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

Ryan G. Tebo and Andrew S. Norton

SUMMARY OF FINDINGS

Squirrel hunting is a popular activity in Minnesota, but hunter perceptions of squirrel declines on publicly-owned land near the Twin Cities Metropolitan Area of Minnesota (hereafter, Metro) has led interested user groups to express concerns 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 July 2015 – 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 models that accounted for uncertainty in fates, we compared differences in annual survival, survival during the hunting season, and survival outside of the hunting season between sites. Annual survival on WWMA and WSP was 0.251 (0.146 – 0.365) and 0.493 (0.368 – 0.624), respectively. During the hunting season (mid-September – February), there was a 0.993 probability survival was higher on WSP. Survival of squirrels on WWMA was 0.492 (0.389 – 0.596), whereas survival on WSP was 0.630 (0.529 – 0.723). Outside of the hunting season, there was little difference in survival rates between the 2 sites. WWMA squirrels had a 0.709 (0.448 – 0.900) survival rate while WSP squirrels had a 0.704 (0.554 – 0.839) rate. On WWMA, we were interested in the relationship between survival and sex, age, or distance to hunter access points (e.g., parking lots, walking trails, roads) during time periods within the hunting season. We found no evidence of differences in survival between sex and age class of squirrels during this time, but distance to hunter access points did affect survival rates. Specifically, squirrels found closer to hunter access points on WWMA had lower survival rates, especially during the first 6-weeks of the hunting season ($p(\beta_{Dist}) < 0 = 0.935$). Survival of squirrels closest to hunter access points was 0.484 (0.345 - 0.624), whereas squirrels 1-km and 2-km from access points had survival rates of 0.687 (0.490 - 0.847) and 0.798 (0.437 - 0.969), respectively. Reduced survival rates due to hunting mortality were clear in this study, but exploited populations are known to respond favorably to high levels of harvest with increased recruitment following removal of a large segment of the population. Those looking to manage properties for adequate squirrel hunting opportunity from year to year need to begin by identifying pathways of recruitment by assessing the site itself as well as properties in the surrounding landscape. In the case of large tracts of land with good squirrel habitat, the site itself may be able to harbor sub-populations of squirrels that act as source populations for more heavily-harvested areas of the property. On smaller properties, the ability to restock populations from neighboring private lands or refuges could be a consideration.

INTRODUCTION

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) by affecting reproduction, immigration, emigration, or mortality. As a game species, hunting mortality is often assumed to be compensatory to natural mortality in determining overall squirrel mortality rates. However, previous research suggests hunting mortality can be additive to non-hunting mortality in other upland game species (Bruggink et al. 2013).

The number of gray and fox squirrels harvested during the 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. 1974, Nixon et al. 1975). A study in Virginia found 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. Hunting accounted for nearly 60% of the annual mortality. 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, fox squirrel annual mortality rates were 79% on a hunted site and 44% and 45% on non-hunted sites whereas 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. In a small Minnesota study, researchers found an annual survival rate of 27% for gray squirrels on a hunted site, with 74% of the mortalities due to hunting (Longley 1963). The annual survival rate was 48% the following year when the site was not hunted. Reproductive rates were 2.4 young per litter regardless of the prior year's squirrel hunt status (Longley 1963).

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 have 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). Survey results indicated more hunters in the Metro believed squirrel populations were declining (51%) than their statewide counterparts (19%). Metro hunters also indicated that they had limited access to private land, and heavy hunting pressure existed on publicly-owned land (Dunbar 2009). The MNDNR Section of Wildlife has considered changes to the squirrel season structure in the Metro based on these 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.

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.

METHODS

Capture and Handling

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 hand-picked black walnuts. To identify initial trapping locations, we used

ArcGIS 10.2 (ESRI, Redlands, California, USA) to select patches of oak habitat that looked to be suitable squirrel habitat. In these areas and 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 locations. Traps were checked at least twice per day (i.e., late morning and late evening) to reduce the amount of time squirrels remained in the traps. Trapping ceased during inclement weather.

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 8-12 h. Optimal battery life was 362 d for the 13-g collar and 302 d 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.

Tracking

Following capture, radiocollared squirrels were monitored for mortality biweekly 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 biweekly until 1 March. When a radiocollar transmitted a mortality signal, researchers used homing techniques in an attempt to recover the collar and determine the cause of mortality. Squirrels remaining on-air beyond 1 March continued to be monitored biweekly until death or battery failure.

Data Analysis

To investigate squirrel survival, we developed survival models based on traditional biostatistical survival analysis approaches (Kalbfleisch & Prentice 1980), and we accounted for uncertainty in fates using data augmentation methods in a Bayesian framework (Walsh et al. 2017). Our data were interval censored because we did not know the exact time squirrels went off-air. We partitioned monitoring intervals to fit biologically-relevant time frames, resulting in approximately 24 2-week intervals. Sources of mortality were placed into 4 categories: harvest, other (natural), dropped collar, and battery failure. Because we included dropped collar and battery failure as mortality sources, this allowed us to forgo assumptions of censoring being independent of fate. To account for uncertainty in fate, we incorporated a data augmentation technique that assigned fates for each Markov chain Monte Carlo iteration based on prior predictive probabilities based on the belief the fate was associated with a specific cause (Walsh et al. 2017). For example, if a squirrel on WWMA was heard during each monitoring event but went missing following the opening weekend of the hunting season, we may assign a 0.9 probability the squirrel was harvested, and a 0.1 probability the squirrel dispersed beyond our search radius or there was a mechanical failure in the collar transmission (i.e., right-censored cause). Using this approach, we modeled yearly survival, survival during the hunting season, survival during the first 6 weeks of hunting season, and survival outside of the hunting season. We ran 3 individual chains for 100,000 iterations each, and discarded the first 50,000 iterations as burn-in. We separately evaluated the relationship between survival and site, sex, age, or distance from hunter access points during relevant time periods. For modeling survival in relation to hunter access points, we chose distances of 0-, 1-, and 2-km from access points to obtain estimates. We did not use DIC values to compare models; instead, we used beta values and credible intervals to evaluate strength of evidence of an effect and effect sizes (Heisey et al. 2010).

RESULTS

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 received radiocollars. 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)

We captured 124 squirrels (123 gray, 1 fox) 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, our trapping success was very low on both sites and we captured only 10 squirrels on each site (3564 trap checks; 0.56% capture rate). However, following this period of low capture success, we switched to fresh-picked walnuts as the main bait type. In the remaining 3 weeks of the 2015 trapping season following the change, we captured 46 and 39 squirrels on WWMA and WSP, respectively (1181 trap checks; 7.2% capture rate). When available, we used walnuts as the predominant bait-type for the remainder of the study. The preference for walnuts may have been due in part to a seasonal change in behavior where caching food became the ultimate goal of squirrels once trees began producing the year's walnut crop. Overall, our 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 definitively harvested by hunters on WWMA (Figure 3). In addition, 9 (8.65%) animals were lost to natural mortality events, 9 (8.65%) dropped their collars, 13 (12.50%) collars were unrecoverable (e.g., in a tree or inaccessible), 1 (0.96%) collar was recovered but fate was uncertain, 19 (18.27%) went missing due to unknown reasons, and 24 (23.07%) 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%) dropped their collars, 20 (19.80%) collars were unrecoverable, 8 (7.92%) went missing due to unknown reasons, and 37 (36.63%) went missing due to presumed collar battery failure (Figure 3). We removed 3 of the 107 radiocollared squirrels on WWMA from the survival analysis due to capture complications.

Of squirrels captured in 2015, all known harvest mortalities (13) occurred within the first 6 weeks of the hunting season. The last observed harvest mortality was 27 October 2015. In 2016, 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.

We placed signs throughout WWMA and at popular parking areas to inform hunters about the study and encourage them to report the harvest of any radiocollared squirrels. Additionally, we placed an ear tag that included a callback telephone number on squirrels captured in 2016. Despite these efforts, only 4 of the 29 (14%) recorded harvests were reported. We found most radiocollars from harvested squirrels 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.

We found the majority (85.29%) of unrecoverable collars in trees and particularly tree cavities. Whether these squirrels died or dropped their collars is unknown; however, we categorized a majority of these losses as dropped collars. Examples that led us to this presumption include numerous cases where collars fluctuated between mortality and normal signal, an indication that the collars were still subject to movement in the tree cavities. On another occasion, a collar was emitting a mortality signal until researchers reached the tree, at which point the collar switched out of mortality mode and an uncollared squirrel exited a cavity in the tree. As a final example, 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.

Squirrel Survival

Annual survival of squirrels on WWMA and WSP was 0.251 (0.146 – 0.365) and 0.493 (0.368 – 0.624), respectively (Figure 4). During the hunting season (mid-September – February), there was a 0.993 probability survival was higher on WSP. Survival of squirrels on WWMA was 0.492 (0.389 – 0.596) whereas survival on WSP was 0.63 (0.529 – 0.723) during the season. Outside of the hunting season, survival rates were similar between the sites. WWMA squirrels had a 0.709 (0.448 – 0.900) survival rate and WSP squirrels had a 0.704 (0.554 – 0.839) survival rate.

On WWMA, we were interested in the relationship between survival and sex, age, or distance to hunter access points during time periods within the hunting season. During the first 6 weeks of the hunting season and during the entire hunting season, we found little evidence that male and female survival differed ($p(\beta_{Sex}) > 0 = 0.542$ and 0.777, respectively). Male survival during the first 6-weeks of the hunting season was 0.553 (0.419 – 0.682) and female survival was 0.563 (0.428 – 0.693). Male and female survival during the entire hunting season was 0.372 (0.249 – 0.504) and 0.435 (0.304 – 0.568), respectively.

We found very little evidence that differences in age class affected survival rates on WWMA during the first 6 weeks of the hunting season and during the entire hunting season ($p(\beta_{Age}) > 0 = 0.518$ and 0.608, respectively). Adult survival during the first 6 weeks of the hunting season was 0.590 (0.452 – 0.722) and juvenile survival was 0.587 (0.442 – 0.723). Adult and juvenile survival during the entire hunting season was 0.430 (0.296 – 0.569) and 0.407 (0.273 – 0.549), respectively.

Our results indicated that squirrels found closer to hunter access points on WWMA had lower survival rates, especially during the first 6 weeks of the hunting season ($p(\beta_{Dist}) < 0 = 0.935$). Survival of squirrels closest to hunter access points was 0.484 (0.345 - 0.624), whereas squirrels 1-km and 2-km from access points had survival rates of 0.687 (0.490 - 0.847) and 0.798 (0.437 - 0.969), respectively.

DISCUSSION

We found annual survival of radiocollared squirrels on WWMA was nearly half that found on WSP. Hunting mortality appeared to account for the differences found between the 2 sites, especially when examining squirrel survival during the first 6 weeks of the hunting season. Prior studies in Ohio, Illinois, and Minnesota (Longley 1963, Nixon et al. 1975, Herkert 1992, respectively) all found marked differences in annual survival rates between hunted and non-hunted sites. In Minnesota, Longley (1963) found squirrel survival was 27% when hunting was open to the public, but increased to 48% when the site remained closed to hunting the following year. Results from Longley (1963) are nearly identical to annual survival rates found on our 2 study sites. Researchers in Illinois concluded that additive mortality was occurring in heavily exploited populations, resulting in reduced squirrel numbers in successive years of high harvest (Herkert 1992).

Nixon et al. (1975) stated that squirrel numbers will decline after several years of hunting pressure when survival rates are low. When hunting mortality reduces resident squirrel numbers to such low levels, compensatory reproduction alone may not be enough to maintain fall-winter squirrel numbers (Nixon et al. 1974, Herkert 1992). With annual survival rates near 25% on our hunted site, we believe that this is unsustainable if relying on the resident squirrel population to replenish numbers from year to year. Instead, it is likely necessary for squirrels to immigrate from other areas to stabilize populations that are subject to heavy hunting mortality similar to WWMA (Nixon et al. 1974, Nixon et al. 1975, Herkert 1992). This colonization is highly dependent on nearby areas that serve as refugia or receive light hunting pressure (Herkert 1992).

The squirrel hunting season in Minnesota opens mid-September and runs through the end of February. We predicted the most detrimental time period to the squirrel population on the hunted site would be during the early months of the season. Our results support our prediction as we did not record a single known harvest beyond October during the first year of the study. The same trend continued in 2016, when the majority of confirmed hunting mortalities occurred during this same 6-week period. Similarly, significant differences in success of hunters in Ohio were found when comparing the months of September (40.1%), October (35.9%), and November (24.9%; Nixon et al. 1975). We believe once the firearm deer season began in Minnesota in early November, much of the attention shifted away from squirrels resulting in limited harvests throughout the remainder of the season. One advantage of the season beginning in mid-September is that summer-born juvenile squirrels should be weaned prior to being subject to harvest (Nixon et al. 1974). Having juvenile squirrels available to hunters for harvest would possibly provide a buffer to adult mortality once the hunting season begins (Nixon et al. 1975).

We also predicted males and juveniles would have higher mortality rates compared to females and adults due to the expanded ranges of males and likelihood of juveniles to travel longer distances to establish a home range (Barkalow 1970). However, we found no evidence for either prediction in our study. Even when hunting pressure was at its peak, we found that males only had a slightly lower survival rate than females. Similarly, juveniles had only slightly lower survival rates than adults. Nixon et al. (1975) also reported no difference in the sex ratios of squirrels shot on their huntable site across their 10-year study. Additionally, Nixon et al. (1975) found little evidence for a difference in survival between juvenile and adult squirrels during the hunting season.

The size of WWMA allowed us to model the effects of distance to hunter access points on survival rates as we were able to capture squirrels that were much less accessible to hunters (i.e., >2 km from the nearest access point) compared to squirrels captured closer to roadways and parking areas. We hypothesized that squirrel survival during the hunting season would be positively associated with distance from access points. Indeed, we found that squirrel survival steadily increased as distance from nearest access points increased. As other studies have noted, a key component for recruitment of squirrels into a population is having a source population that helps restock local populations annually (Nixon et al. 1974, Nixon et al. 1975, Herkert 1992). WWMA is large enough that many areas within the boundaries of the site may receive comparatively light squirrel hunting pressure which in turn may help with recruitment of squirrels into more heavily-hunted areas of the site. Because these areas likely exist on WWMA, we believe a huntable annual population is retained. However, very few public lands in the Metro have acreages as large as WWMA which may lead to potential problems if similar squirrel survival rates occur on these smaller tracts. Public lands that are isolated pockets of habitat with no nearby population sources are especially at risk (Nixon et al. 1974), and years of consistent harvest may be detrimental to squirrel populations on these properties.

MANAGEMENT IMPLICATIONS

Many factors cause squirrel populations to fluctuate annually. Mast abundance is one of the most important and well-documented factors in annual squirrel survival, with favorable seed crops leading to increases in survival, reductions in emigration of young squirrels, and increases in fecundity of females the following year (Nixon et al. 1975). As a result, managing squirrel populations on public lands via harvest can become challenging because these sometimes drastic fluctuations are hard to predict. However, our results show that one potential way to offset high hunting mortality is to have areas that act as refuges for squirrels. In the case of large tracts of land with good squirrel habitat, the site itself may be able to harbor sub-populations of squirrels that act as source populations for more heavily harvested areas of the property. On smaller properties, the ability to restock populations from neighboring private lands or refuges would be a necessity (Nixon et al. 1974).

On the surface, a 25% annual survival rate of squirrels on our hunted site seems lower than what would be considered sustainable. However, exploited populations are known to respond favorably to high levels of harvest with increased recruitment following removals of a large segment of the population (Allen 1954, Jordan 1971, Herkert 1992), and rapid recolonization can occur if a source population of squirrels is available nearby (Herkert 1992). Using this information, managers can identify pathways of recruitment by assessing surrounding private lands or refuges. Doing so will allow them to make management-unit decisions regarding season length and harvest strategies so that squirrel hunting opportunities are retained across time.

ACKNOWLEDGMENTS

We would like to thank the employees at Whitewater State Park and Whitewater WMA, especially Brent Anderson, Colin Wright, Don Nelson, Christine Johnson, Dave Dahl, and Steve Elringer for their 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

Allen J. M. 1954. Gray and fox squirrel management in Indiana. Second edition. Indiana Department of Conservation Division of Fish and Game Pittman-Robertson Bulletin 1, Indianapolis, Indiana, US.

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.

Bruggink, J.G., E. J. Oppelt, K.E. Doherty, D.E. Andersen, J. Meunier, and R. S. Lutz. 2013. Fall survival of American woodcock in the western Great Lakes region. Journal of Wildlife Management 77:1021-1030.

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., E. E. Osnas, P. C. Cross, D. O. Joly, J. A. Langenberg, and M. W. Miller. 2010. Rejoinder: sifting through model space. Ecology 91:3503-3514.

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.

Jordan, J.S. 1971. Dispersal period in a population of eastern fox squirrels (*Sciurus niger*). U.S. Department of Agriculture, Forest Service Research Paper NE-216, Broomall, Pennsylvania, USA.

Kalbfleisch, J.D. and R.L. Prentice. 1980. The statistical analysis of failure time data. John Wiley, 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.

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., A. S. Norton, D. J. Storm, T. R. Van Deelen, and D. M. Heisey. 2017. Using expert knowledge to incorporate uncertainty in cause-of-death assignments for modeling of cause-specific mortality. Ecology and Evolution 8:509-520.

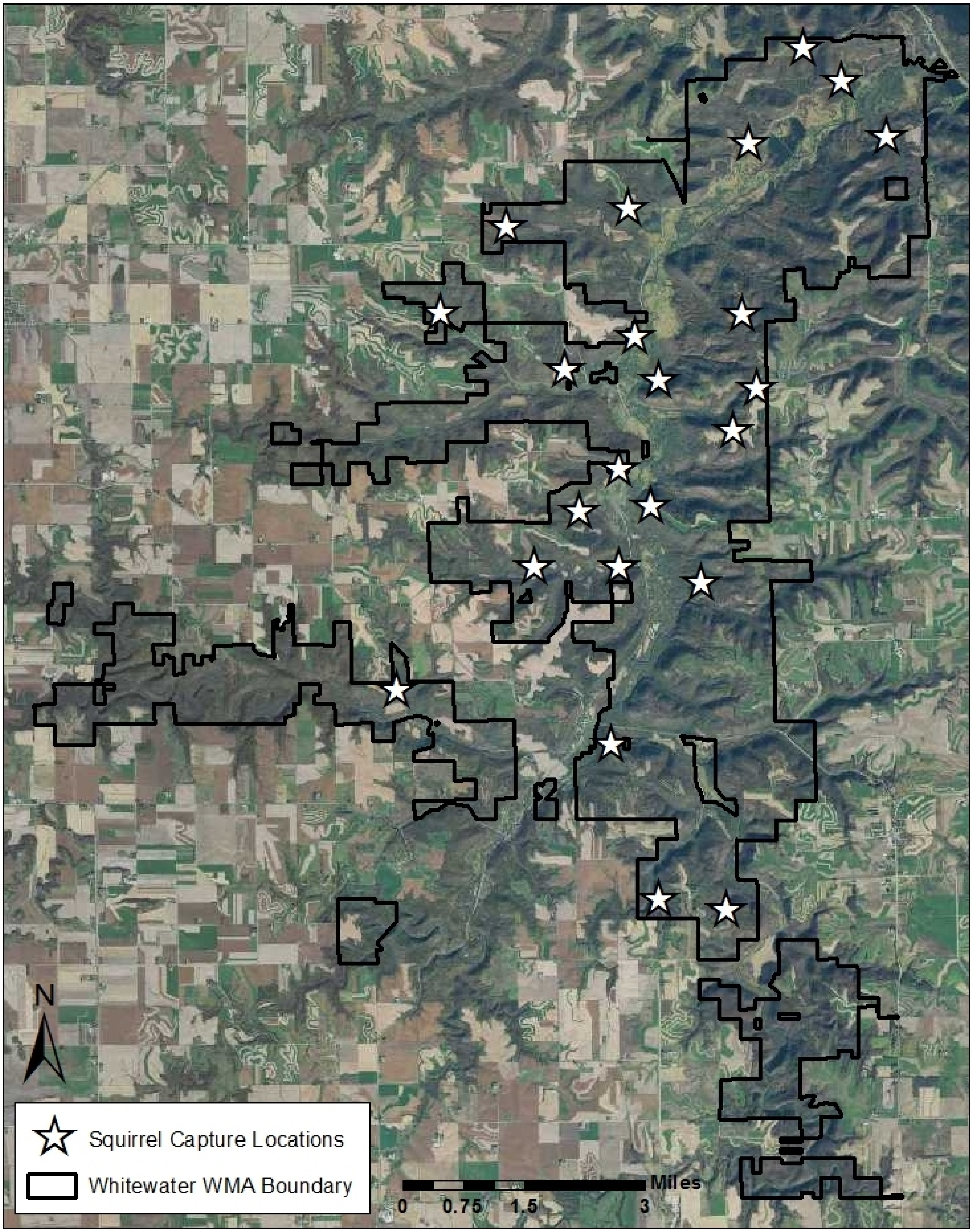

Figure 1. Capture locations for gray and fox squirrels (as indicated by white stars) during 6 July 2015 – 14 September 2016 in Whitewater Wildlife Management Area, Minnesota (outlined in black).

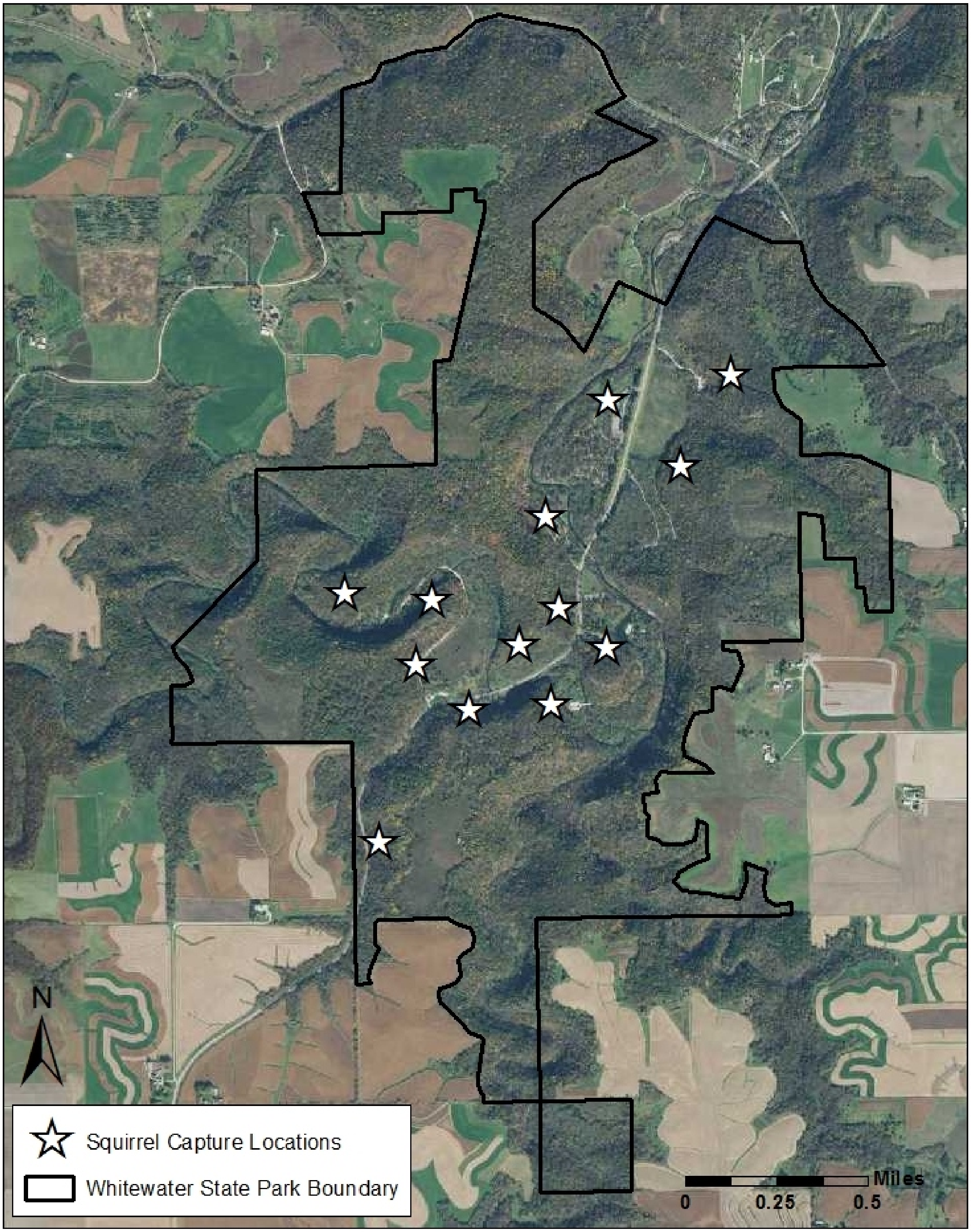

Figure 2. Capture locations for gray and fox squirrels (as indicated by white stars) during 4 August 2015 – 15 September 2016 in Whitewater State Park, Minnesota (outlined in black).

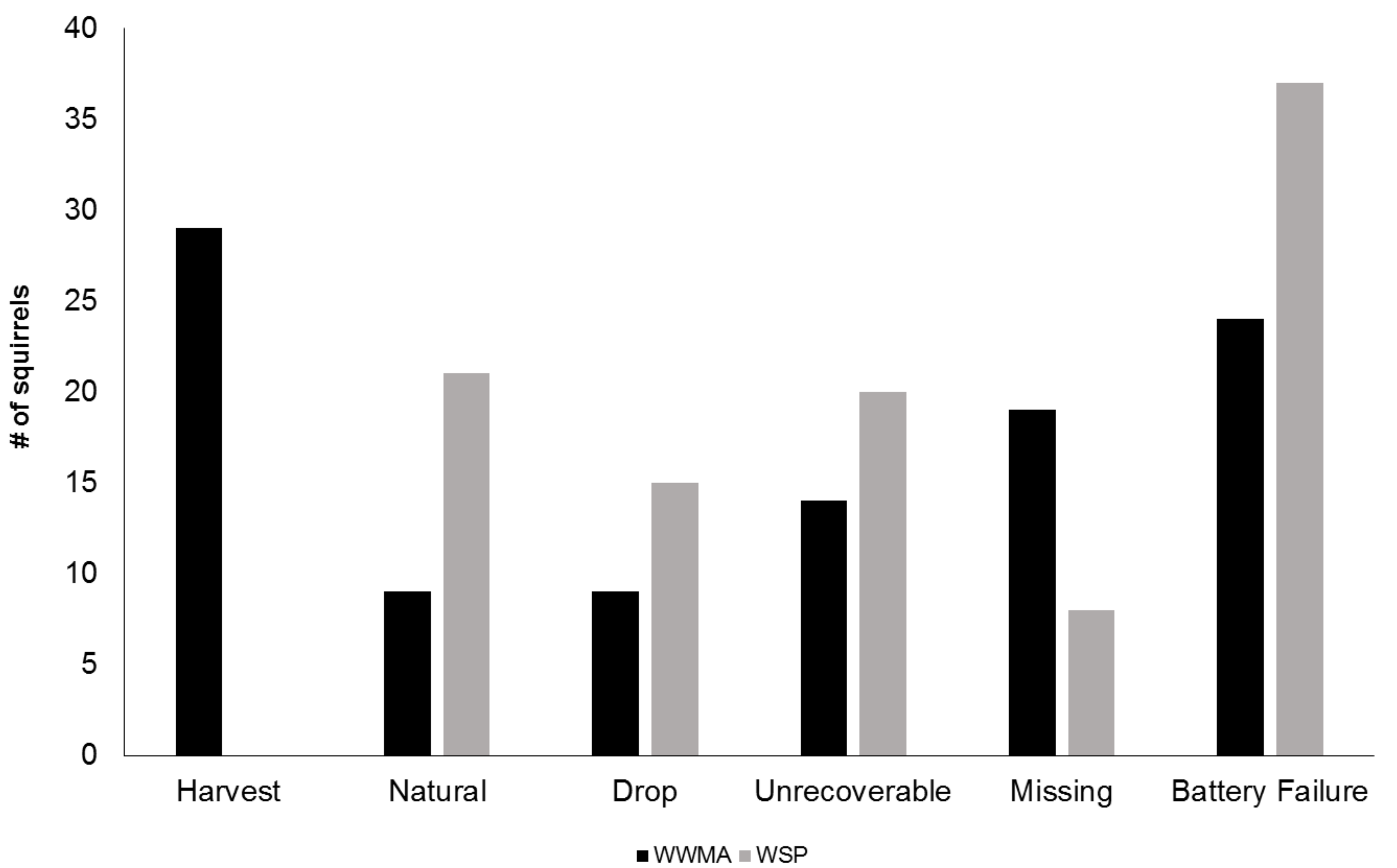

Figure 3. Fates of gray and fox squirrels in Whitewater Wildlife Management Area (*n* = 104; black bars) and Whitewater State Park (*n* = 101; gray bars), Minnesota during 2015 – 2017.

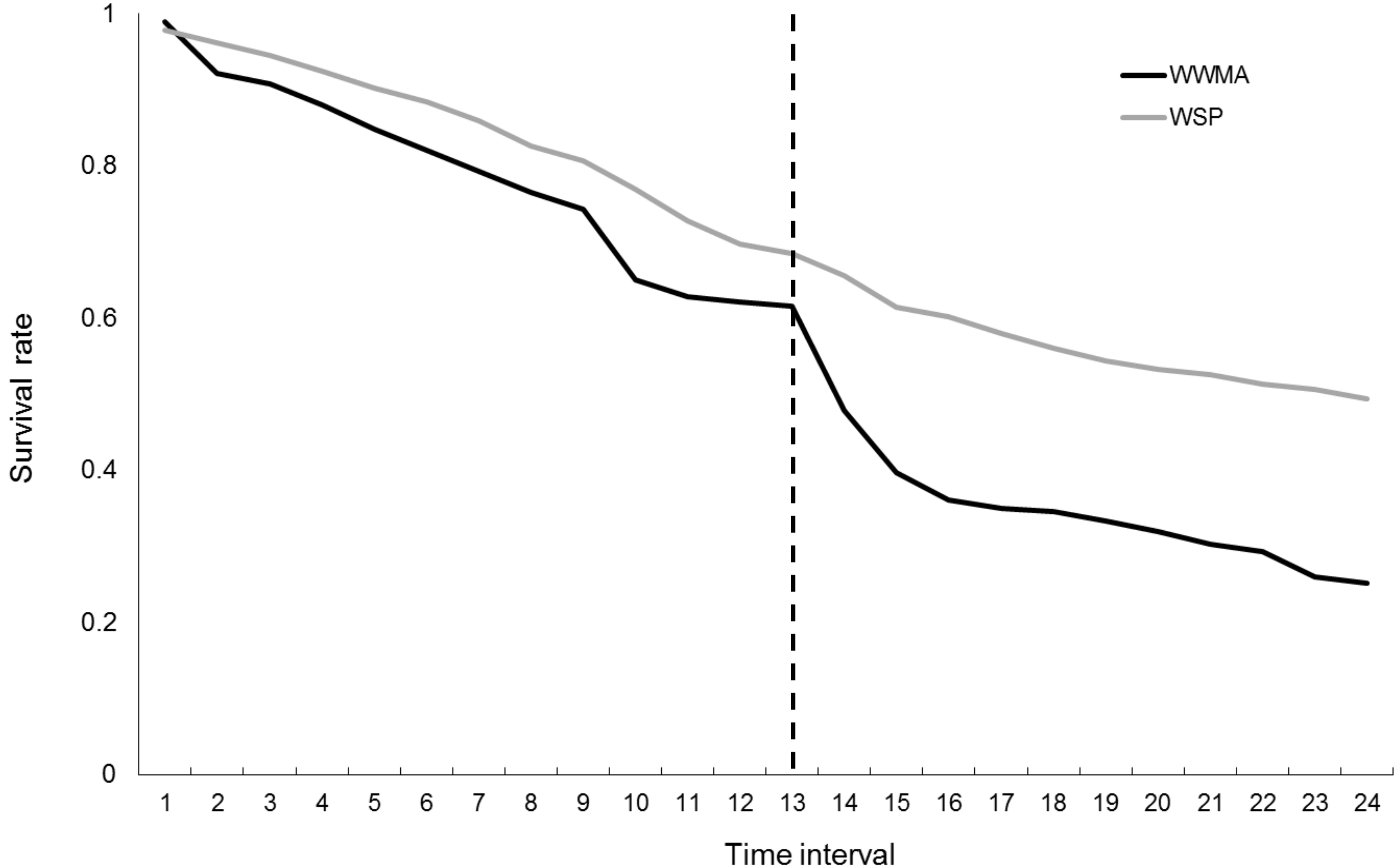

Figure 4. Annual survival curve of gray and fox squirrels on Whitewater Wildlife Management Area (*n* = 104; black line) and Whitewater State Park (*n* = 101; gray line), Minnesota during 2015 – 2017. Intervals are each approximately 2 weeks in length. The vertical dashed line indicates the beginning of the squirrel hunting season.