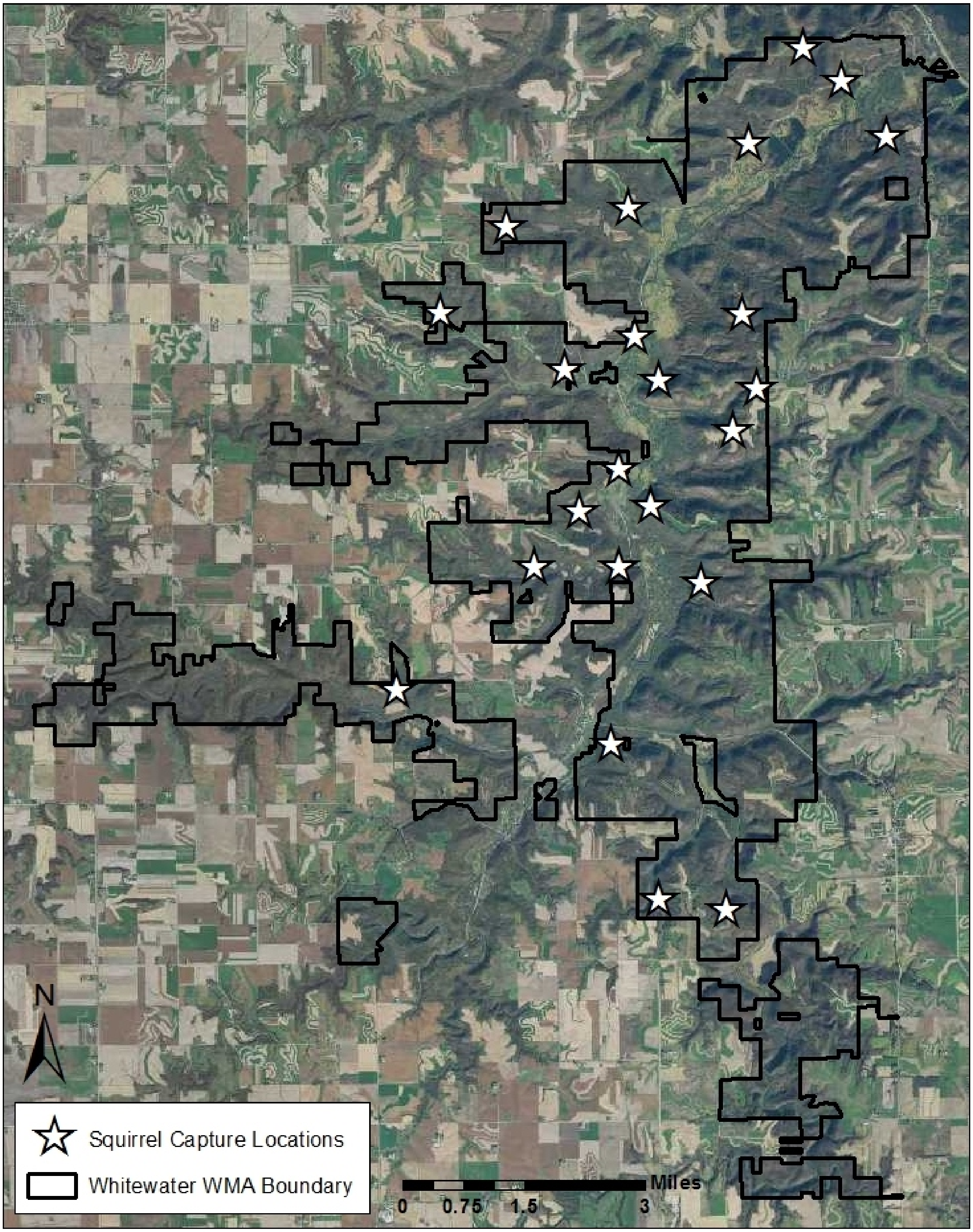

Figure 1. Capture locations of gray and fox squirrels (as indicated by white stars) during 11 July – 17 September 2015 and 24 May – 14 September 2016 in Whitewater Wildlife Management Area (WWMA), Minnesota (outlined in black).

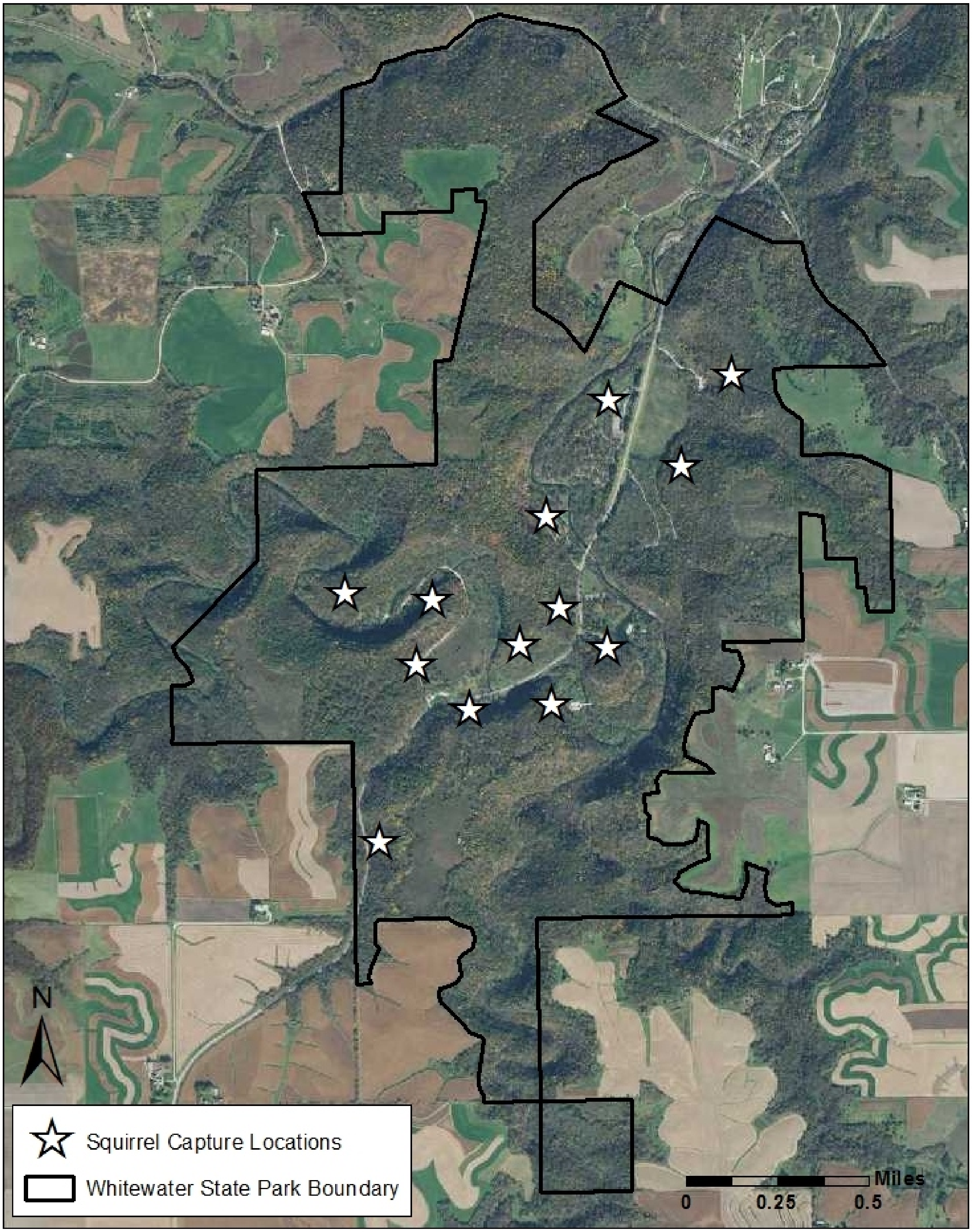

Figure 2. Capture locations of gray and fox squirrels (as indicated by white stars) during 6 August – 16 September 2015 and 2 May – 15 September 2016 in Whitewater State Park, Minnesota (outlined in black).

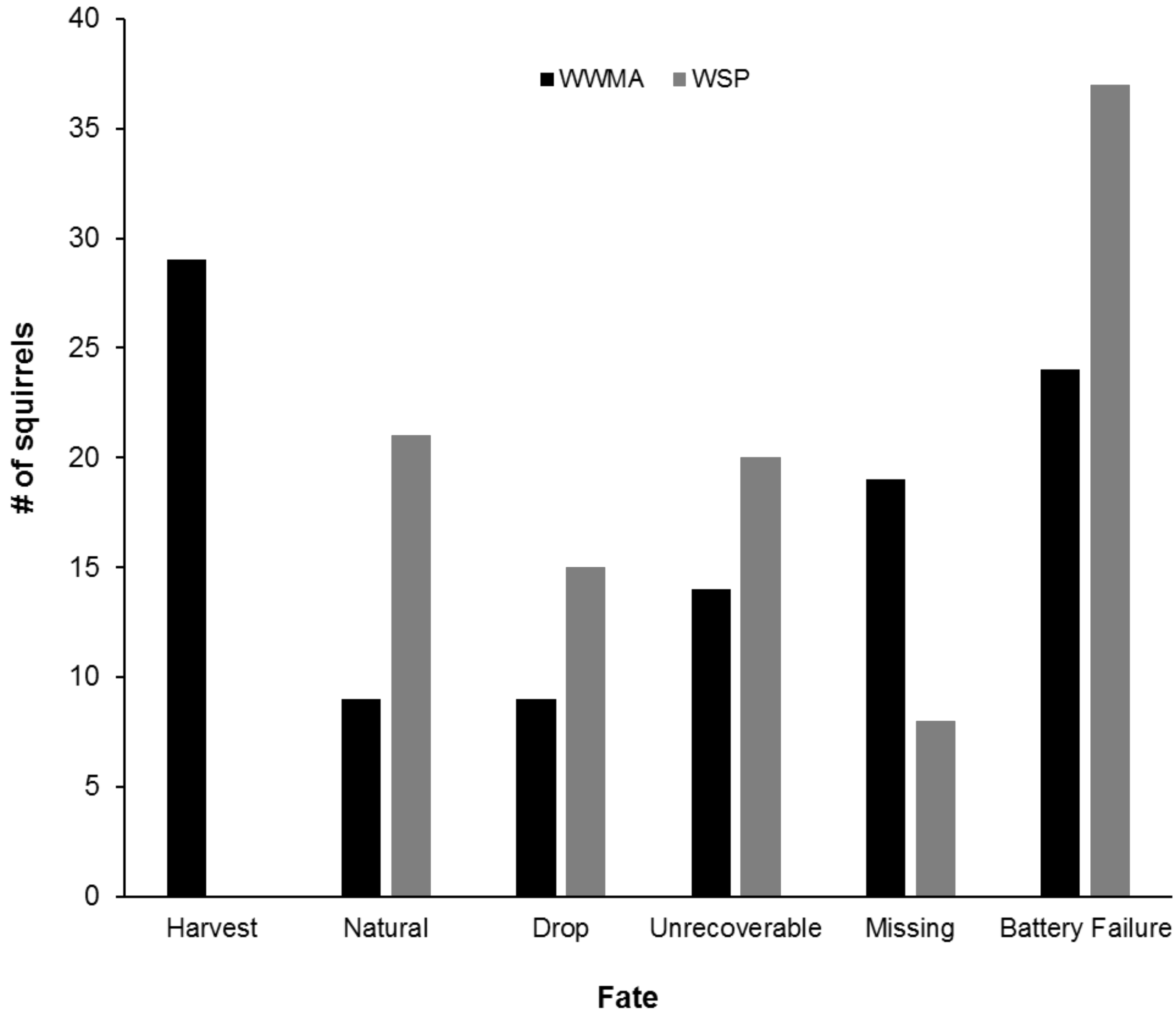

Figure 3. Fates of radiocollared gray and fox squirrels on Whitewater Wildlife Management Area, Minnesota (WWMA) and Whitewater State Park, Minnesota (WSP) 11 July 2015 – 25 May 2017.

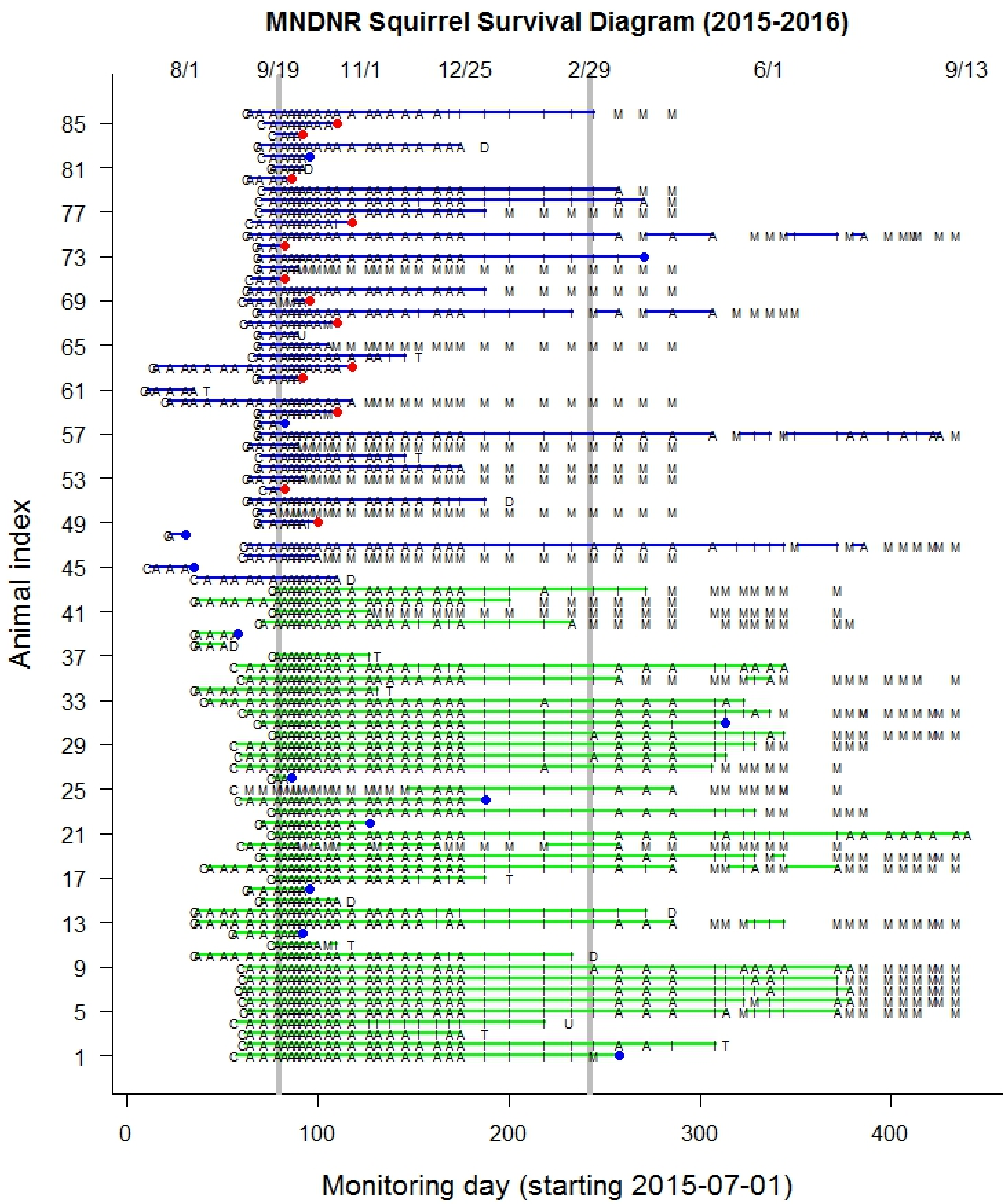

Figure 4. Life history diagram of radiocollared gray and fox squirrels captured in 2015 at Whitewater Wildlife Management Area, Minnesota (blue lines, n = 43) and Whitewater State Park, Minnesota (green lines, n = 43). Solid lines indicate continued survival across monitoring intervals. Fates of squirrels during the 2015-2016 hunting season are found within the gray vertical lines. Fate codes are as follows: red dot = harvest, blue dot = natural mortality, C = date of capture, A = active alive, I = inactive presumed alive, T = mortality in tree, D = dropped collar, U = undetermined collar loss, M = missing/signal not heard.

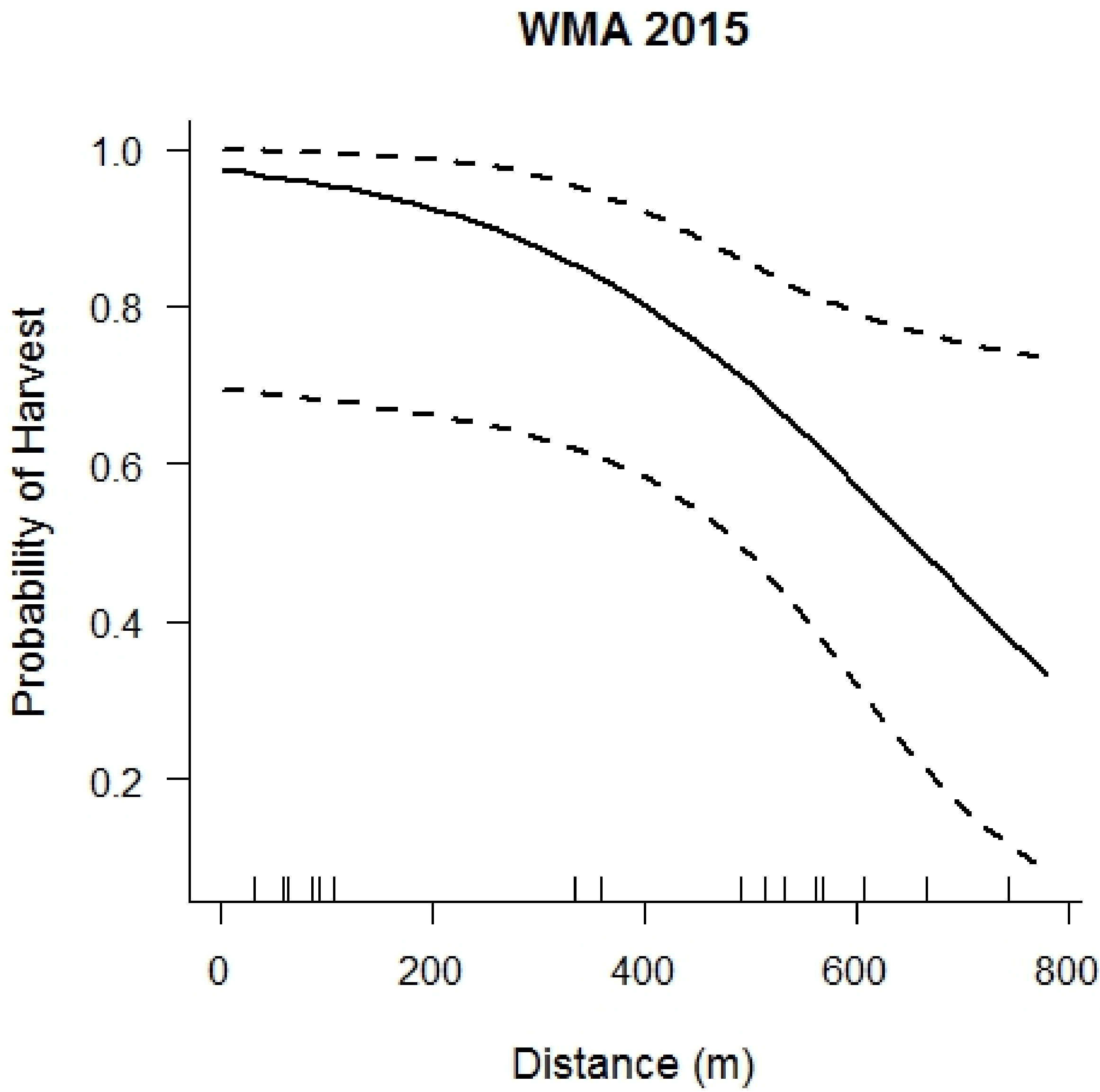

Figure 5. Probability of harvest of gray and fox squirrels (n = 44) in relation to distance from capture site to nearest hunter access point in Whitewater Wildlife Management Area (WWMA), Minnesota during 19 September 2015 – 29 February 2016.

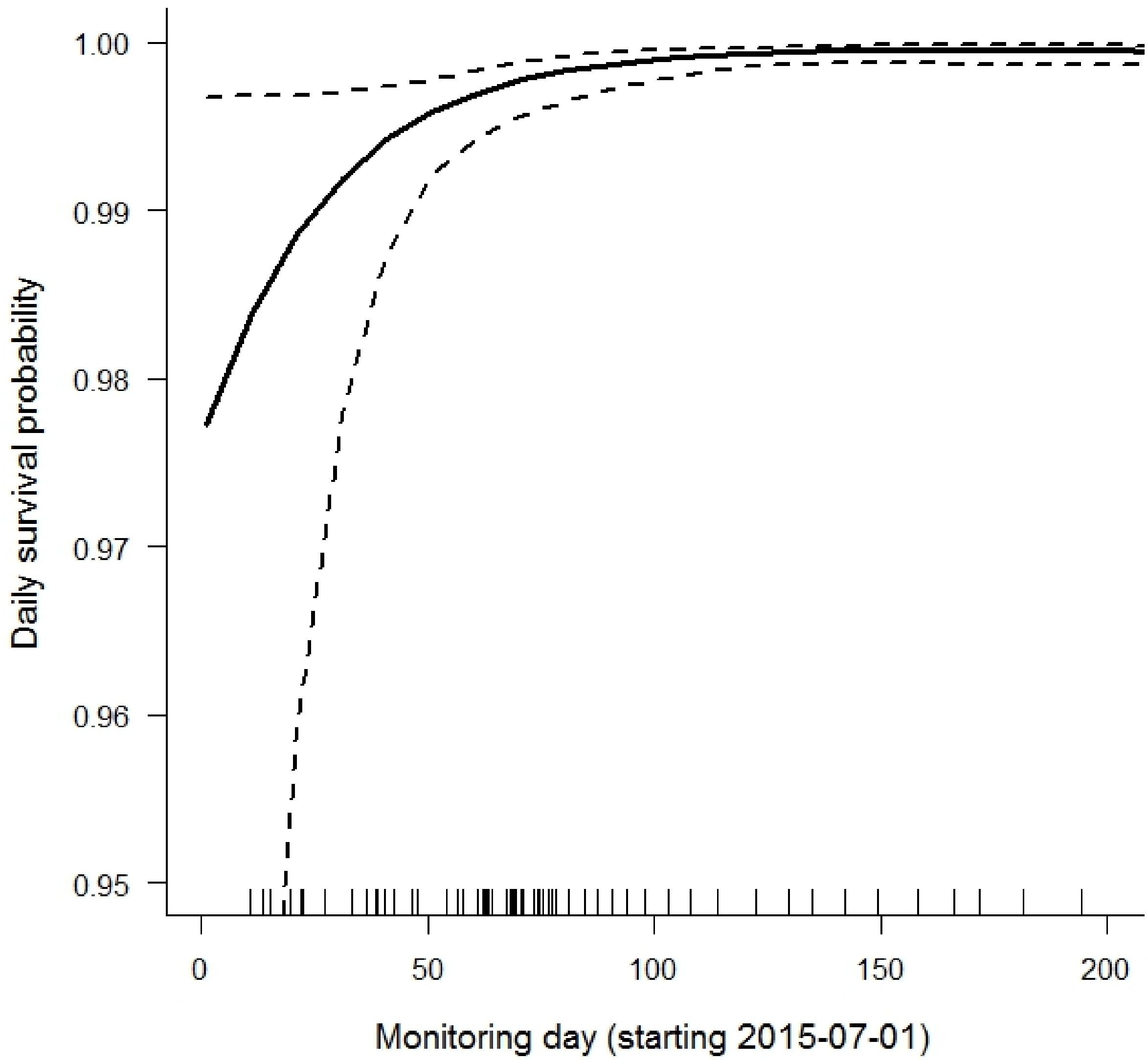

Figure 6. Daily survival probability (excluding the first 6 weeks of hunting season) of gray and fox squirrels in Whitewater Wildlife Management Area, Minnesota (n = 44) and Whitewater State Park, Minnesota (n = 43) during late summer, fall, winter, and early spring 2015-2016.

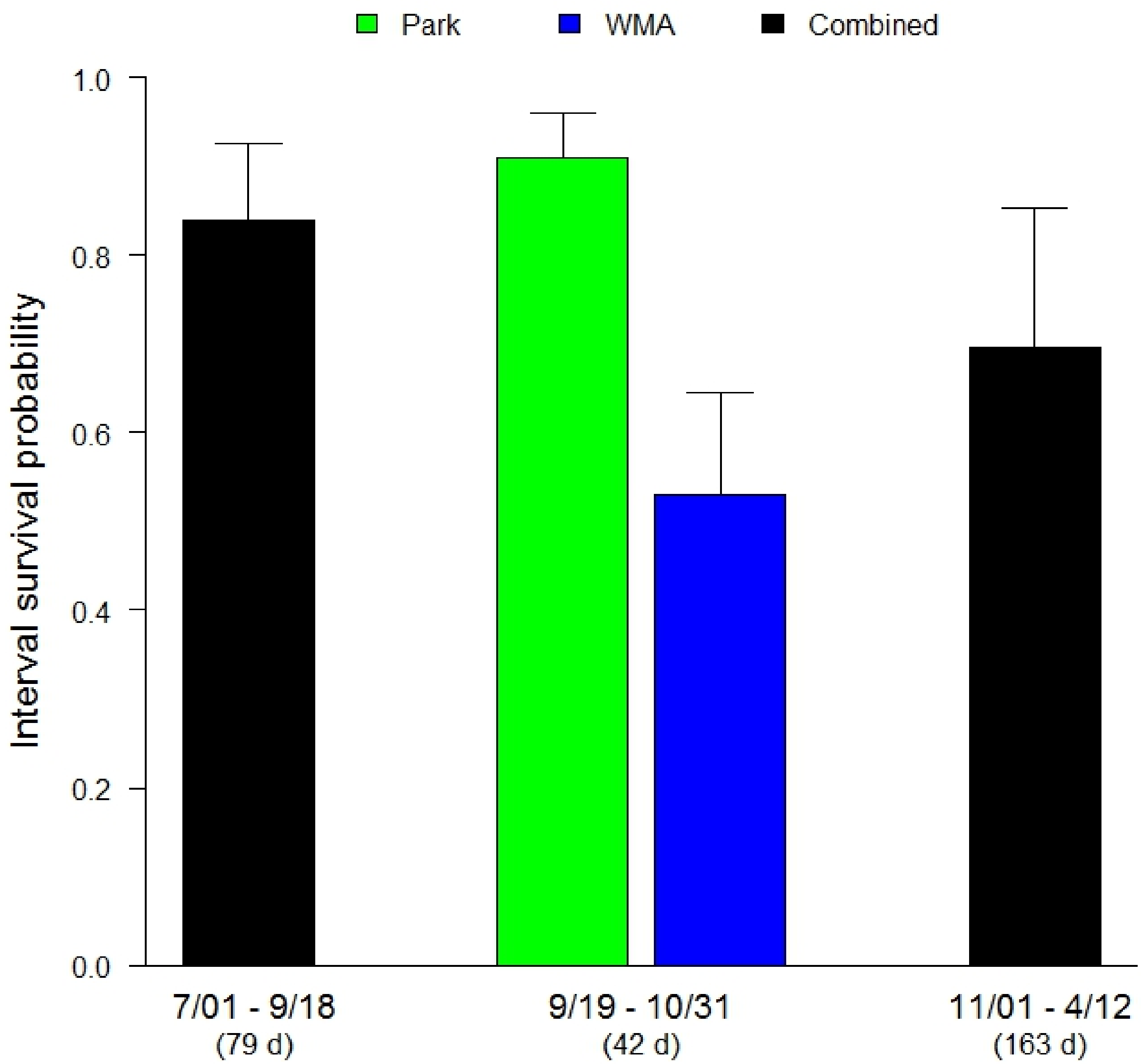

Figure 7. Estimates of combined squirrel survival (black, n = 87) and by site (green = Whitewater State Park, Minnesota (WSP, n = 43); blue = Whitewater Wildlife Management Area, Minnesota (WWMA, n = 44) during the pre-hunt time period (1 July 2015 – 18 September 2015), first 6 weeks of hunting season (19 September 2015 – 31 October 2015), and winter-spring time period (1 November 2015 – 12 April 2016).

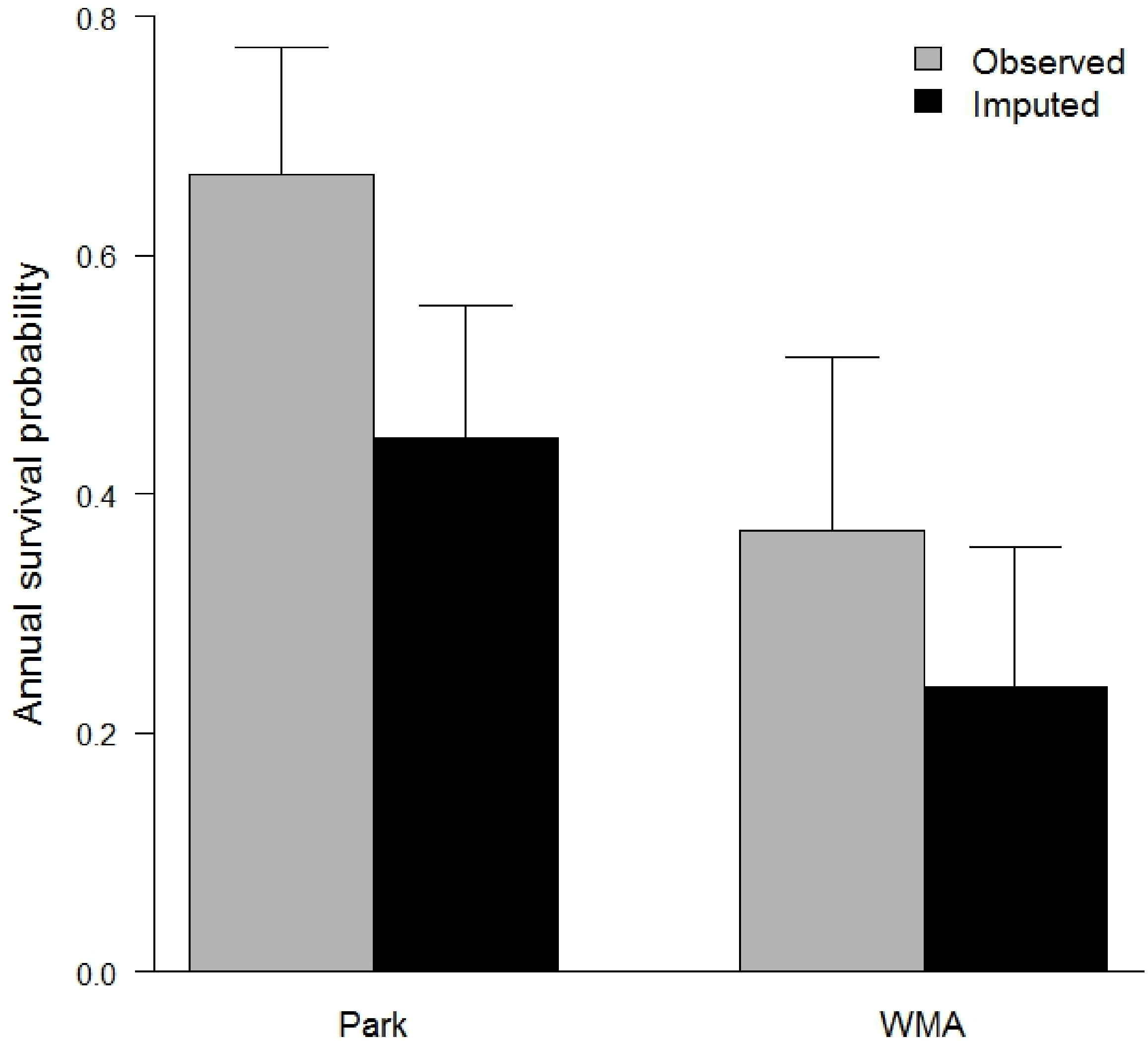

Figure 8. Imputation analysis indicating positive bias of observed annual survival probability due to non-independence of censoring and fate caused by high proportion of gray and fox squirrels with unknown fates. Sixteen of 43 and 22 of 44 squirrels had unknown fates on Whitewater State Park (WSP), Minnesota and Whitewater Wildlife Management Area (WWMA), Minnesota, respectively, during 2015-2016.