GAME REPORT

Evaluation of elk movement, nutritional condition, pregnancy rates, and calf survival in the southern Black Hills of South Dakota

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ABSTRACT

Studies indicate that annual survival of elk (*Cervus canadensis nelsoni*) calves varies considerably when compared to the constant rates of adult female survival. Collecting vital rates of calves and adult females and understanding how such rates influence population growth are important for resource managers. Our case investigation was stimulated by a decreasing elk population in Custer State Park and adjacent management units with a focus on evaluating nutritional condition of dams, fecundity, and calf recruitment. We captured, radio-marked, and monitored 58 female elk ≥2 years of age, 125 calves, and 14 yearlings. Pregnancy rates of female elk aged 2-7 years (prime-aged) varied from 0.92 to 1.00 (SE = 0.00-0.013) and 0.71 to 0.90 (SE = 0.015-0.031) for female elk aged 8+ years (old-aged). Annual survival of female elk aged 2-7 years varied from 0.76 to 0.95 (SE = 0.045-0.085) and annual survival for female elk aged 8+ years varied from 0.79 to 0.90 (SE = 0.069-0.098). Survival was highest for adults the final year of the study and steadily increased every year of the study for prime-aged females. Annual survival of calves varied from 0.07 to 0.27 (SE = 0.042-0.081). Most cause-specific mortality for adult female elk was from hunting (7%) and most cause-specific mortality for calves was from predation by puma (*Puma concolor*) (63%). Winter nutritional condition of dams was on the lower end of the range for studied populations, but does not appear to influence demographics. Daily survival of calves was a function of both age and quadratic time trend. A high percentage of calves (26%) were predated during the hiding phase (≤5 days age), and most calves (71%) were predated when <60 days of age. We demonstrated that predation by puma was the most important

proximate mortality factor for elk calves from birth through August in the southeastern portion of the Black Hills. Activities that limit puma predation during parturition and the following summer months may benefit elk calf survival. However, reducing female elk hunting harvest appears to be the most effective technique to improve elk population demographics in our study area. We found no evidence of differential movements based upon corresponding winter home range size between elk of higher and lower nutritional condition. Winter fecal glucocorticoid (FG) hormone levels appear to be in the normal range but summer FG hormone levels appear to be higher during our study when compared to data collected in 1995-97. Higher stress metabolite levels can be associated with increased human activity and decreasing the amount of human disturbance such as providing area closures in important calving areas may provide disturbance buffers for elk during the summer months.

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INTRODUCTION

With large herbivores there has been emerging knowledge that vital rates of low elasticity can sharply influence λ values if they are highly variable (Mills et al. 1999, Wisdom et al. 2000, Coulson et al. 2005, Raithel et al. 2007). Long-term investigations of large herbivores reveals annual survival of young varies considerably due to disparate environments and changes in cause-specific mortality sources when compared to the constant rates of adult female survival (Gaillard et al. 1998, Gaillard et al. 2000). Recruitment of juveniles can be the most variable vital rate affecting population growth of elk (Raithel et al. 2007, Harris et al. 2008, Sargeant et al. 2011). Elk (*Cervus canadensis nelsoni*) calf survival demonstrates a high level of variability compared to relatively constant rates of adult female survival and calf elk survival can explain as much as 4 times more of the variation in λ than adult female survival (Wisdom and Mills 1997, Wisdom et al. 2000, Mills et al. 2001, Raithel et al. 2007, Griffin et al. 2011). Because adult female survival have a strong effect on population dynamics managers typically closely monitor and manipulate human harvest, particularly in areas with abundant or diverse carnivores (Brodie et al. 2013).

Other factors involved with survival and reproduction of elk include habitat quantity and quality which can be indexed through nutritional condition (Kohlmann 1999, Parker et al. 1999, Cook 2002, Cook et al. 2004). Timing of parturition, calf birth weight, gender of calf, and age of calf may influence calf survival and elk population dynamics (Smith and Anderson 1996, Singer et al. 1997, Smith et al. 2006, White et al. 2010). Associations among neonate survival and resource availability can be

confounding when predation is a pronounced source of mortality (Gasaway et al. 1983, Boutin 1992).

Predation can influence elk demographics (Rearden 2005, Rearden et al. 2011, Sargeant et al. 2011) and some case studies have found predator reductions can improve survival of ungulate neonates (Gasaway et al. 1983, Boutin 1992, Hayes et al. 2003, White et al. 2010). Several studies documented predator reductions did not influence ungulate neonate survival (Ballard et al. 2001, Ballard et al. 2003).

A study of neonatal mortality of elk related to climate and predator community composition indicated mortality hazards were significantly lower in systems with only coyotes (*Canis latrans*), puma (*Puma concolor*) and black bears (*Ursus americanus*) compared to higher mortality hazards experienced with gray wolves (*Canis lupus*) and grizzly bears (*Ursus horribilis*) (Griffin et al. 2011). Further, only bear predation appeared additive and occurred earlier than other predation events, which may render later mortality by other predators compensatory as calves age (Griffin et al. 2011).

Elk may respond negatively to human disturbance with displacement from preferred habitats (Edge and Marcum 1985), influence movements particularly in relation to roads (Millspaugh et al. 2001, Montgomery et al. 2013), and potential diet changes (Morgantini and Hudson 1985). Elevated stress may influence immunity to disease, survival, and reproductive performance (Dunlap and Schall 1995, Verme and Doepker 1988, Wingfield 1988). Therefore, obtaining a metric of physiological responses of elk to any disturbance is important to quantify and non-invasive techniques such as fecal cortisol metabolites can measure stress responses in free-ranging animals (Miller et al. 1991, Creel et al. 1997, Wasser et al. 1997, Wasser et al. 2000, Millspaugh et al. 2001).

Our case investigation was stimulated by a decreasing elk population with poor elk calf recruitment in Custer State Park (CSP) and adjacent management units. Estimates of roughly 1,100 elk were observed in 2003 and declined to under 400 in 2013 in CSP (South Dakota Department of Game, Fish, and Parks [SDGFP], unpublished data). Harvest of antlerless elk was significant in CSP from 2002-2006 and annual harvest ranged from 82-127 elk over those 5 years and certainly was a factor contributing to the population decline (South Dakota Elk Management Plan 2015-2019). Including previous antlerless harvest, initial hypotheses related to this decreasing elk herd were focused on nutritional condition of dams, fecundity, and poor calf recruitment, given calf:cow ratios in CSP were below 0.29 since 2006 (SDGFP, unpublished data).

Objectives

1. Determine nutritional condition during winter and pregnancy rates of reproductive aged female elk.
2. Determine calf and adult female survival and cause-specific mortality rates.
3. Quantify stress hormone metabolites in reproductive aged cow elk.
4. Quantify movements of adult female elk in CSP and adjacent hunting units.
5. Compare movements between elk of excellent condition and elk in poor condition.

STUDY AREA

The study was in Custer and Pennington counties of South Dakota in the southern and central parts of the Black Hills physiographic region (Flint 1955). Land ownership included private and public land including CSP which encompasses 286 km^2 in the central part of the study area (Fig. 1). Elevations ranged from 1108 m to 2208 m. CSP

average road density was 2.1 km/km^2 (CSP Land Cover GIS Database, Custer, SD 2014) and the Black Hills National Forest averaged 3.2 km/km^2 (T. Mills, GIS Specialist, Black Hills National Forest, personal communication). The climate was semiarid and varied northwest to southeast with average annual precipitation ranging from 52-54 cm and average annual temperature ranging from 6-9º C across the study area (National Climatic Data Center 1989-2011). Vegetation varies considerably from northwest to southeast where forests dominate the landscape at higher elevations and grasslands dominate the southeastern portion of the study area. The forested portions of study area were dominated by ponderosa pine (*Pinus ponderosa*) forest. Smaller patches of deciduous forest were characterized by aspen (*Populus tremuloides*), bur oak (*Quercus macrocarpa*), and paper birch (*Betula papyrifera*). Wildfire and mountain pine beetle (*Dendroctonus ponderosae*) infestations created natural disturbance throughout the study area. Western snowberry (*Symphoricarpos occidentalis*) and common juniper (*Juniperus communis*) were common shrubs in the understory of pine forests (Hoffman and Alexander 1987). The eastern 1/3 of the study area was primarily a prairie ecosystem with native mixed-grass prairie, agriculture fields and prairie woodlands comprised of green ash (*Fraxinus pennsylvanica*), cottonwood (*Populus deltoides*), and boxelder (*Acer negundo*). Common native grasses in the mixed-grass prairie included needle and thread (*Stipa comata*), western wheatgrass (*Pascopyrum smithii*), blue grama (*Bouteloua gracilis*), little bluestem (*Schizachyrium scoparium*), and prairie dropseed (*Sporobolus heterolepis*; Larson and Johnson 1999).

Potential non-human predators of elk included coyotes, puma, and bobcats (*Felis rufus*). Adult and sub-adult population estimates of puma for the Black Hills of South

Dakota in 2011 were 124–435, 125–291 in 2012, and 111-206 in 2013 (SDGFP 2014, unpublished data). Elk numbers in CSP and adjacent lands decreased from 900–1,100 in 2005 to 300–500 in 2011 (SDGFP, unpublished data). CSP was surrounded by a 1.5–1.8 m-tall bison-proof fence, but elk could move in and out of CSP and were part of a larger Black Hills population. CSP was bordered to the south by Wind Cave National Park, on the west and north by Black Hills National Forest, and on the east and north by private lands.

METHODS

Capture and Radio-telemetry

We captured female elk using tranquilizer dart guns from helicopters (QuickSilver, Peyton, Colorado) during February 2011–2013. Elk were sedated using butorphanol, azaperone, and medetomidine sedation protocol (Mich et al. 2008). After elk were sedated, we blindfolded and fitted elk with Global Positioning System (GPS)–very high frequency (VHF) telemetry collars (Telonics Inc., Mesa, AZ., Advanced Telemetry Systems Inc., Isanti, MN). During captures, roughly 18 ml of blood was drawn by venipuncture and centrifuged. Cow elk were inspected for pregnancy using rectal palpation (Greer and Hawkins 1967, Vore and Schmidt 2001). Females suspected of being pregnant were fitted with a vaginal implant transmitter (Advanced Telemetry Systems, Isanti, MN). Additionally, serum from blood was also used to verify pregnancy after being analyzed for protein B specific for pregnancy via radioimmunoassay (Noyes et al. 1997). Vaginal implant transmitters (VIT) were used to determine parturition dates and locate calves post-partum (Barbknecht et al. 2009). A veterinarian assisted for testing for pregnancy and implanting transmitters.

We located female elk using radio-transmitters by direct observation and triangulation with hand-held yagi antenna daily each week from 1 April - 31 October. From 1 November – 31 March, elk were located 5 days per week. Starting 1 May, we closely monitored cow elk behavior and if females were located alone or started to localize in one area we located those elk twice daily and checked VIT signals in morning and evening hours. Once the VIT signal indicated a calf was born we used one investigator with telemetry gear to locate and visually see the female that had the calf. After the female elk was visually located additional investigators were brought into the area to begin searching for the calf. The group of investigators searched the location of the female elk in a grid-like manner to find the hiding calf. Once found, the calf was fitted with an expandable VHF radio-collar (Advanced Telemetry Systems, Isanti, MN). We monitored calf survival daily through 31 October, and 5 days per week the rest of the year. We recorded the gender, collected blood and an ear notch, measured chest girth and body length, and weighed the calf to the nearest 0.1 kg. Birth date of the calf was estimated on when the VIT signal indicated parturition. Additionally, we evaluated the appearance of umbilicus and hoof formation (Johnson 1951) to confirm the initial estimate of timing from the VIT signal.

All handling, marking, and monitoring procedures were approved by the South Dakota State University Research Committee (Animal Care and Use Committee Approval Number 11-012A).

Physical Metrics and Nutritional Condition

We collected all live-animal measurements while elk were anesthetized during winter captures. We aged females as adults (>20 months) or subadults (≤20 months) by

extracting an upper canine tooth and cementum annuli were evaluated in a lab (Matson's Lab, Milltown Montana; Hamlin et al. 2000). A veterinarian assisted with extraction of teeth. We measured chest girth with a cloth tape measure. We collected rump nutritional condition scores (rBCS) as described for elk by Cook et al. (2001a). We collected MAXFAT measurements as described by Stephenson et al. (1998, 2002) and Cook et al. (2001a, 2001b, 2007) via ultrasonography using a University Medical Systems 900 ultrasonagraph with a 5.0-MHz, 7.0-cm probe (Universal Medical Systems, Bedford Hills, NY). Brightness mode real-time ultrasonography generates gray scale 2-dimensional images that readily distinguish tissue layers (Stephenson et al. 1998). We estimated nutritional condition during winter using the LIVINDEX, an arithmetic combination of rBCS and MAXFAT (Cook et al. 2010). We estimated live weight using chest girth and a regression equation (Millspaugh and Brundige 1996). We used program R (R Version 3.01.0, 2014, www.R-project.org/, accessed 25 Apr 2014) to conduct Analysis of Variance (ANOVA) to compare nutritional condition among years.

Vital Rates and Cause-specific Mortality

We estimated pregnancy rates for prime-aged adult (2-7 years) and old adult (8+) females from our winter captures using rectal palpations and females were verified pregnant using serum from blood and protein B. We estimated annual survival of calf elk from born date through 365 days, yearling survival (2nd year of life), survival of female elk aged 2-7 (prime-aged), and survival of female elk aged ≥8 (old-aged) from capture date in February through 365 days each year. Annual survival parameters for radio-telemetry data were generated using a daily known-fate-model routine (Nest Survival module) in Program Mark (White and Burnham 1999). We also provide 90-day survival

estimates for calves each year. We right-censored individuals due to collar loss or unknown fate if this occurred before the 365-day period ended. We tested for differences in annual survival among years for prime-aged adults, old-aged adults, and calves using chi-square procedures described by Sauer and Williams (1989) using the program CONTRAST (Hines and Sauer 1989).

We determined cause-specific mortality of elk using several diagnostics. When a mortality signal was detected we investigated the mortality, and the carcass was located, photographed, and necropsied immediately. Mortality sites were examined for predator sign. We classified cause of mortality as: 1) predation when evidence at the mortality site indicated that the elk had been alive when attacked (e.g., hemorrhaging), (2) hunter harvest, 3) dystocia (Lehman et al. 2012), 4) vehicle collision, 5) sepsis infection, 6) abnormal birth, 7) poor body condition, and (8) unknown if mortality could not be determined.

Predation-caused mortalities were further classified to species of predator based on characteristics of predator kills (O'Gara 1978). Further, we investigated the area for cache sign, drag marks, scat, and searched shrubs, downed woody debris, and other vegetation at the site for hairs of predators. Remains of elk were necropsied for signs of hemorrhaging and bite marks, and bite marks were measured to the nearest mm. Saliva, predator hairs, and scat were sent to the Laboratory for Ecological, Evolutionary and Conservation Genetics at the University of Idaho for mitochondrial DNA analysis to determine species presence at the predation site (Onorato et al. 2006). The species of origin for each sample was determined using mitochondrial DNA fragment analysis (De Barba et al. 2014). Infrared cameras were also placed at predation sites to photograph

and determine predator species returning to the carcass immediately following the predation event. We classified the mortality as unknown predation if we observed hemorrhaging but could not identify any additional predator characteristics.

Additionally, we collected organs, blood, and tissue for disease analysis at a diagnostic lab. All elk that had viable brain tissue remaining were tested for chronic wasting disease. All elk that had viable blood and spleen organs were tested for epizootic hemorrhagic disease. Animals that tested positive for bacteria species in lymph nodes were classified as sepsis infection (Williams and Barker 2001). Elk that lacked subcutaneous, mesenteric, and kidney fat and had femur marrow that appeared translucent but gelatinous and tested negative for infection or disease were classified as poor body condition (Sargeant et al. 2011).

We estimated cause-specific mortality using cumulative incidence functions (CIF; Heisey and Patterson 2006). We used the "wild1" package of Program R (Sargeant 2014) to estimate CIFs which allow the estimation of cause-specific mortality in the presence of competing mortality factors (Heisey and Patterson 2006). Competing factors occur when an animal is exposed to more than one potential cause of mortality, and the incidence of one event prevents others from occurring.

Calf Elk Survival Modeling

We developed a set of a priori biological hypotheses used to construct specific models to explain variation in daily survival of calves. We outline our hypotheses about the eight sources of variation we incorporated into our models:

1) Year. Annual variation can result from influences such as changes in weather patterns or variation in predator composition or numbers, and many other factors. We

attempted to account for annual variation that was not specifically addressed in any other sources of variation outlined below.

2) Gender of calf. We were interested in a possible gender bias because a maternal investment in male calves indicates greater maternal nutritional condition (Kohlmann 1999) which may have implications for subsequent survival. Gender can be an important predictor of calf survival and a study in Wyoming reported that summer survival of female calves was 83% greater than males (Smith et al. 2006).

3) Age of calf. Calves are more at risk for predation at early ages versus late (Smith and Anderson 1996, Singer et al. 1997, White et al. 2010). We wanted to reduce confounding age effects and temporal variation in daily calf survival rates by monitoring elk calves of variable ages across the entire calving season.

4) Weight of calf. Birth mass has been documented to be an important predictor of calf survival and heavier calves may have higher survival than lighter calves (Singer et al. 1997, Smith et al. 2006, White et al. 2010).

5) Previous winter nutritional condition of dam. Nutritional condition reveals adequacy of forage quantity and quality which may strongly effect reproduction and survival (Kohlmann 1999, Parker et al. 1999, Cook 2002, Cook et al. 2004).

6) Timing of parturition. Summer calf survival can decline with later birth dates (Clutton-Brock et al. 1987, Singer et al. 1997).

7) Harvest of puma. Predator reductions can improve survival of ungulate neonates (Gasaway et al. 1983, Boutin 1992, Hayes et al. 2003). Experimental harvest of black bears (*Ursus americanus*) and puma increased elk calf survival in Idaho (White et al. 2010).

8) Temporal variation during calving. Based on observations made from previous research (Smith and Anderson 1996, Singer et al. 1997, White et al. 2010) the assumption of constant within-season calf survival seemed unlikely; we evaluated three potential time trends and first we fit a simple constant daily survival model to our data. We then evaluated a linear time trend in which we hypothesized that daily survival would increase across the calving season because older calves are less vulnerable to predation (Smith and Anderson 1996, Singer et al. 1997, White et al. 2010). We also fit a quadratic model that allowed daily calf survival to track a curvilinear time trend.

Daily survival of calves was modeled with several biologically relevant factors using a daily known-fate-model routine (Nest Survival module) in Program Mark (White and Burnham 1999). We used the product of daily calf survival rates across the 365-day annual survival period as an estimate of calf survival. During our study, elk calves were born from 9 May to 4 September, regardless of year, and to encompass the entire annual period for all calves resulted in 425 days and 424 estimates of daily calf survival for the age covariate. Additional individual covariates included year, gender, weight of calf (kg), nutritional condition from the previous winter for each calf's dam, number of puma harvested from the study area for the previous hunting season, and timing of parturition. For timing of parturition we set the median date of parturition equal to 0 for each year. Then for each calf we used the number of days deviating from 0. For example, if the calf was born on the median date we gave it a value of "0", if it was born 10 days before or after the median date we gave it a value of "10".

We limited our analyses to a small set of 10 models (see Table 1). Our simplest model (Model 1) was a single daily calf survival rate estimated using the logit link. We

then modeled daily survival with individual covariates separately (Models 2-8). We fit two additional additive models with the age covariate, one with a linear and one with a quadratic time trend on daily nest survival (Models 9 and 10). We ranked and compared models using Akaike's Information Criterion and the Information-Theoretic approach (Burnham and Anderson 2002).

Elk Movements

We used the "BBMM" package (Nielson et al. 2014) in Program R to fit a Brownian bridge movement model (BBMM) to observed elk locations in space and time. We estimated a 99% contour and area of utilization from mid-February, or at date of capture, through the day before parturition for each radio-marked elk. We fit BBMMs to animal location data obtained by a Global Positioning System (GPS) from satellite radio-transmitters. The BBMM package provides an empirical estimate of the movement path of an animal using location data obtained at short time intervals. The Brownian bridge probability density connecting each pair of successive locations is an estimate of the relative time spent in an area during the time interval between each location.

We compared winter BBMM areas between elk with higher nutritional condition (≥4.0 body fat %) and elk with lower nutritional condition (<4.0 body fat %). Within each year, we used program R (R Version 3.01.0, 2014, www.R-project.org/, accessed 25 Apr 2014) to conduct Analysis of Variance (ANOVA) to compare BBMM areas of use between elk categorized as either high or low in nutritional condition.

Additionally, we provide figures for GPS collar waypoints annually for each elk where we had the data in relation to each female elk's winter capture site and parturition location. We generated calving area polygons using 80% fixed kernel isopleths around

parturition locations. We also computed the linear distance (km) for individuals from each winter capture location to the subsequent parturition location. We provide means, standard errors, and ranges for parturition dispersal distances from capture locations.

Stress Hormones

Fecal samples were collected from individually radio-collared elk during winter captures (February) and during summer (August) in areas where we observed radio-marked elk to evaluate fecal glucocorticoid (FG) hormone. Because hormones may be distributed unevenly in feces, we homogenized each sample in the field prior to freezing (Wasser et al. 1988, Wasser et al. 1996). We froze samples at –20˚ C, typically within 2 hours of collection (Millspaugh et al. 2001).

Frozen fecal samples were thawed and we placed ~10 g subsample in a lyophilizer for 4 days. Once the samples were freeze-dried, we ground them, sifted each through a stainless steel mesh to remove large particles, and thoroughly mixed them. Freeze-drying and grinding preserved FG, controlled for dietary changes in steroid excretion (Wasser et al. 1994), and allowed for thorough mixing of the sample prior to extraction (Wasser et al. 1996). We extracted glucocorticoids from feces using a modification of Schwarzenberger et al. (1991). We placed dried feces (0.2 g) in a test tube with 2.0 ml of 90% methanol and vortexed at high speed in a multi-tube pulsing vortexer for 30 minutes. Samples were then centrifuged at 2,200 rpm for 20 minutes, and the supernatant was saved and stored at –20˚ C until assayed (Wasser et al. 2000).

We compared FG metabolite (ng/g) concentration levels from our study with previous levels taken in CSP from 1995-1997 by evaluating overlapping confidence intervals (Millspaugh et al. 2001).

RESULTS

We captured and radio-marked 58 female elk ≥2 years of age with helicopters during winter and 125 calves during calving, 2011-2013. For yearlings, 14 were monitored for annual survival one year after they survived their initial year of life as a calf.

Physical Metrics and Nutritional Condition

Average age of females monitored during the study was 7.3 years (SE = 0.3) (Table 2). Metrics such as chest girth and estimated body weight varied little among years. Winter nutritional condition differed among years ($F_{2, 120} = 6.25$, $P = 0.003$), and nutritional condition was highest in 2012 and lowest in 2013 (Table 2).

Vital Rates and Cause-specific Mortality

Pregnancy rates of female elk aged 2-7 years (prime-aged) varied from 0.92 to 1.00 and 0.71 to 0.90 for female elk aged 8+ years (old-aged) (Table 3). For survival, we right censored 2 adult female elk for survival analysis in 2011, 0 in 2012, and 0 in 2013. For calves we right censored 12 in 2011, 7 in 2012, and 5 in 2013. Loss of calf collars to barbed wire fences and early expansion was the primary cause (88%) for censoring of collared calves, followed by collar malfunction (12%). Annual survival of female elk aged 2-7 years differed between 2011 and 2013 ($\chi^2 = 3.99$, df = 1, $P = 0.045$) and varied from 0.76 to 0.95. Annual survival for female elk aged 8+ years varied from 0.79 to 0.90 and did not significantly differ among years ($\chi^2 = 0.90$, df = 2, $P = 0.64$). Survival was highest for all adults the final year of the study and steadily increased every year of the study for prime-aged females. Survival for all adult females combined was 0.80 (SE = 0.06) in 2011, 0.83 (SE = 0.06) in 2012, and 0.93 (SE = 0.04) in 2013. Annual survival

of calves differed among years (χ^2 = 8.57, df = 2, P = 0.013) and varied from 0.07 to 0.27 (Table 3). Survival for calves at 90 days, or roughly 3 months, was 0.31 (SE = 0.09) in 2011, 0.25 (SE = 0.08) in 2012, and 0.41 (SE = 0.07) in 2013. Most cause-specific mortality for adult female elk was from hunting (7%) and most cause-specific mortality for calves was from predation by puma (63%). Hunting mortality steadily decreased every year of the study for adult females (Table 4).

Calf Elk Survival Modeling

We monitored calves for a total of 18,029 exposure days across a 425-d interval during the three-year study. Median dates for parturition were 1 June in 2011, 28 May in 2012, and 3 June in 2013. Ninety percent of calf births occurred by 15 June over the 3-year period of the study. Daily survival of calves was a function of both age and quadratic time trend (Table 5). Daily calf survival increased with age and followed a curvilinear pattern (Fig. 2). A high percentage of calves (26%) were predated during the hiding phase (≤5 days age), and most calves (71%) were predated when <60 days of age (Fig. 3). Models incorporating the daily age of the calves received considerable support and in the best model β_{age} = 0.014 (SE = 0.01, 95% CL = –0.007, 0.035) on a logit scale. Also, quadratic trend was a significant coefficient in the best model, β_T = 0.014 (SE = 0.01, 95% CL = –0.008, 0.035) – β_{TT} = 0.00005 (SE = 0.00001, 95% CL = –0.00008, –0.00002). Means and standard errors for covariates used in modeling calf survival appear in Table 6.

Elk Movements

Overall across years, winter home range size was similar for female elk in high winter nutritional condition (mean = 43.3 km^2, SE = 3.0) versus elk in lowered winter

nutritional condition (mean = 45.4 km^2, SE = 6.6) (Table 7). Brownian bridge movements did not differ between elk at high and low nutritional condition in 2011 ($F_{1, 15}$ <0.01, P = 0.98), 2012 ($F_{1, 37}$ = 0.04, P = 0.84), and 2013 ($F_{1, 32}$ = 0.11, P = 0.75) (Table 7). Distances moved from winter capture sites in February of each year to subsequent parturition locations varied considerably among elk and across the study area (Appendix A). Mean distance from winter capture site to subsequent parturition location was 12.9 km in 2011 (SE = 2.06; Range = 0.54-32 km), 6.8 in 2012 (SE = 0.9; Range = 0.31-29.8 km), and 8.04 in 2013 (SE = 1.13; Range = 1.6-36.2 km). Primary calving areas based on 2011-2013 parturition locations are displayed as 80% contours (Fig. 4).

Stress Hormones

We collected 39 feces samples during winter and 15 samples during summer from radio-marked female elk during the course of our study. Mean FG metabolite was 47.78 ng/g (SE = 2.37) during summer. Compared to data collected in 1995-97 (mean = 34.21 ng/g, SE = 3.71) 95% confidence intervals did not overlap and summer FG levels appear to be higher in this study when compared to the 1995-97 data set (Fig. 5). Mean FG metabolite was 24.94 ng/g (SE = 2.39) during winter. Compared to data collected in 1995-97 (mean = 18.90 ng/g, SE = 2.85) 95% confidence intervals did overlap and winter FG levels appear to be similar in this study when compared to the 1995-97 data set (Fig. 5).

DISCUSSION

Understanding how elk vital rates influence population growth rate (λ) is important to discover. Matrix models that simulate population dynamics tell us about the transitions in the life cycle to which the population growth rate is sensitive or elastic, and

changes in those vital rates may or may not have a big impact on population growth rate. Sensitivity analysis has been used to identify and target the vital rate that exerts the largest influence on the population growth rate, which in turn has greatly improved the management of wildlife populations (Heppell et al. 1994, Buenau and Gerber 2004, Raithel et al. 2007). In large herbivores, adult female survival is regularly identified as the vital rate with the highest elasticity; however in contrast, λ is fairly insensitive to calf survival (Escos et al. 1994, Gaillard et al. 1998, Gaillard et al. 2000, Eberhardt 2002, Garrott et al. 2003). There is growing recognition that vital rates of relatively low elasticity can strongly impact λ if they are highly variable (Mills et al. 1999, Wisdom et al. 2000, Coulson et al. 2005). In elk, calf survival demonstrates a high level of variability and can strongly influence λ (Raithel et al. 2007). The focus of our report was to present the needed demographic information in this document and future matrix modeling efforts will explore the "sensitivity" of our collected vital rate information for this elk herd and for future management.

Contrary to the premise that elk calf survival can demonstrate a high level of variability compared to constant adult female survival (Wisdom and Mills 1997, Wisdom et al. 2000, Mills et al. 2001, Raithel et al. 2007), we found high variability in survival for both calves and prime-aged adult females during our 3 year study. Annual elk calf survival demonstrated a range of 20%, and prime-aged adult females ranged 19% across years, indicating nearly identical variability for these age classes during our study. Hunting was the primary cause of death for adult females and hunting pressure was steadily removed during the course of our study and most likely contributed to the increased survival of adults toward the end of the study. CSP was closed to antlerless elk

hunting during the entire duration of the study. Unit 4 was closed to elk hunting for fall of 2012 and remained closed for the remainder of the study. Additionally, licenses allocated in Unit 2 were steadily reduced during the course of our study. Both of these actions removed and reduced hunting mortality and were important in increasing female survival. Female elk survival in our study was near the mid-range of what can be expected from previous studies for adult female elk in the west (range = 0.640–0.999; Raithel et al. 2007).

Calf elk survival in our study was at the lower end of the range (range = 0.060–0.720; Raithel et al. 2007) and predation was the primary cause of lowered calf survival. One bobcat and some coyotes killed elk calves, but puma were the primary predator of elk calves. An analysis of several neonate studies indicated high variability in calf survival related to predation and weather variables evaluating compensatory versus additive mortality (Griffin et al. 2011). Estimated 3-month (90 days) calf survival over 3 years in our study averaged 0.32 (SE = 0.08) and was lower than most 3-, 4-, and 5-predator community systems evaluated in the west (Barber-Meyer et al. 2008, Griffin et al. 2011). Only one 3-month survival rate in Yellowstone National Park at 0.31 (SE = 0.04) was lower and that system had 5 predators (Barber-Meyer et al. 2008). It was suggested that early predation of elk calves by bears (*Ursus americanus* and *Ursus arctos*) was strongly additive. Phenology of predation may dictate juvenile survival patterns, and the 3-month survival rate documented in this study followed a similar juvenile survival pattern to other additive systems (Griffin et al. 2011). Calf survival appears to vary across the Black Hills as annual survival of calves in a study area further west averaged 75% (SE = 0.03) over 2 years (SDGFP Elk Management Plan 2015).

Variability of calf survival has been documented over large landscapes in the west (Rathiel et al. 2007, Griffin et al. 2011), but can also occur at local levels within a smaller geographic area.

Further analysis of calf survival indicated age and quadratic time trend were important for daily calf survival. Survival followed a curvilinear pattern where calf survival was lower immediately following parturition and increased as calves aged. Calf elk lived under precarious conditions immediately following parturition as 26% of predation mortality occurred within 5 days of parturition, or during the hiding phase (Geist 1982). Reardon (2005) found less predation on hiding phase neonates, and 11% of calf predation events were on neonates ≤5 days old. In our study, most predation (74%) did occur when neonates were using the fleeing strategy, but was less than what was observed in Oregon at 89% (Reardon et al. 2011). Reardon et al. (2011) surmised that elk calves >5 days of age are at heel with the female and in family groups of elk which would draw more attention from stalking predators than hiding phase calves. Our results do support this conclusion; however, our results also indicate predators, and particularly puma can be effective predators of calves during the hiding phase.

Nutritional condition is an index of nutritional intake and expense, and may influence survival and reproduction and, thus, is a gauge of habitat quality (Parker et al. 2009). Nutritional condition, or ingesta-free body fat of female elk in our study is on the lower end of the range for elk in the west (Cook et al. 2010). However, survival and pregnancy rates are in the normal range (Raedeke et al. 2002, Raithel et al. 2007) and the nutritional condition levels we documented in the study does not appear to be influencing fitness of female elk. Our index of condition was only collected during winter and there

could be possible nutritional limitations acting on this herd through summer–autumn forage conditions (Cook et al. 2004), but we were unable to detect that in our design. We found no evidence of differential movements based upon corresponding winter home range size between elk of higher and lower nutritional condition. Further, we found no evidence that winter condition of dams was an important factor in survival of calves.

For movements, 10 marked female elk left their winter capture location of the northeast corner of CSP and moved northwest to their parturition locations near Hill City, South Dakota in 2011. The large movements of these elk were the primary explanation for the greater parturition dispersal distances in 2011 versus subsequent years. However, during each year of the study there was at least one elk that moved at least 29 km from their winter capture site to their subsequent parturition location.

Following the predicted pattern of previous work in CSP, FG levels of female elk were higher in summer than in winter (Millspaugh et al. 2001). Winter FG levels appear to be in the normal range when compared to previous data, but summer FG levels appear to be higher during our study when compared to data collected in 1995-97 (Millspaugh et al. 2001). It was surmised that higher FG levels were associated with high human activity and higher temperatures in summer versus winter (Millspaugh et al. 2001). The amount of human activity (i.e., vehicle use on primary roads) was correlated with FG levels in CSP. Visitation during summer has increased since 1995 as there were roughly 1.2 million visitors in 1995, but in 2012 there was an estimate of 1.6 million summer visitors. Perhaps the increase in visitors and potential activities such as hiking, biking, and horseback riding may have provided some disturbance which has increased summer

FG levels. Further, other activities such as National Guard helicopter and ground training operations may contribute to increased levels.

Females in better condition typically give birth to larger calves which can improve survival of calves (Thorne et al. 1976, Clutton-Brock et al. 1982, Singer et al. 1997, Cook et al. 2004). Further, timing of parturition, gender of calves, and age of calves may influence calf survival and elk population dynamics (Smith and Anderson 1996, Singer et al. 1997, Smith et al. 2006, White et al. 2010). In most instances, low juvenile survival can result from a combination of factors, including predation, adverse weather conditions, and low birth weights (Schlegel 1976, Clutton- Brock et al. 1982, Clutton- Brock et al. 1987; Singer et al. 1997, Cook et al. 2004, Smith et al. 2006). We did not find a strong correlation among timing of birth, birth mass, gender, or dam condition to survival of calves, unlike the previous studies cited above. However, age of calves was an important factor in survival similar to previous studies (Smith and Anderson 1996, Singer et al. 1997, White et al. 2010). Our data suggested predation, especially by puma, was the most important proximate cause of elk calf mortality immediately following parturition and during the summer months. Hunting mortality was the most important proximate cause of mortality of adult females, and substantial reductions in female elk harvest can improve survival over a short time period.

MANAGEMENT IMPLICATIONS

Our results may provide insights that can be applied to other areas where managers are dealing with a declining elk population with associated low calf elk recruitment. We demonstrated that predation by puma was the most important proximate mortality factor for elk calves from birth through August in the southeastern portion of

the Black Hills. Our modeling efforts indicate that puma harvest from the previous season did not influence calf survival at those harvest levels. Because calves were most susceptible to puma predation in the first 60 days of life, activities that limit puma predation from parturition through the summer months (1 May- 31 August) should be considered in calving areas (Fig. 4) where the goal is to improve calf survival. Activities such as targeted removal of puma could be an alternative considered for evaluation in areas experiencing higher puma predation (i.e., calf:cow ratios ≤ 30 calves per 100 cows, or calf survival ≤ 27%). A research design could include a control and treatment area where puma are radio-marked and studied for prey selection by individual animals. The treatment area would have targeted removal of radio-marked puma consuming high proportions of elk calves (≥3 elk calves consumed during June-August time period). The response of elk calf survival would be compared with the control area. Puma are also managed for a sustainable population in South Dakota (SDGFP Mountain Lion Management Plan 2010) and creative management alternatives are needed which balance both puma and elk populations in the Black Hills. In absence of activities related to enhancing elk calf survival, reducing adult female elk harvest from hunting appears to be the most effective technique to improve elk population demographics. Higher stress metabolite levels can be associated with increased human activity (Millspaugh et al. 2001). Decreasing the amount of human disturbance such as closing roads and providing area closures for human disturbance in important calving areas may provide buffers for elk during the summer months.

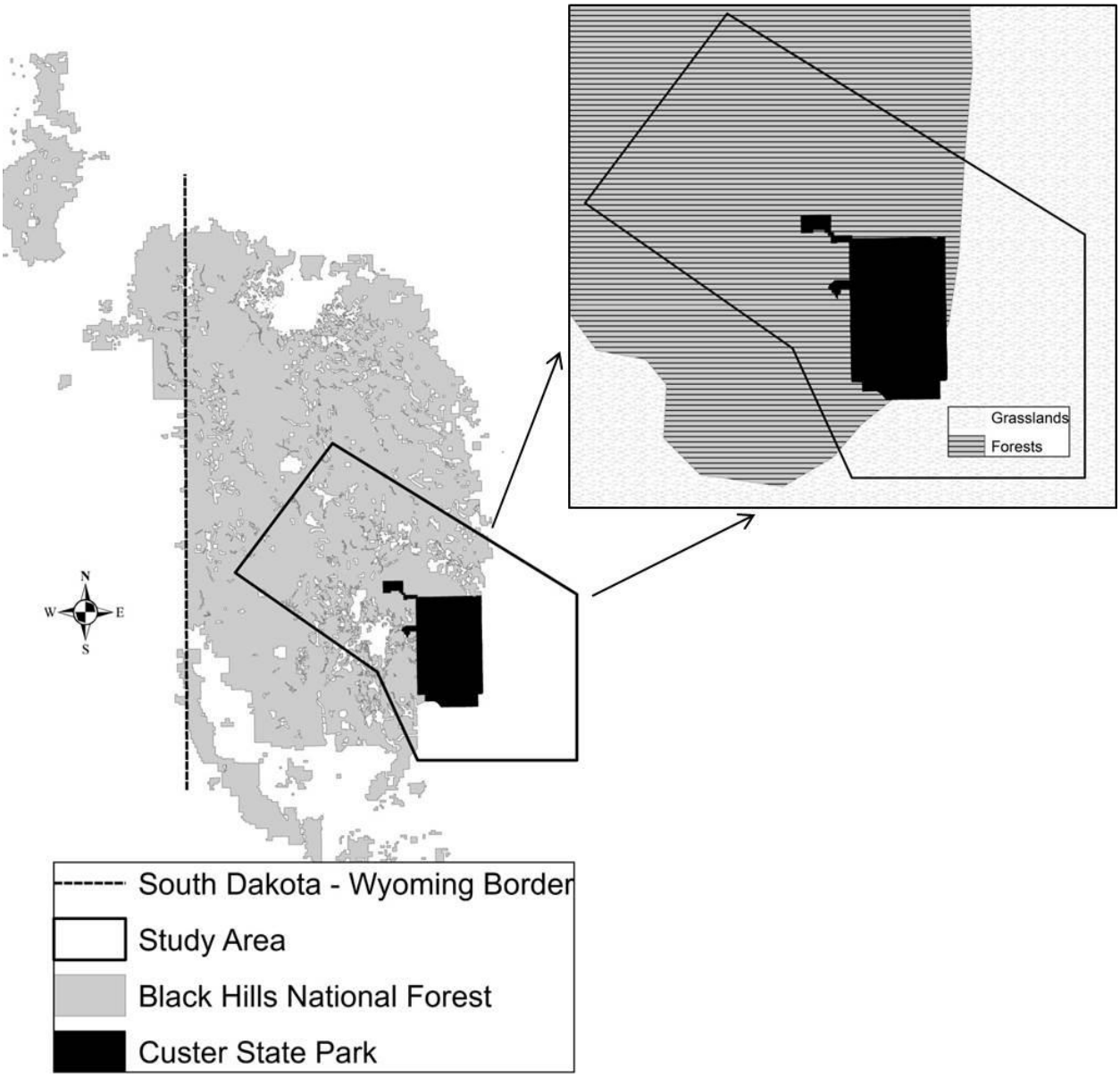


Figure 1. Location of study area along the forest-grassland ecotone in the Black Hills, South Dakota, USA.

Table 1. Description of daily survival models developed to test competing hypotheses of elk calf survival in the Black Hills, South Dakota 2011-2013.

Model	Notation
1) Single estimate of daily survival	$S_{(.)}$
2) Effect of year	S_{year}
3) Effect of gender of calf	S_{gender}
4) Effect of puma harvest the previous year	S_{puma}
5) Effect of timing of parturition	$S_{\text{parturition}}$
6) Effect of dam's winter nutritional condition	$S_{\text{nutrition}}$
7) Effect of calf weight when born	$S_{\text{calf_w}}$
8) Effect of calf age	S_{age}
9) Effect of calf age + linear trend	$S_{\text{age} + T}$
10) Effect of calf age + quadratic trend	$S_{\text{age} + T + TT}$

Table 2. Mean values and standard errors for age, body metrics, and nutritional condition of female elk in southeastern Black Hills, South Dakota 2011-2013.

Year	Age[a]	SE	Chest girth (cm)	SE	Weight (kg)[b]	SE	Body score	SE	Rump fat (mm)	SE	Body fat %[c]	SE
2011	6.7	0.6	146.6	0.9	276.1	2.4	2.8	0.1	4.9	0.6	5.9	0.4
2012	7.4	0.6	150.2	1.0	286.0	2.7	3.5	0.1	6.0	0.5	7.0	0.2
2013	7.9	0.5	151.6	0.8	290.0	2.3	2.7	0.1	4.5	0.5	5.8	0.2
Overall	7.3	0.3	149.5	0.6	284.1	1.5	3.0	0.1	5.1	0.3	6.2	0.2

[a]Age based on canine teeth cementum annuli.

[b]Weight estimated using chest girth and regression equation from Millspaugh and Brundige (1996).

[c]Nutritional condition (Body fat %), is estimated using the LIVINDEX, an arithmetic combination of body score (rBCS) and rump fat (MAXFAT) (Cook et al. 2010).

Table 3. Vital rate data for elk which includes sample size (*n*), mean values for estimates, and variance (SE) in Black Hills, South Dakota 2011-2013.

Vital rate	*n*	2011	SE	*n*	2012	SE	*n*	2013	SE
Annual calf survival	30	0.067	0.042	37	0.271	0.081	58	0.239	0.057
Annual yearling survival[a]	14	0.938	0.059	14	0.938	0.059	14	0.938	0.059
Annual adult female survival (2-7 years)	25	0.762	0.085	22	0.864	0.073	22	0.954	0.045
Annual adult female survival (8+ years)	14	0.849	0.098	18	0.787	0.094	20	0.897	0.069
Pregnancy rate for yearling females	-	-	-	-	-	-	-	-	-
Pregnancy rate for adult females (2-7 years)	25	0.920	0.011	22	1.000	0.000	22	0.909	0.013
Pregnancy rate for adult females (8+ years)	14	0.714	0.031	18	0.900	0.017	20	0.900	0.015
Proportion female calves born to dams	30	0.567	0.017	37	0.676	0.013	58	0.397	0.008

[a]For yearling survival we used annual data from 2012-13 for every year. Here we used an informative prior and assume the number of calves surviving a year is a binomial random variable with parameters p (to be estimated) and *n* = 14 yearling elk. Our prior distribution for p is beta (1, 1), and our posterior distribution for p is beta (*n*, 1).

Table 4. Cause-specific mortality for elk including sample size (*n*), estimates (CSM), and 95% confidence intervals (CI) in the Black Hills, South Dakota 2011-2013.

Age class	2011			2012			2013			Overall		
Mortality factor	*n*	CSM	CI	*n*	CSM	CI	*n*	CSM	CI	*n*	CSM	CI
Adult (2 + years of age)												
Puma	2	0.05	–0.02-0.13	3	0.05	–0.02-0.12	0	0.00		5	0.04	0.01-0.08
Hunter harvest	4	0.11	0.01-0.21	2	0.08	–0.01-0.16	2	0.05	–0.02-0.12	8	0.07	0.02-0.11
Dystocia	1	0.025	–0.03-0.08	0	0.00		0	0.00		1	0.008	–0.007-0.02
Vehicle collision	1	0.025	–0.03-0.08	0	0.00		1	0.02	–0.02-0.07	2	0.02	–0.01-0.04
Infection septicemia	0	0.00		1	0.025	–0.02-0.07	0	0.00		1	0.009	–0.008-0.03
Unknown	0	0.00		1	0.025	–0.02-0.07	0	0.00		1	0.008	–0.007-0.02
TOTAL	8	0.21	0.08-0.35	7	0.18	0.06-0.29	3	0.07	–0.01-0.16	18	0.155	0.09-0.22
Calf												
Puma	16	0.80	0.60-1.00	16	0.56	0.33-0.78	27	0.60	0.40-0.79	59	0.63	0.51-0.76
Coyote	1	0.09	0.07-0.23	2	0.04	–0.04-0.12	4	0.10	–0.03-0.23	7	0.06	–0.01-0.13
Bobcat	0	0.00		0	0.00		1	0.05	–0.04-0.14	1	0.015	–0.03-0.06
Unknown predation	1	0.03	–0.05-0.12	0	0.00		0	0.00		1	0.005	–0.01-0.02
Total predation	18	0.92	0.77-1.07	18	0.60	0.42-0.78	32	0.75	0.60-0.89	68	0.71	0.61-0.81
Poor body condition	0	0.00		0	0.00		2	0.02	–0.01-0.06	2	0.01	–0.01-0.03
Unknown	0	0.00		0	0.00		1	0.01	–0.01-0.03	1	0.01	–0.01-0.02
Other[a]	0	0.00		1	0.25	–0.24-0.74	1	0.01	–0.01-0.03	2	0.05	–0.10-0.20
TOTAL	18	0.92	0.77-1.07	19	0.85	0.67-1.03	36	0.79	0.66-0.91	73	0.78	0.70-0.88

[a]For the Other category we had one calf that was born with a defect and abnormally developed in 2012. In 2013, we had one calf that fell into a rock crevice and died.

Table 5. Model selection results for daily survival of calf elk in the Black Hills, South Dakota, USA, 2011–2013.

Model	Deviance	K	AIC_c	ΔAIC_c	w_i
$S_{age + T + TT}$	874.606	4	882.608	0.000	0.974
S_{age}	886.459	2	890.459	7.852	0.019
$S_{age + T}$	886.383	3	892.385	9.777	0.007
S_{year}	934.450	2	940.451	57.843	0.000
S_{puma}	937.887	2	941.888	59.280	0.000
$S_{nutrition}$	941.507	2	945.508	62.900	0.000
S_{calf_w}	941.932	2	945.932	63.325	0.000
$S_{(.)}$	945.912	1	947.912	65.304	0.000
$S_{parturition}$	944.873	2	948.874	66.266	0.000
S_{gender}	945.877	2	949.878	67.270	0.000

[a]Models are ranked by increasing ΔAICc; *wi* is the model weight and *K* is the number of parameters. Factors in models included year, gender of calf (gender), puma harvest from previous year (puma), timing of parturition (parturition), dam's previous winter nutritional condition (nutrition), calf weight (calf_w), calf age (age), a linear time trend (*T*), a quadratic time trend (*T* + *TT*), and a model with constant daily survival (.).

Figure 2. Daily survival probability for elk calves as they age and as a function of quadratic time trend in the Black Hills, South Dakota, 2011-2013.

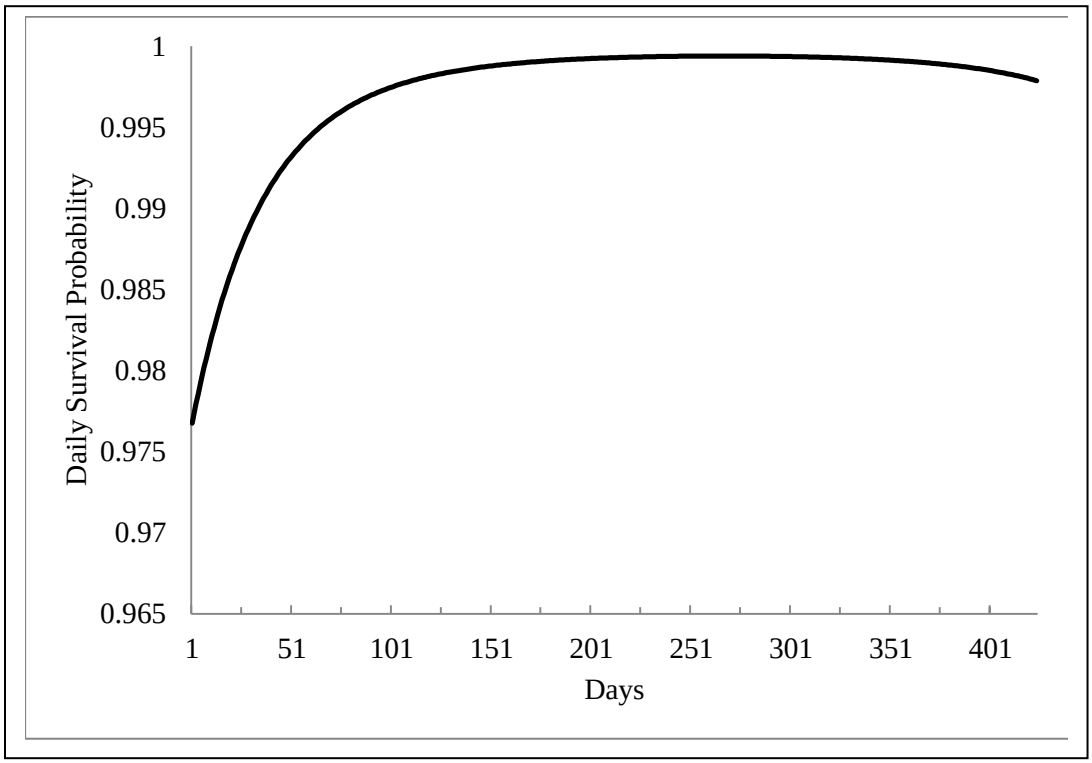


Figure 3. Number of predation events by age categories for elk calves through their annual life cycle in the Black Hills, South Dakota, 2011-2013.

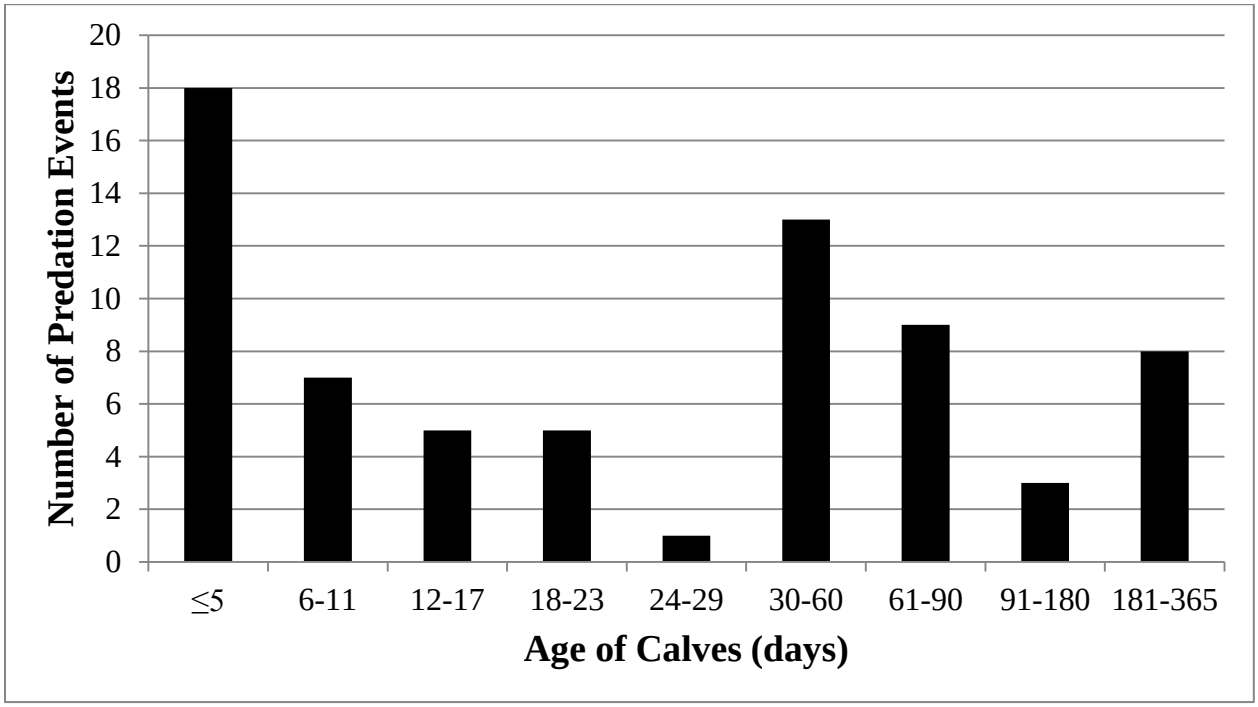


Table 6. Mean covariate values and standard errors (SE) used for modeling daily elk calf survival in the Black Hills, South Dakota 2011-2013.

Year	Parturition date[a]	Calf weight (kg)	SE	Body fat %[b]	SE	Puma harvest[c]
2011	1 June	16.310	0.753	5.909	0.394	9
2012	28 May	14.784	0.322	6.976	0.207	15
2013	3 June	16.376	0.369	5.771	0.235	18
Overall	1 June	15.888	0.272	6.161	0.162	42

[a]Median parturition date.

[b]Nutritional condition of dam (Body fat %) that birthed calf from the previous winter. Data collection followed methods from Cook et al. (2010) and was collected in February of each year.

[c]Number of puma harvested during the previous hunting season within the study area. Season dates occurred from December 26-March 31.

Table 7. Mean values for number of satellite locations (*n*), location error (m), Brownian bridge winter home range size (BBMM; km^2), and associated winter nutritional condition (Condition) for female elk comparing high versus low nutritional condition (Condition class) in southeastern Black Hills, South Dakota 2011-2013.

Year	Condition class[a]	*n*	SE	Location error	SE	BBMM[b]	SE	Body fat %[c]	SE
2011		1218.1	14.2	23.1	0.9	40.8	4.4	6.0	0.4
	High	1239.5	14.3	22.2	0.9	40.8	5.3	7.4	0.5
	Low	1166.8	21.3	25.2	1.7	41.0	9.0	2.9	0.6
2012		1206.3	93.4	16.8	2.1	43.9	3.5	7.1	0.2
	High	1204.4	98.3	16.6	2.2	44.1	3.6	7.3	0.2
	Low	1241.5	150.5	19.9	13.	40.7	17.	3.9	0.0
2013		1219.7	93.5	16.3	2.2	45.4	5.8	5.5	0.4
	High	1150.9	131.8	14.6	3.1	43.6	7.5	7.2	0.2
	Low	1297.1	134.2	18.2	3.3	47.4	9.1	3.1	0.3
Overall		1213.6	53.4	17.8	1.3	43.9	2.8	6.2	0.2
	High	1196.3	64.3	17.1	1.5	43.3	3.0	7.3	0.1
	Low	1264.0	93.7	19.9	2.5	45.4	6.6	3.2	0.2

[a]Elk movements were compared between elk of high nutritional condition (≥4.0 body fat %) versus low (<4.0 body fat %) nutritional condition.

[b]Brownian bridge movement model based on home range movements collected from mid-February through day before each radio-marked elk initiated parturition.

[c]Nutritional condition (Body fat %) is estimated using the LIVINDEX, an arithmetic combination of body score (rBCS) and rump fat (MAXFAT) (Cook et al. 2010).

Figure 4. Primary calving areas based on 80% fixed kernel contours of elk parturition locations in the Black Hills, South Dakota 2011-2013.

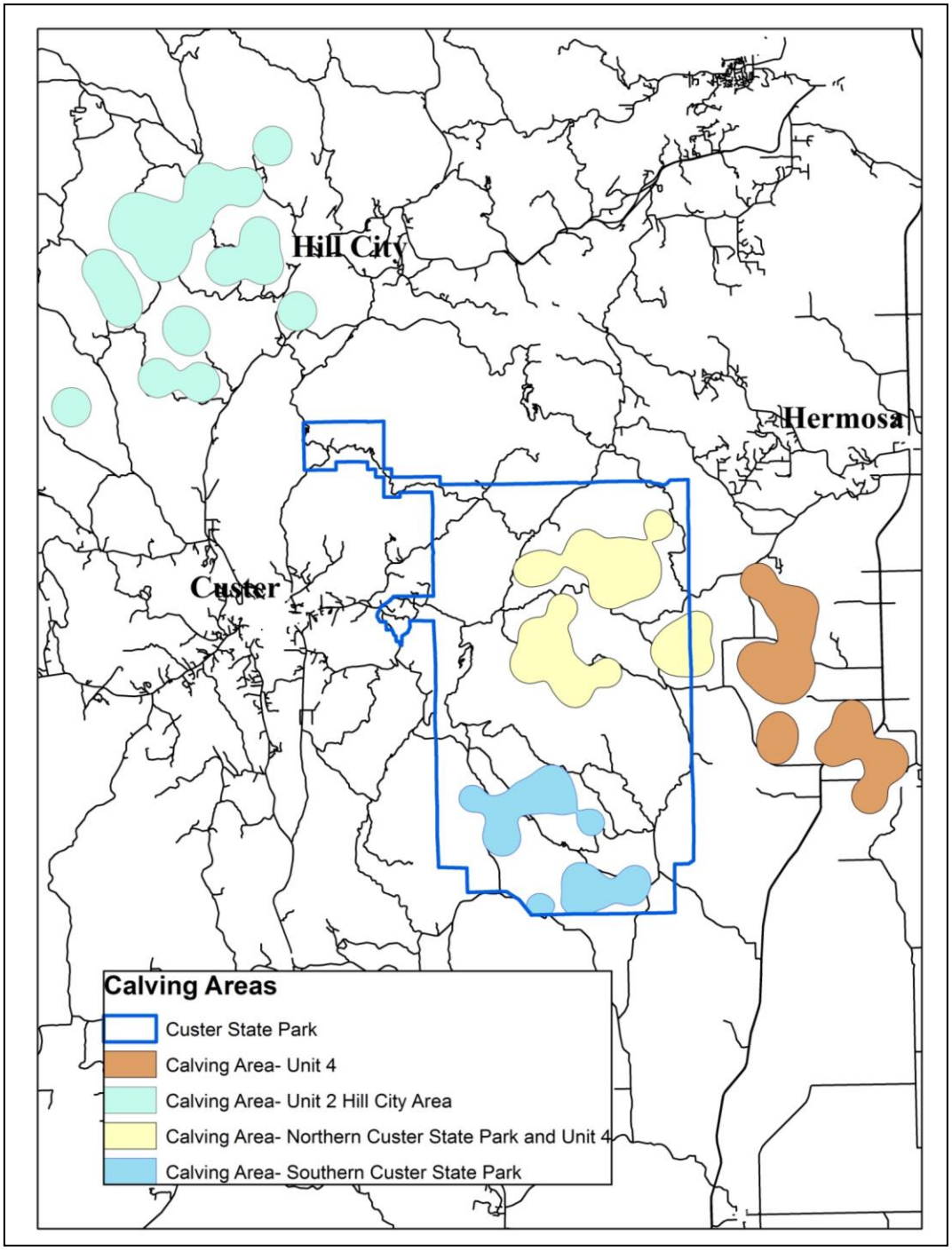
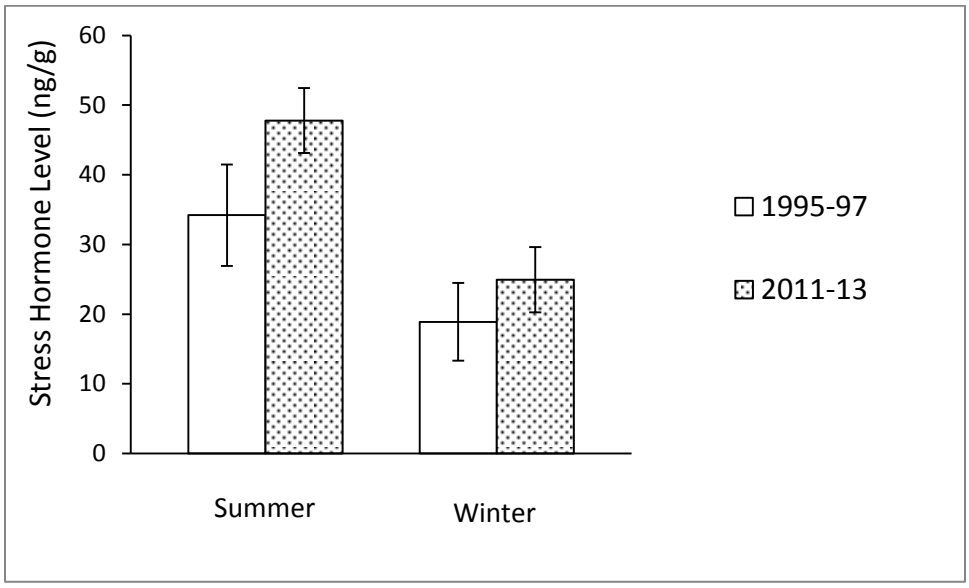


Figure 5. Mean fecal glucocorticoid hormone metabolite levels (ng/g) plus 95% confidence interval error bars from a Custer State Park elk herd in1995-97 (Millspaugh et al. 2001) and from elk in southeastern Black Hills, South Dakota 2011-2013.



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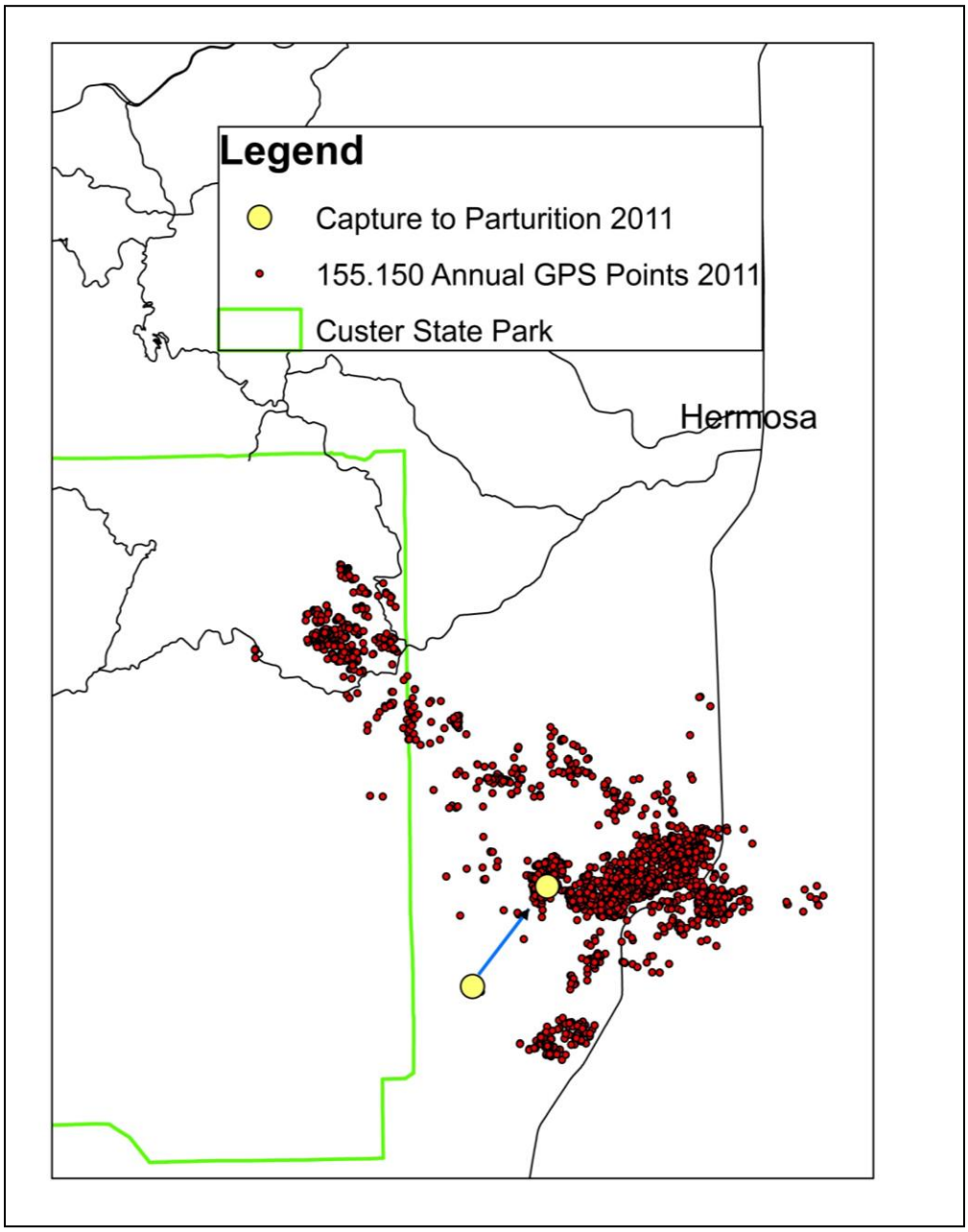
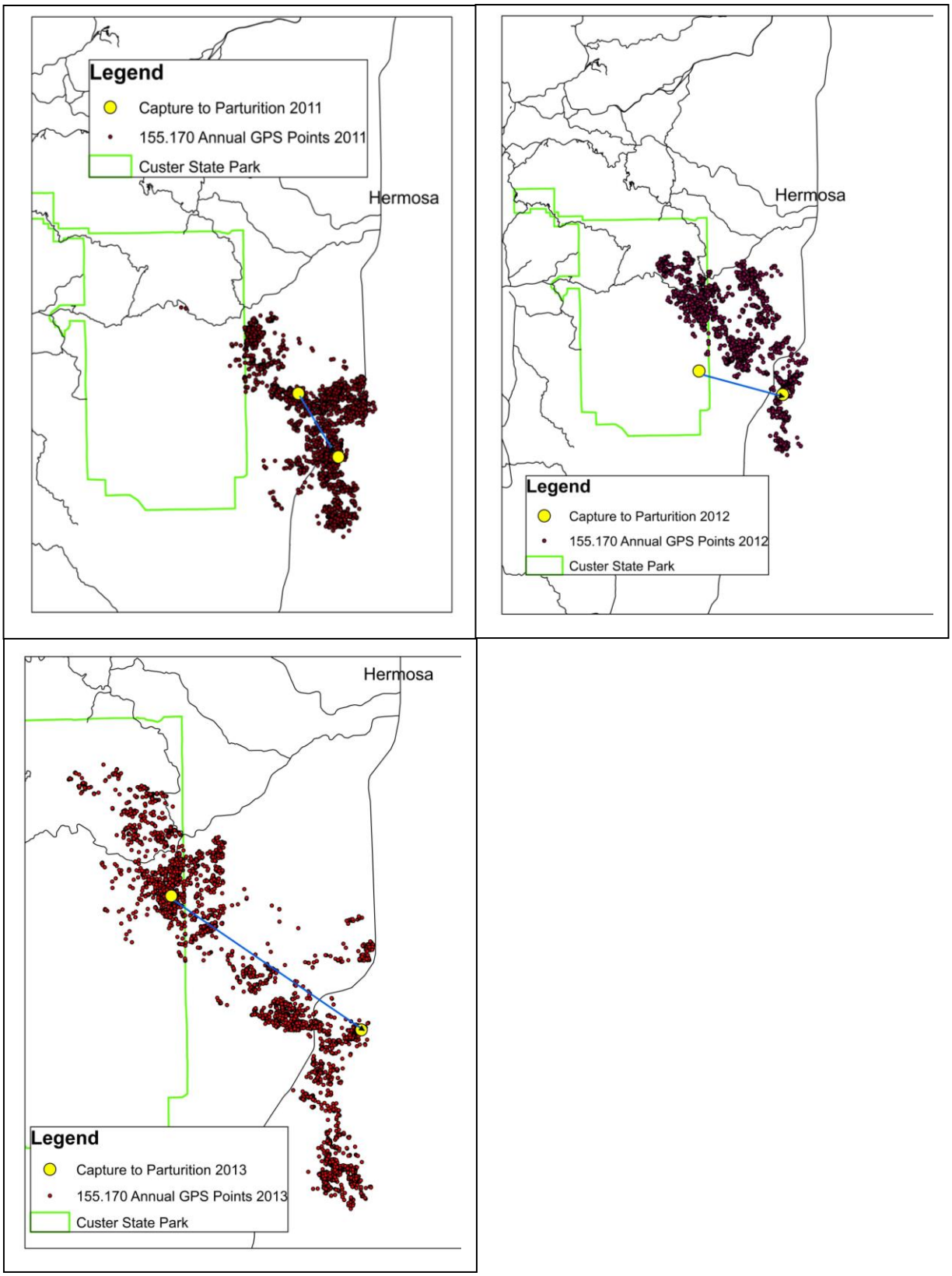
Appendix A. Satellite locations from GPS collars of female elk in the Black Hills of South Dakota, 2011-2013. Locations represent annual home range locations for each individually marked elk. Figures include winter capture locations that occurred in February of each year and that proximity to subsequent parturition locations (arrow points to direction of parturition site). Each page represents data for one individual, and for some individuals we have 3 years of data, but for some we only have 1 or 2 years of annual data. In some years, some individuals were not pregnant and will not have parturition locations.

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Custer State Park
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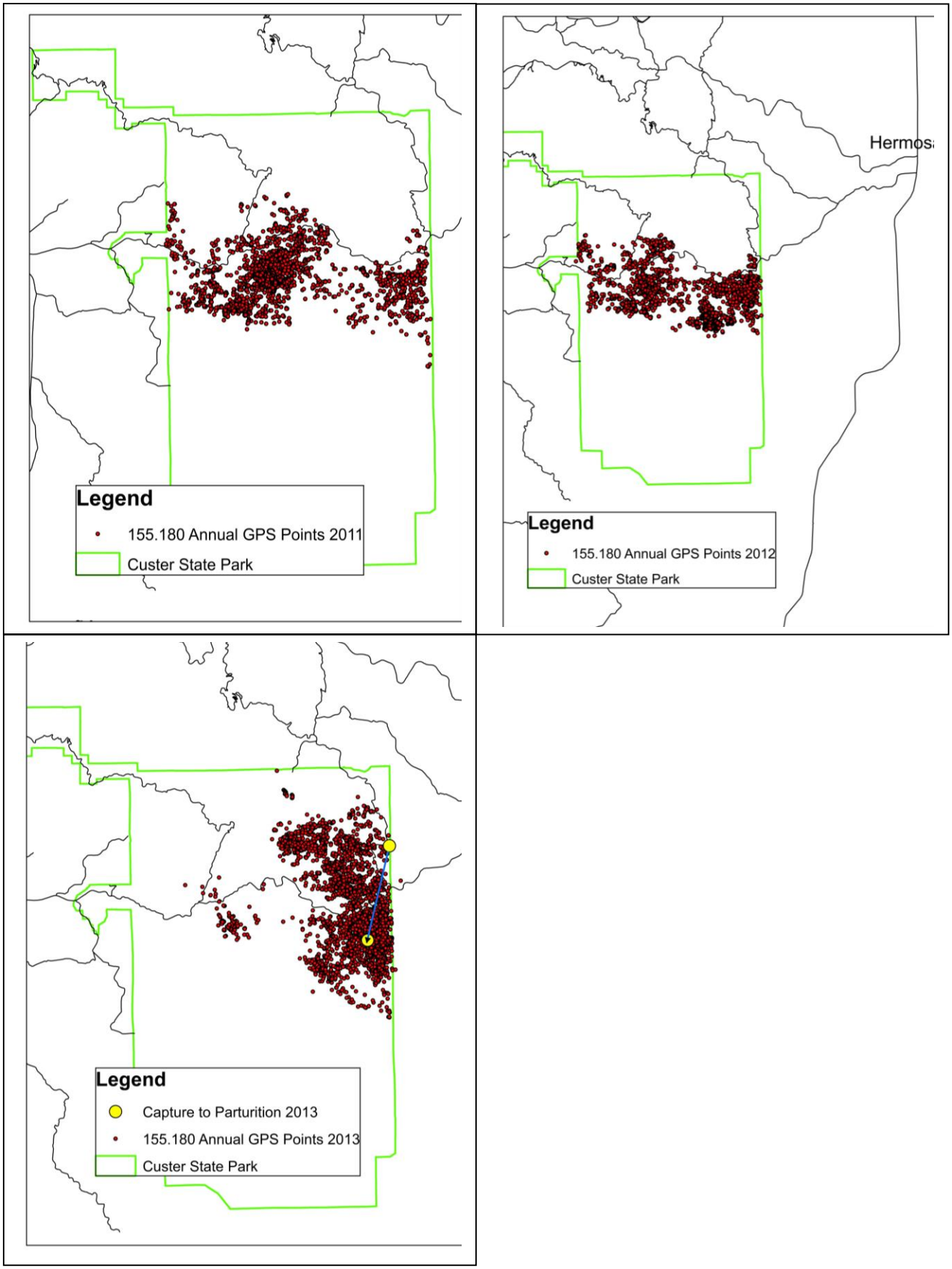
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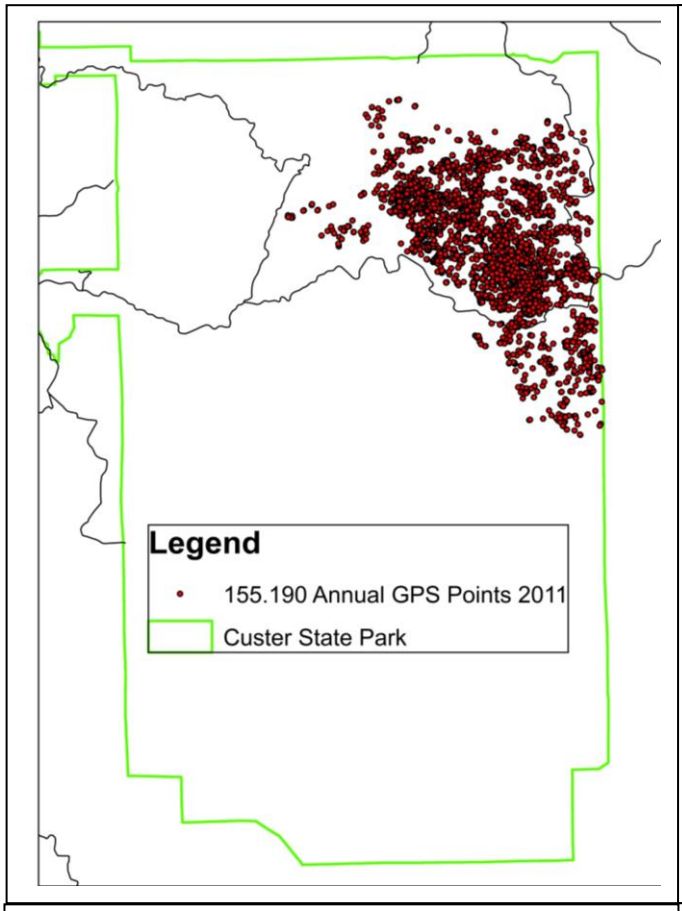
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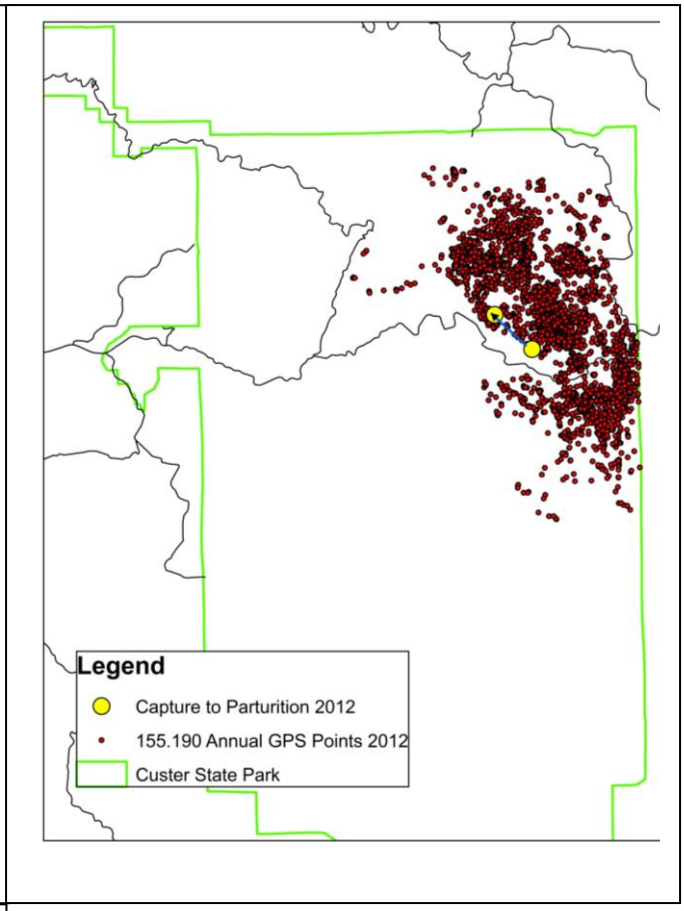
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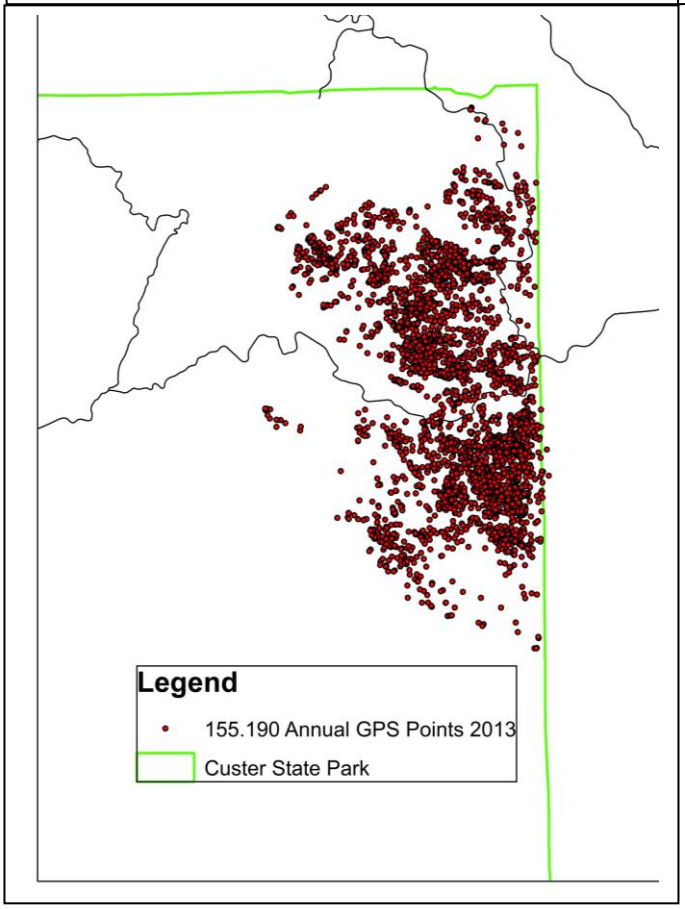
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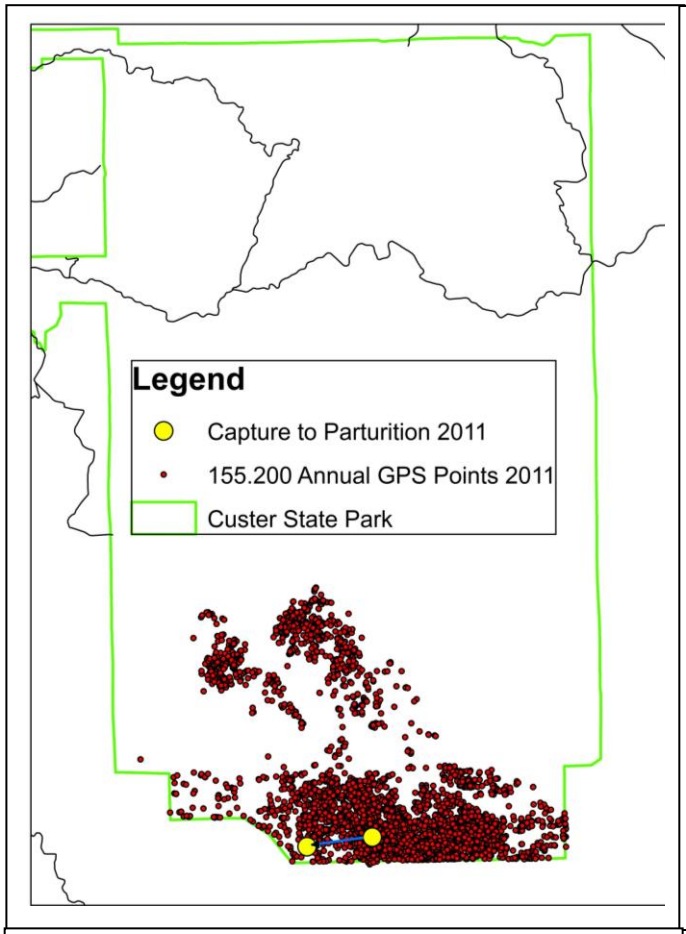
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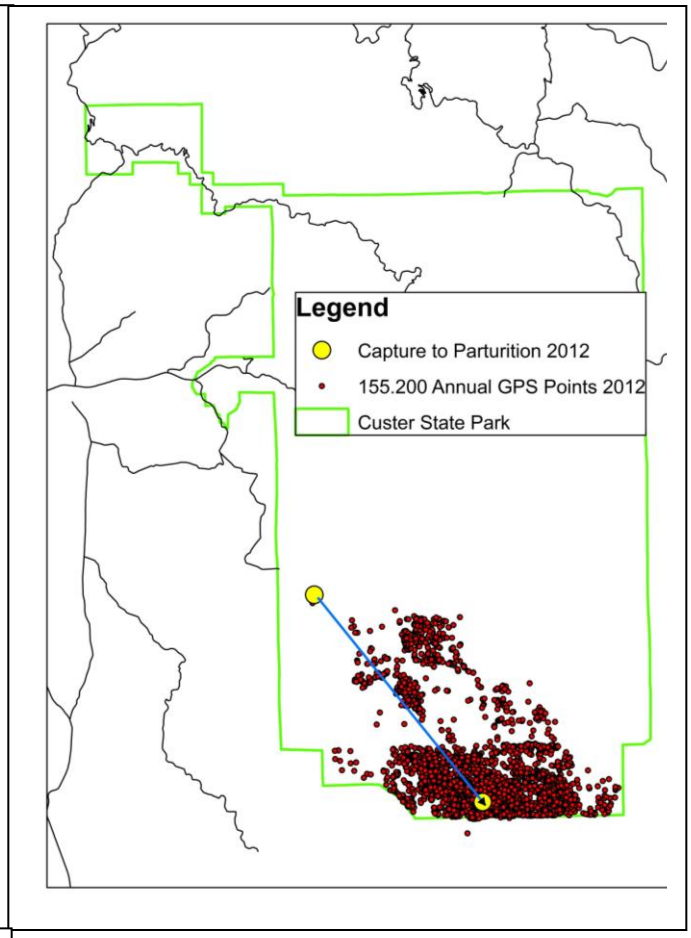
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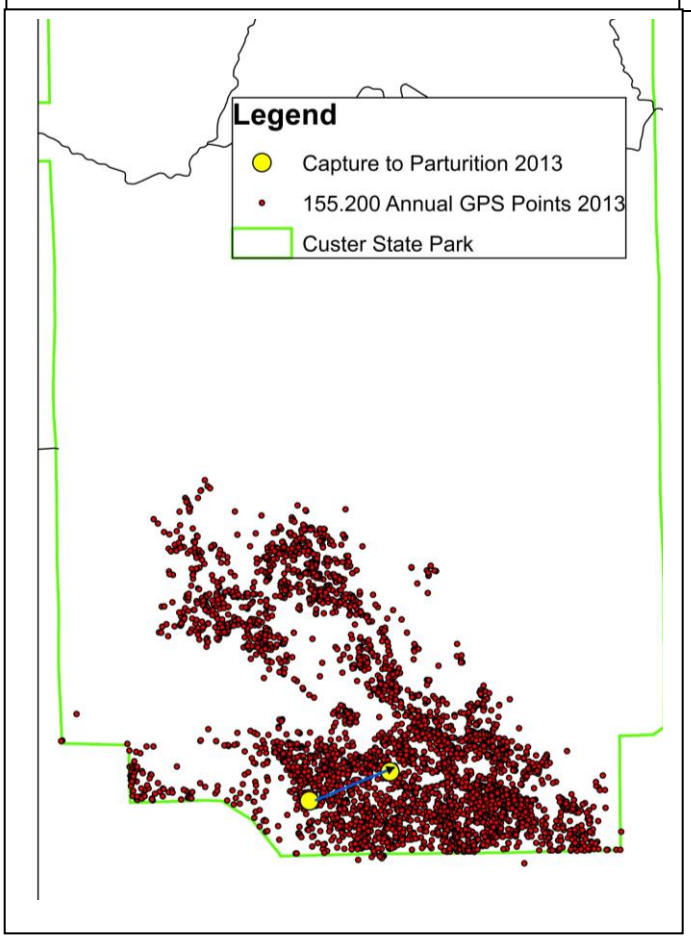
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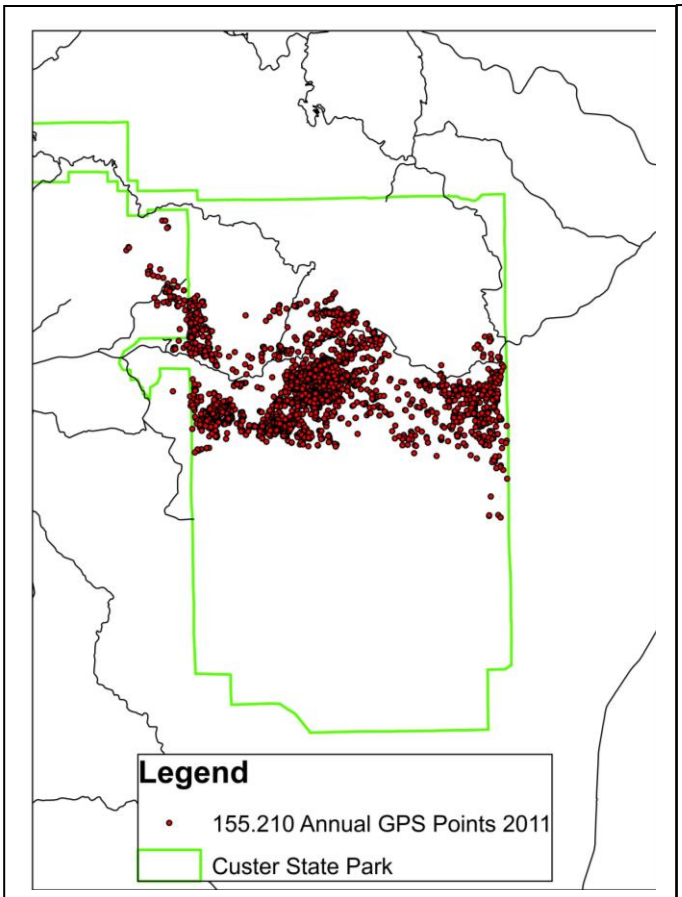
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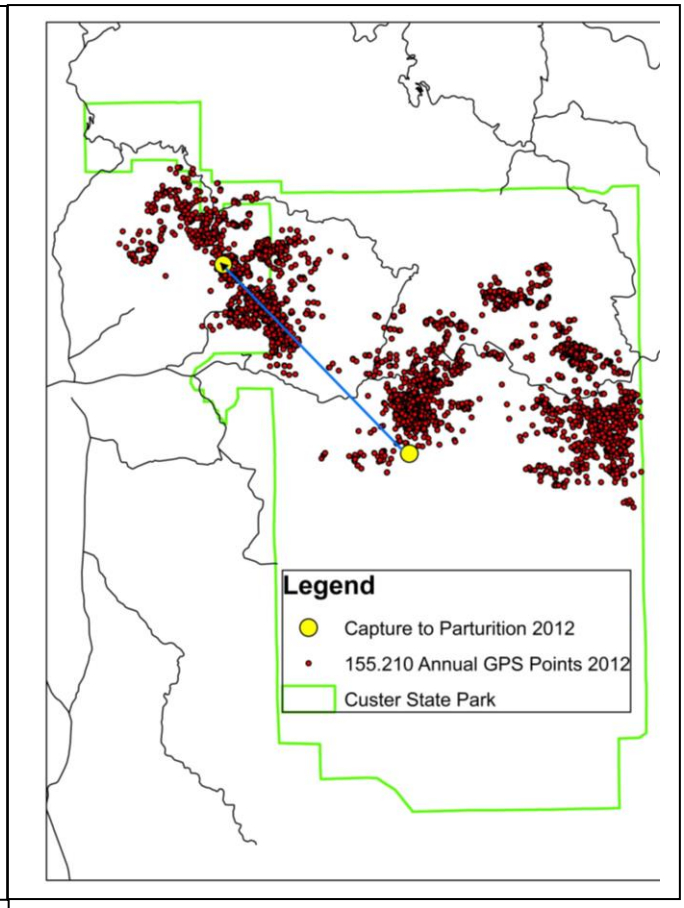
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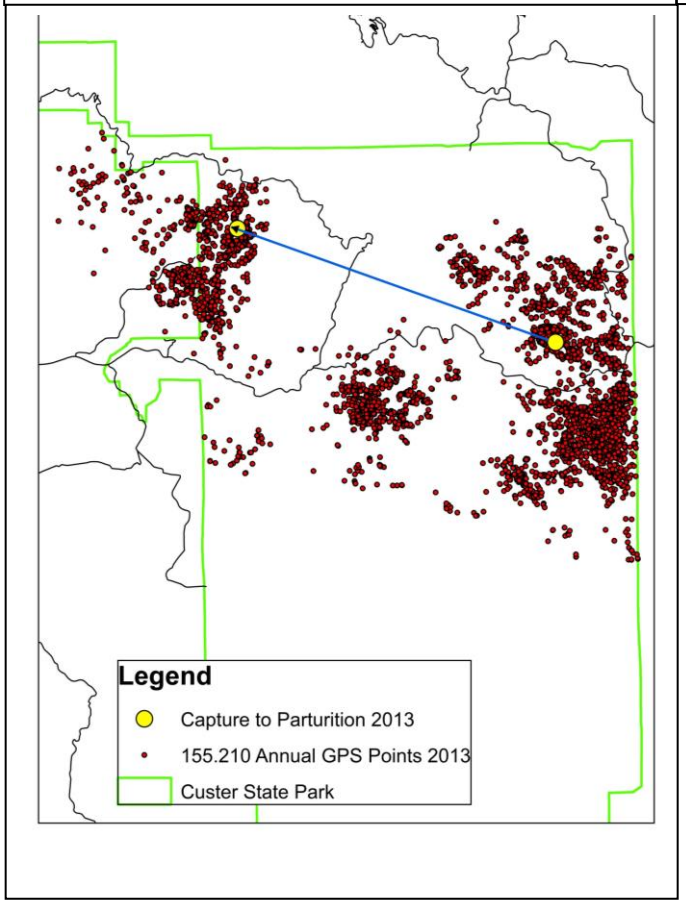
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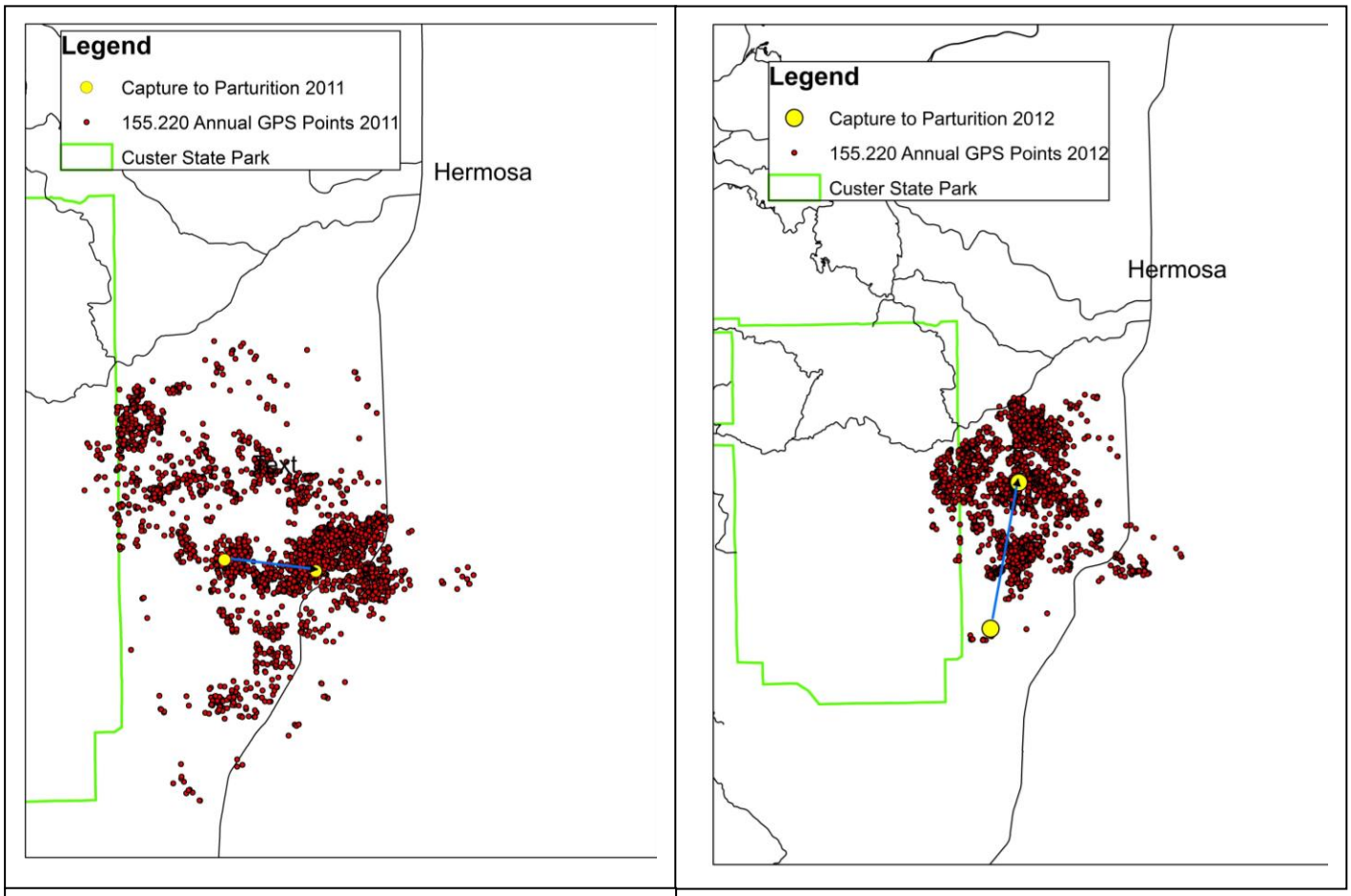
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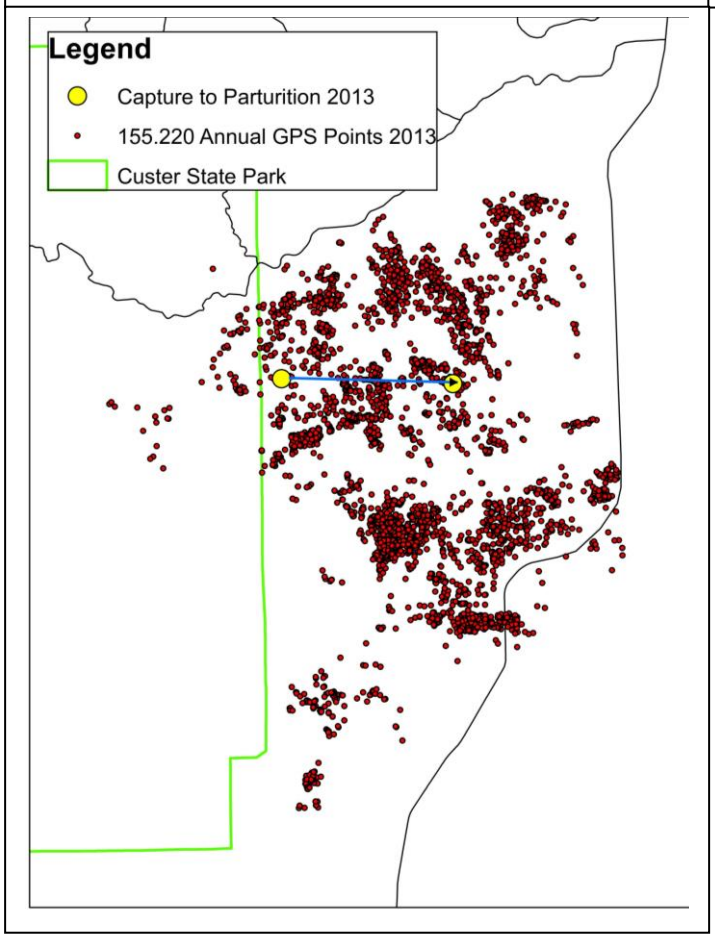
Hermosa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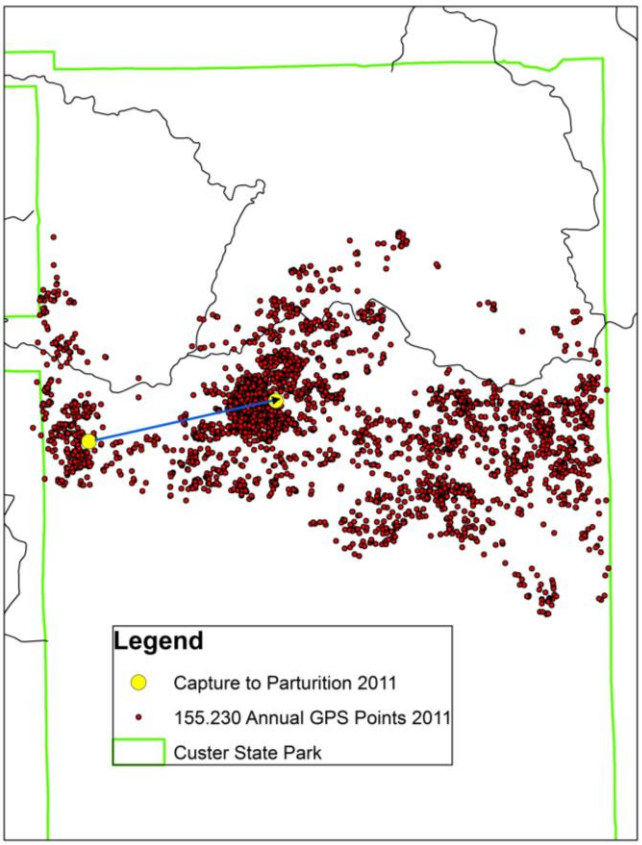
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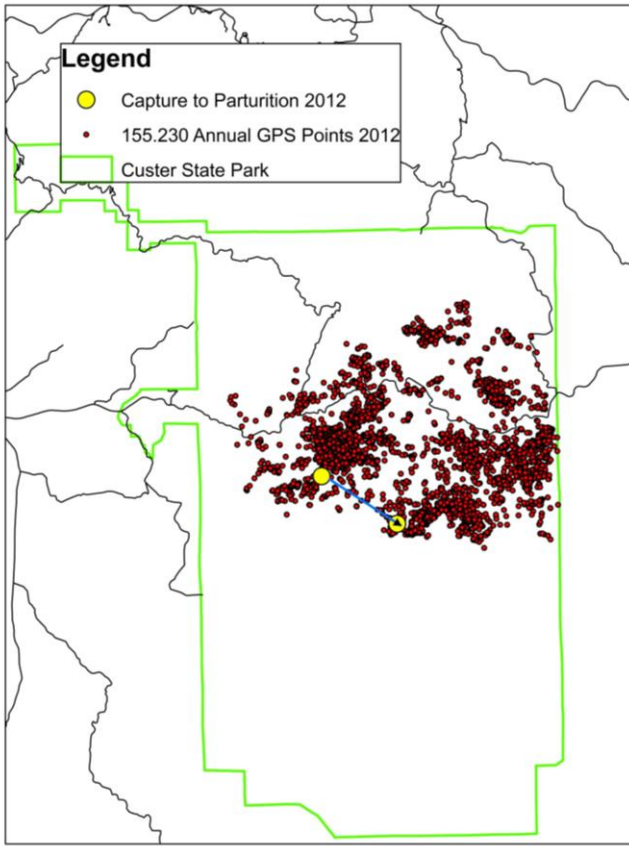
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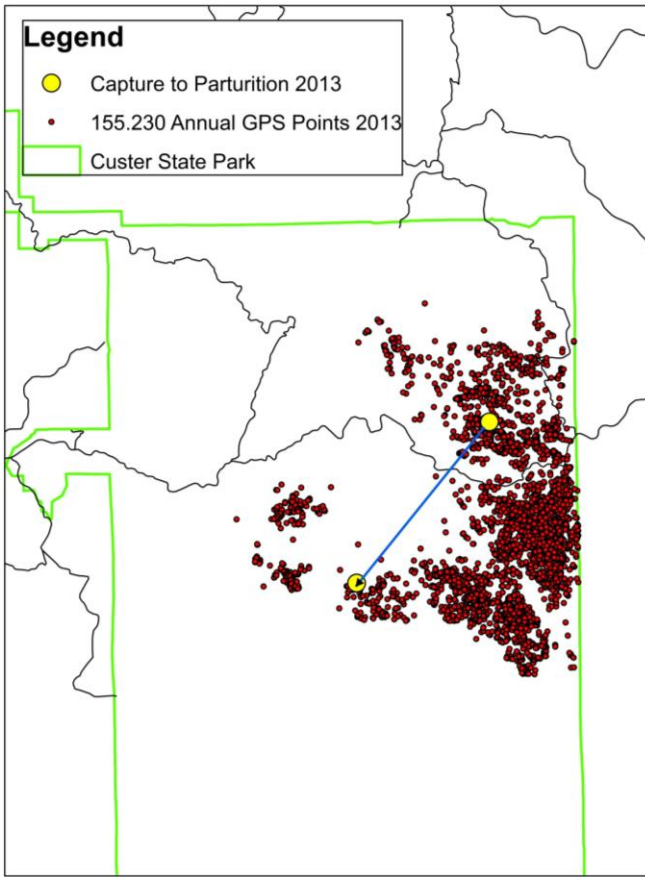
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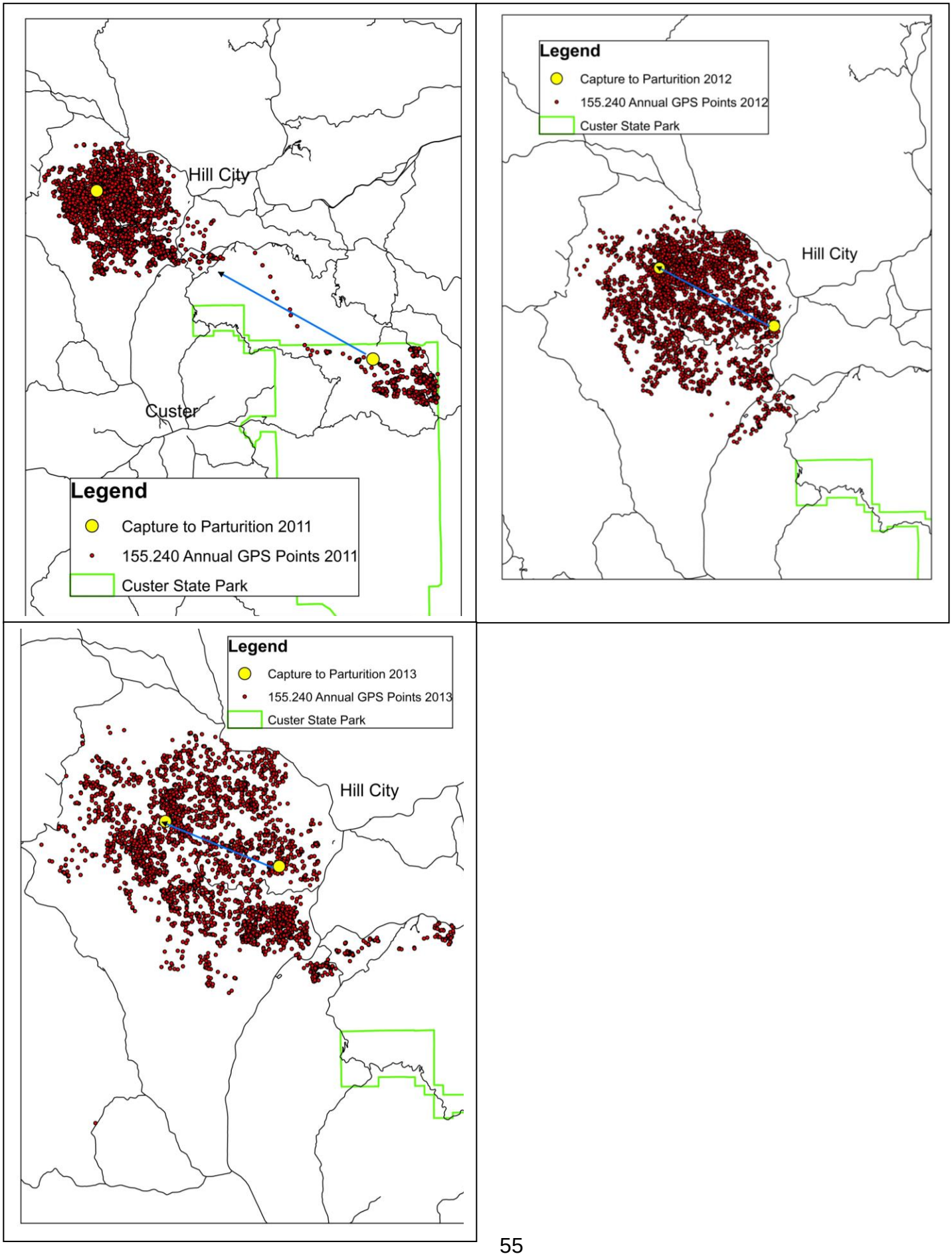
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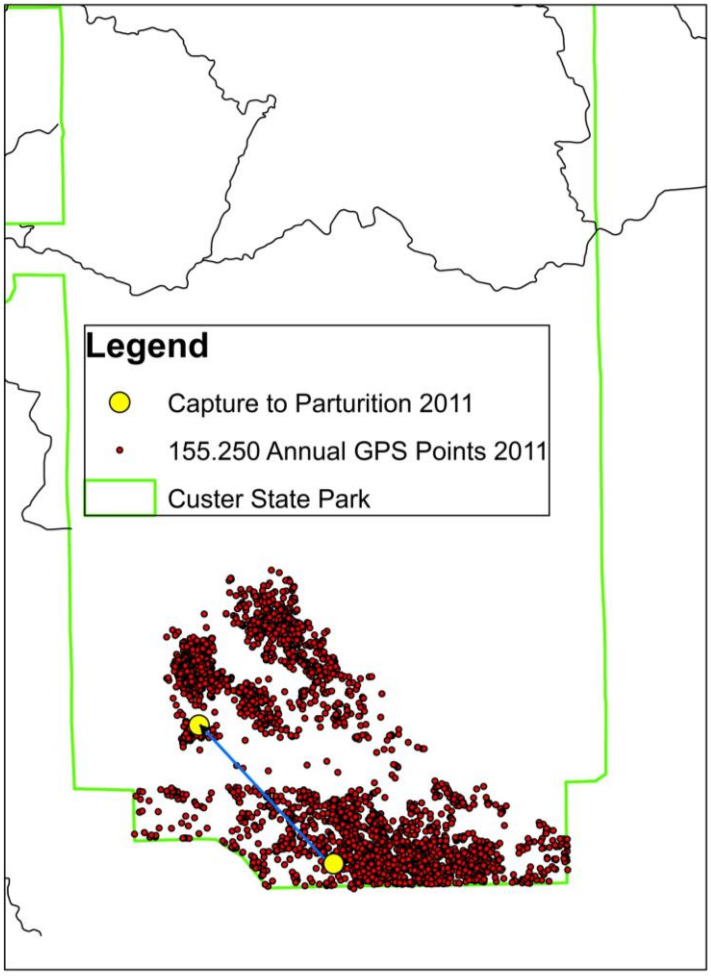
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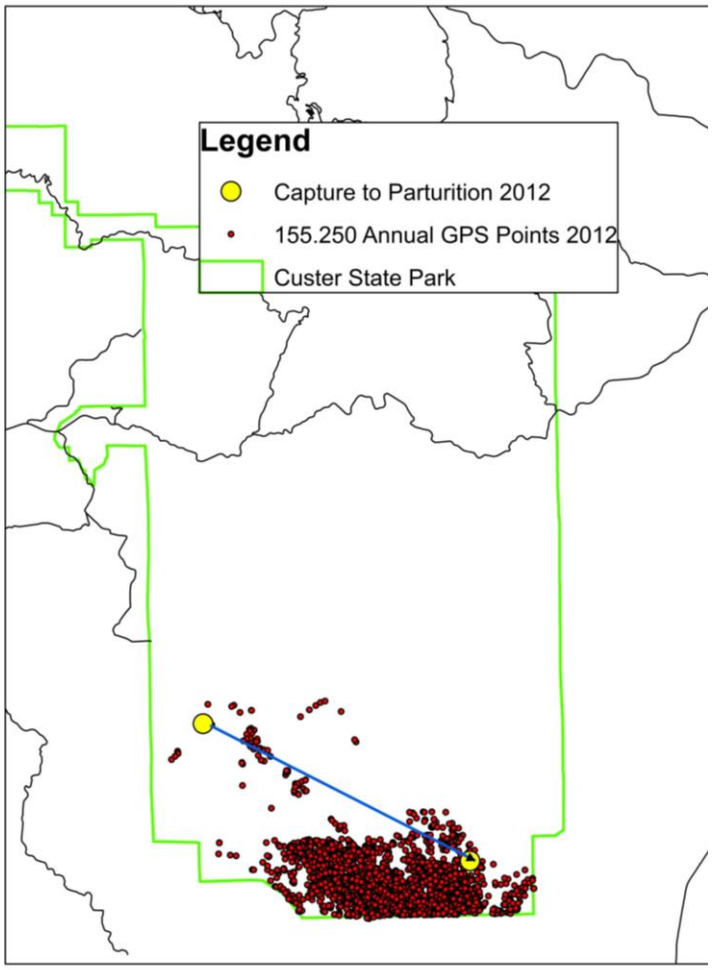
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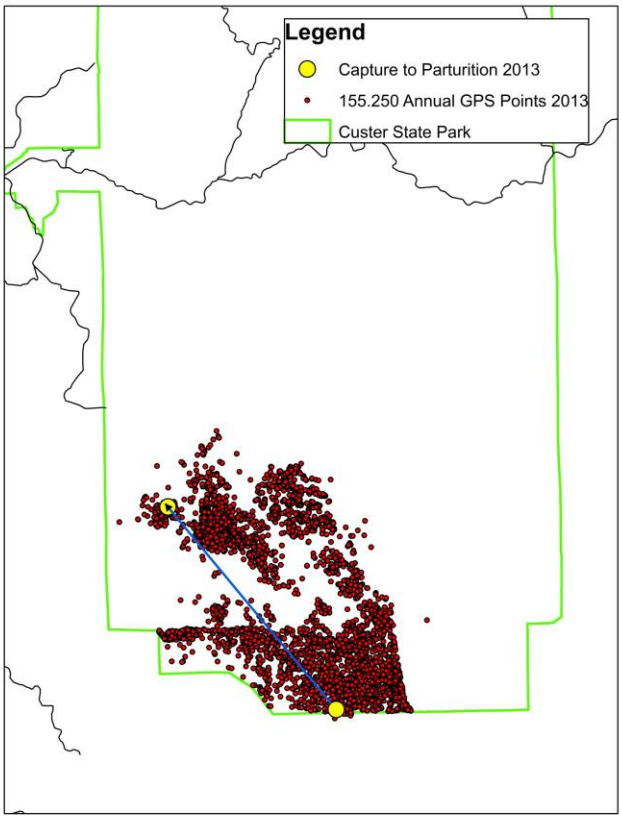
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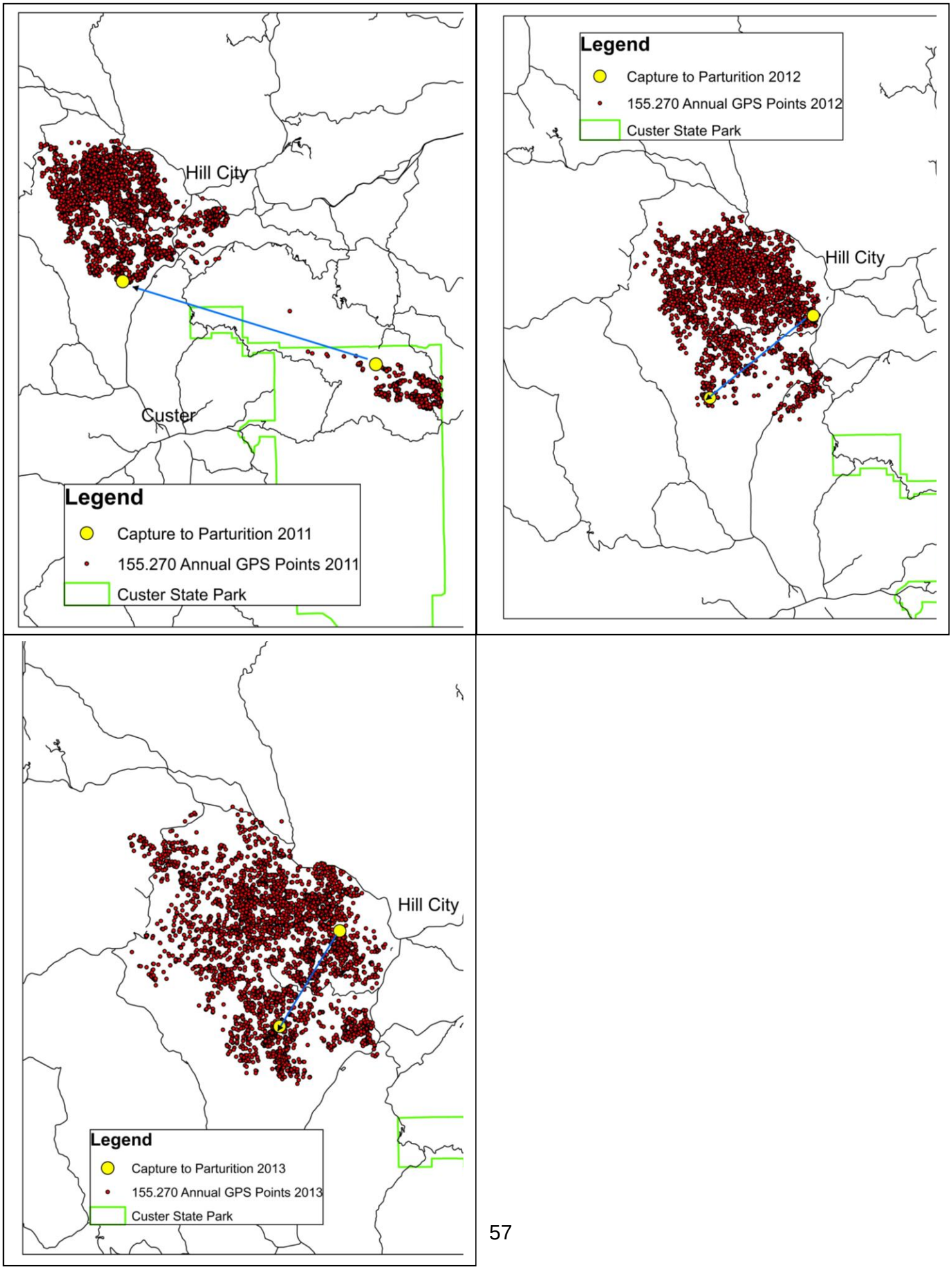
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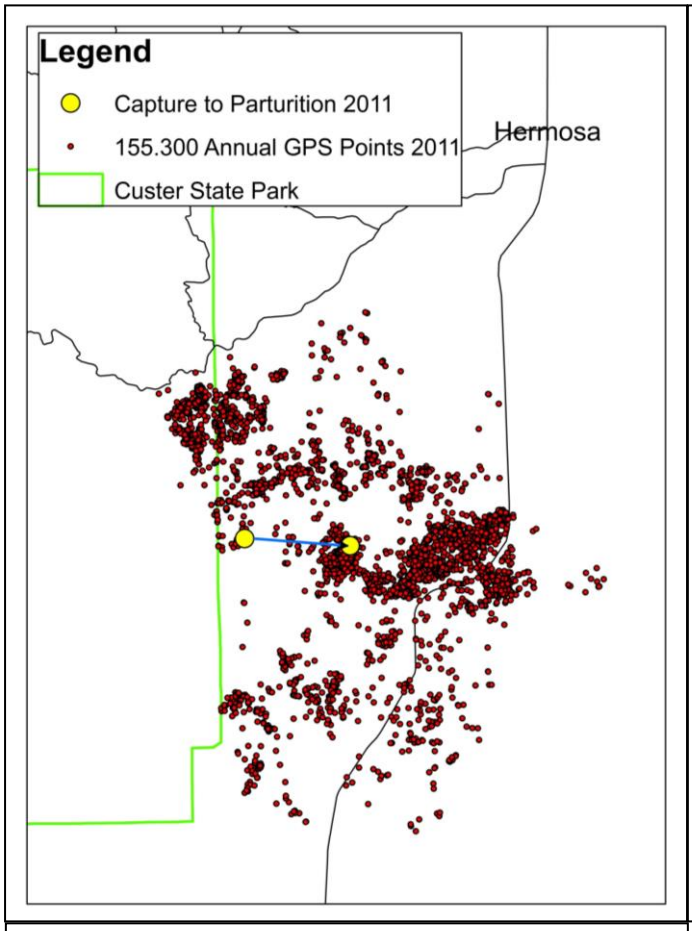
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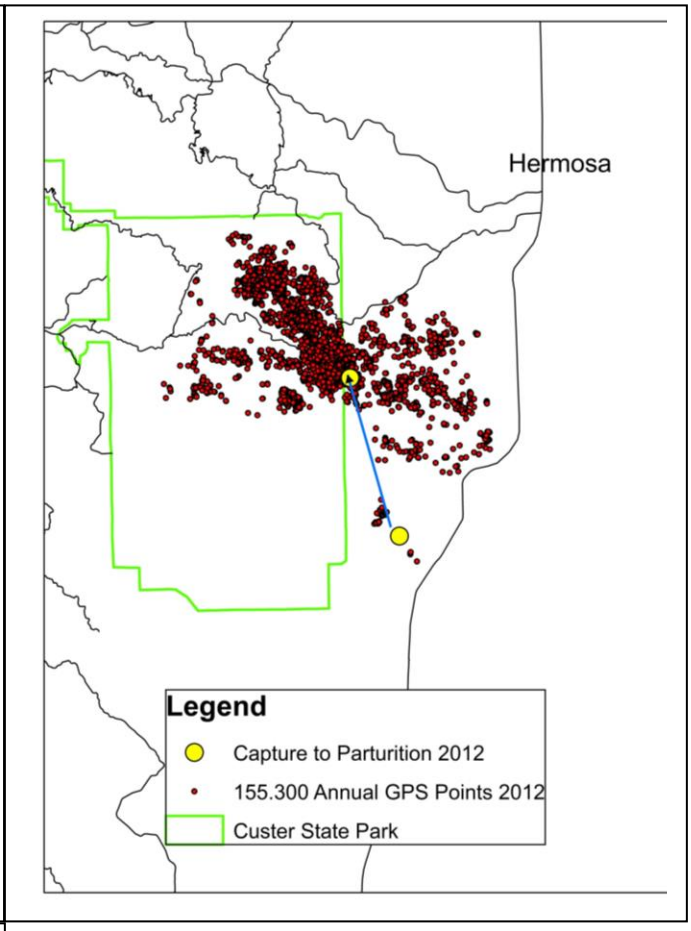
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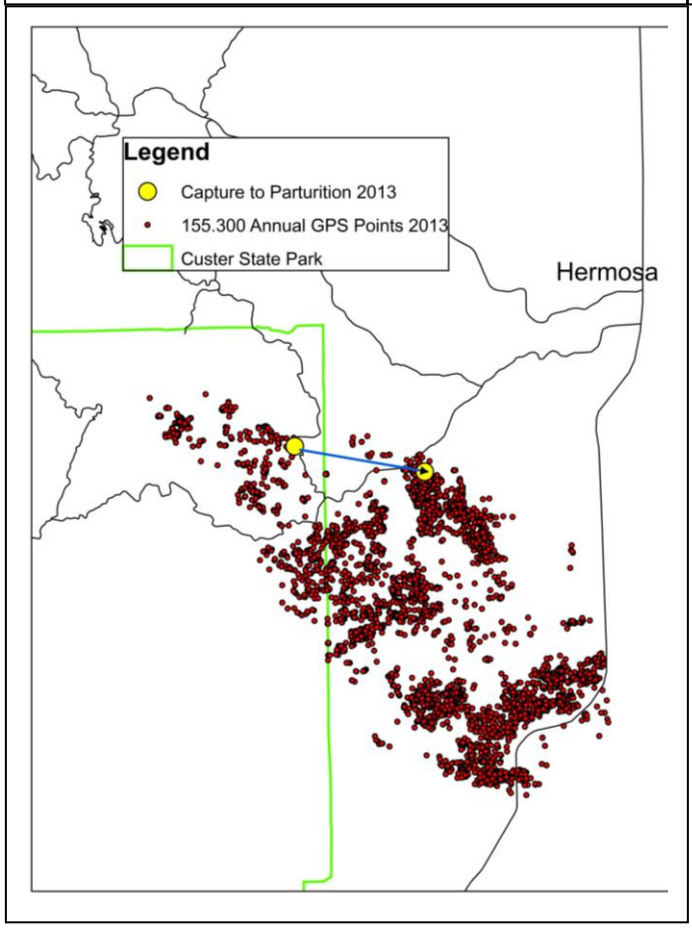
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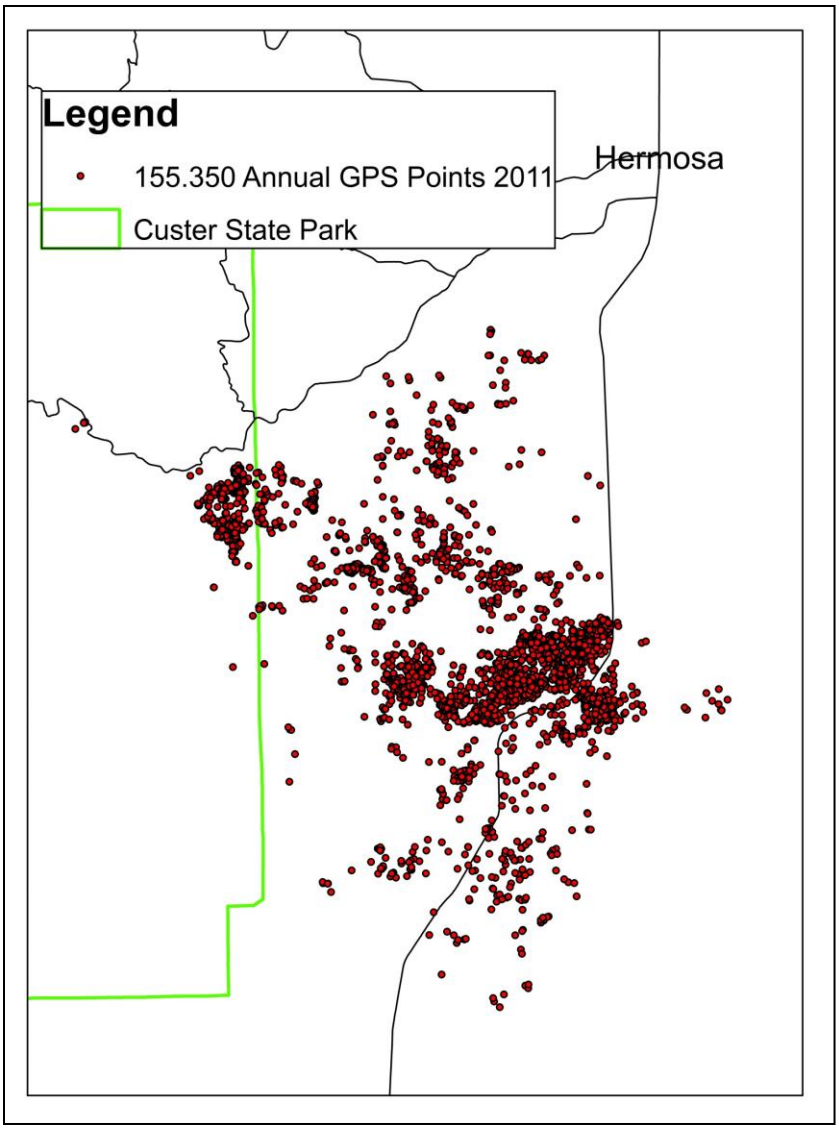
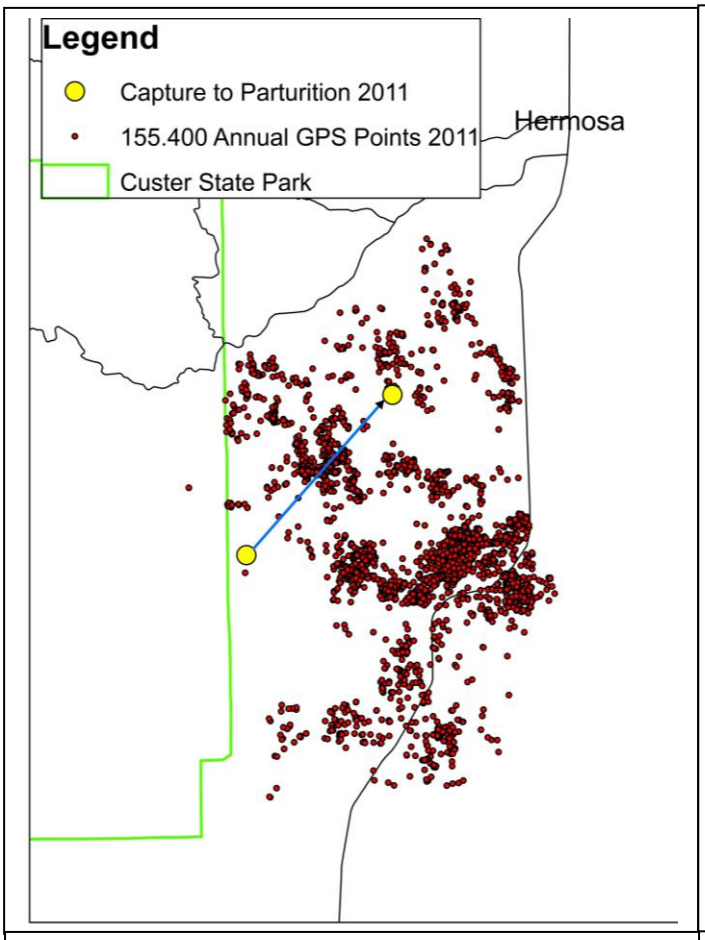
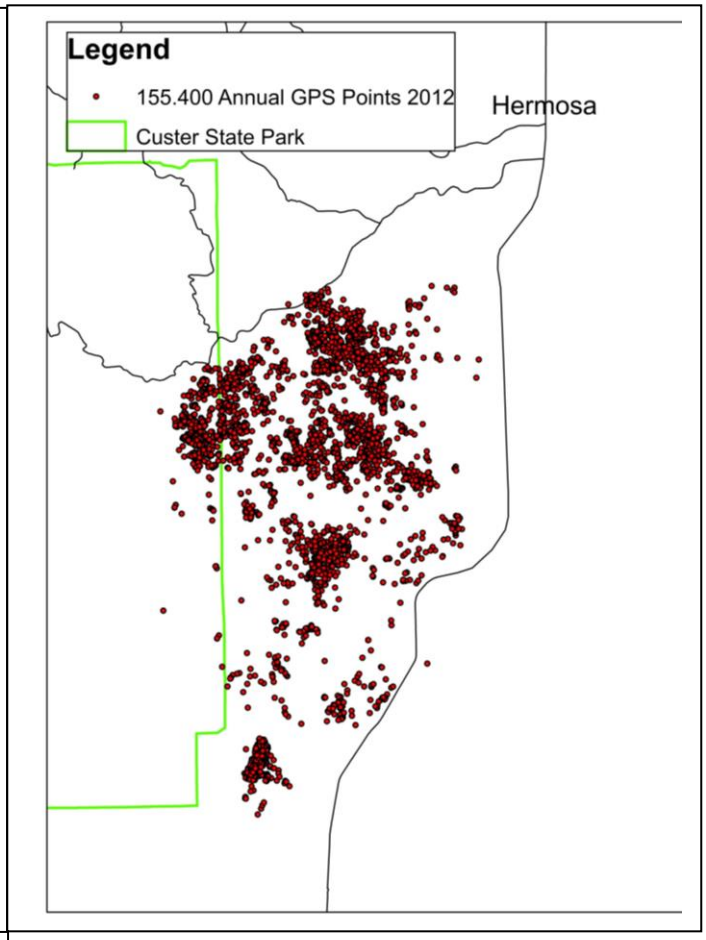
Custer State Park
Hermosa


Legend
155.350 Annual GPS Points 2011
Custer State Park
Hermosa


Legend
Capture to Parturition 2011
155.400 Annual GPS Points 2011
Custer State Park
Hermosa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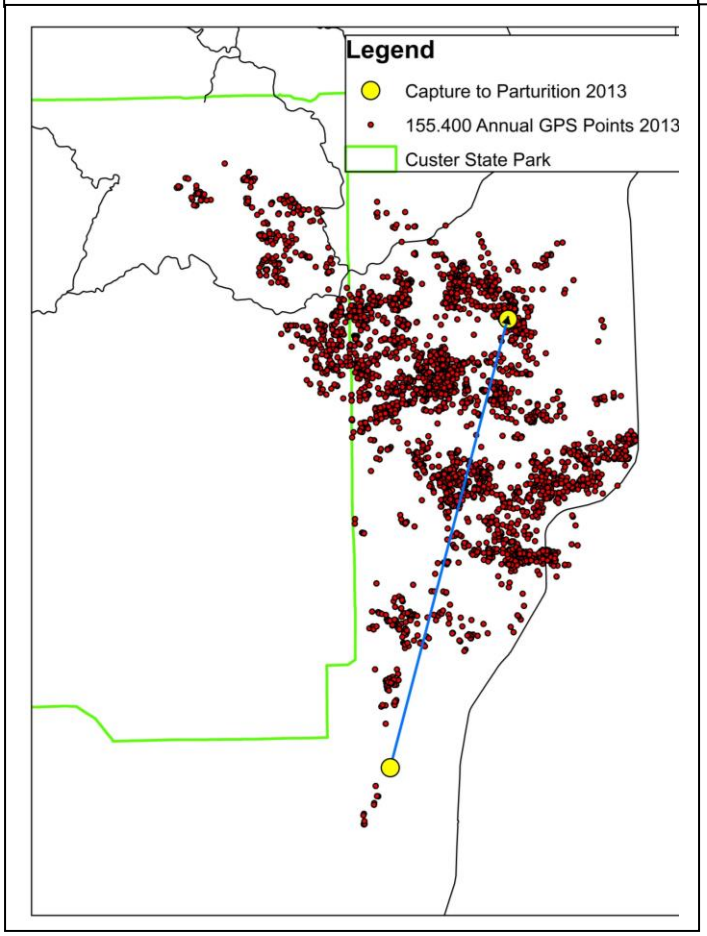
Custer State Park
Hermosa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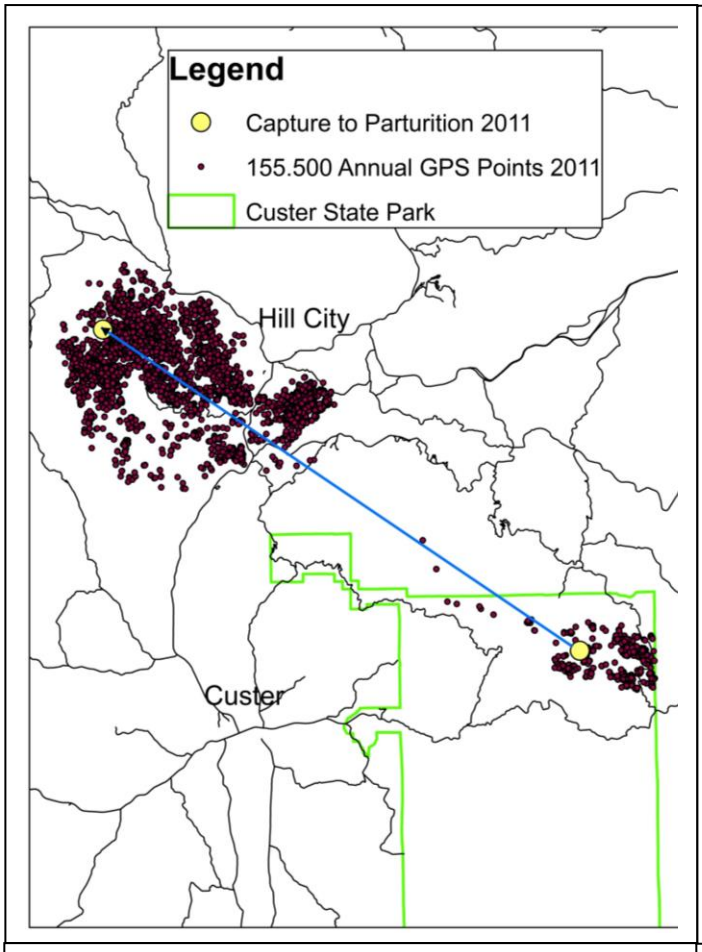
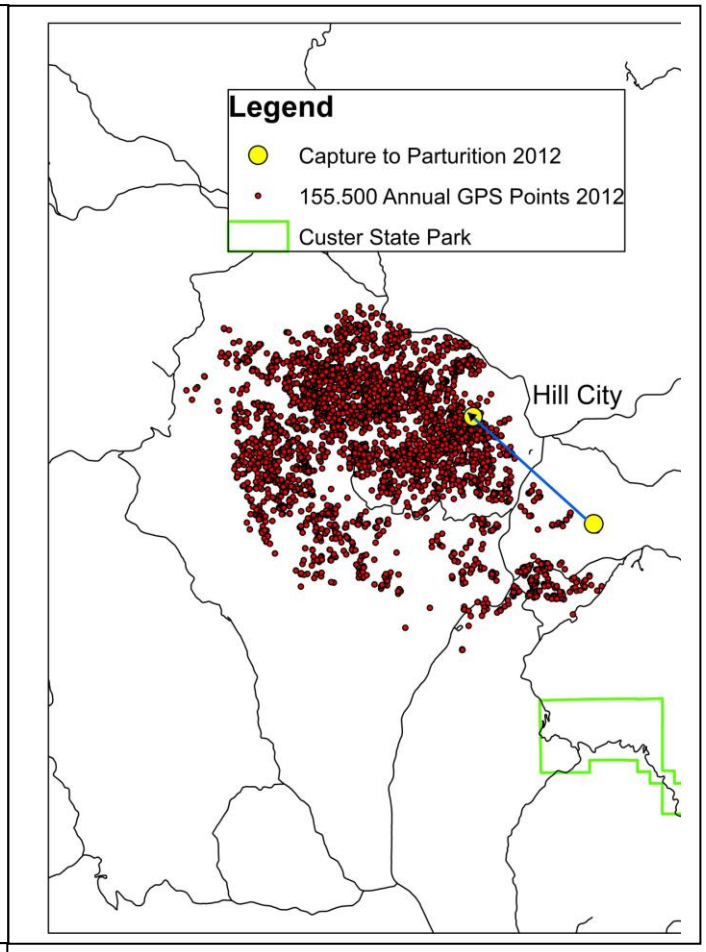
Capture to Parturition 2013
155.400 Annual GPS Points 2013
Custer State Park


Legend
Capture to Parturition 2011
155.500 Annual GPS Points 2011
Custer State Park
Hill City
Custer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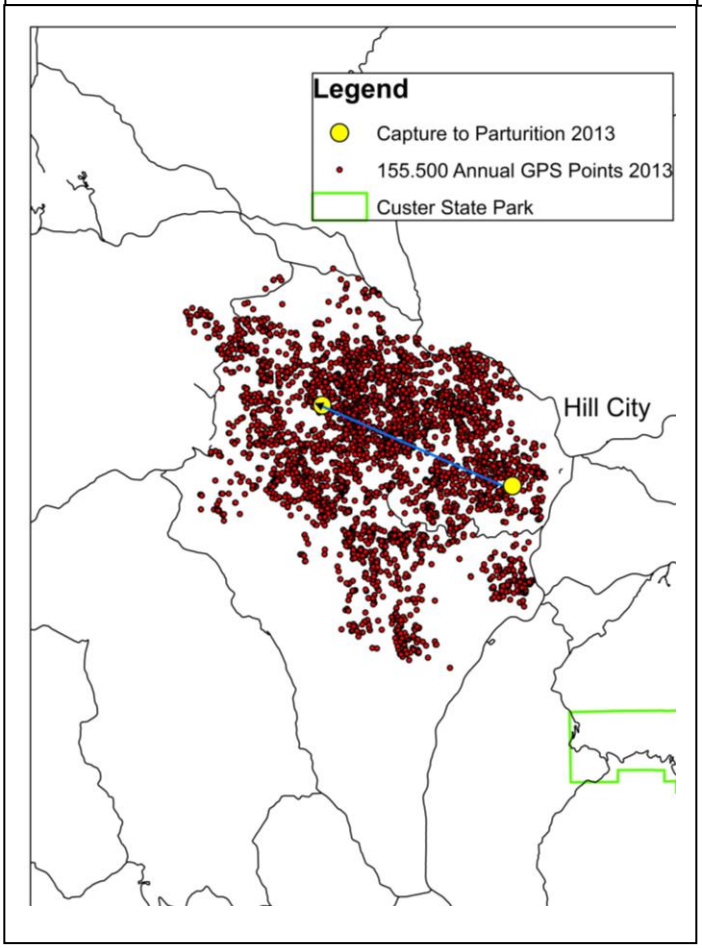
Capture to Parturition 2012
155.500 Annual GPS Points 2012
Custer State Park
Hill City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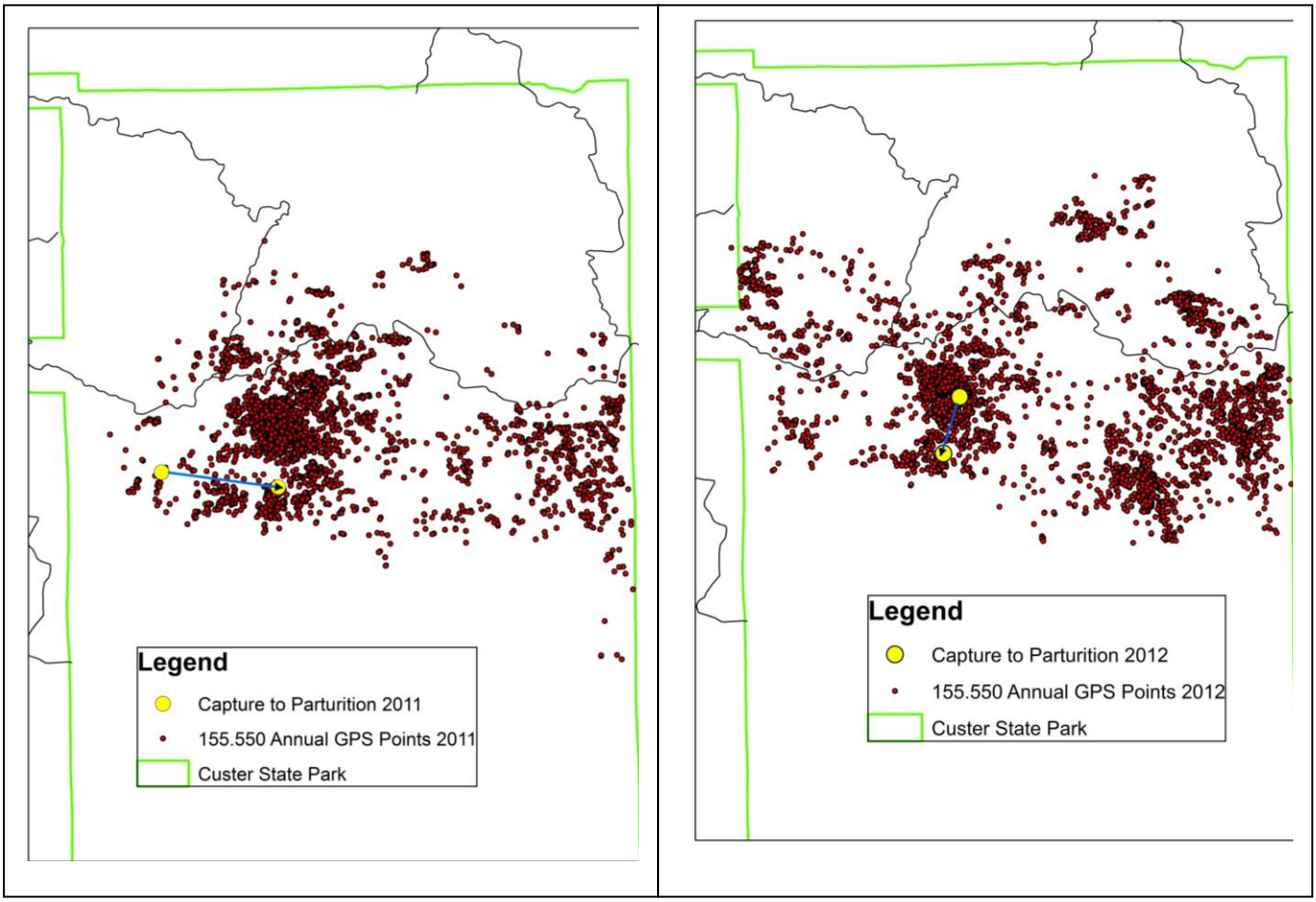
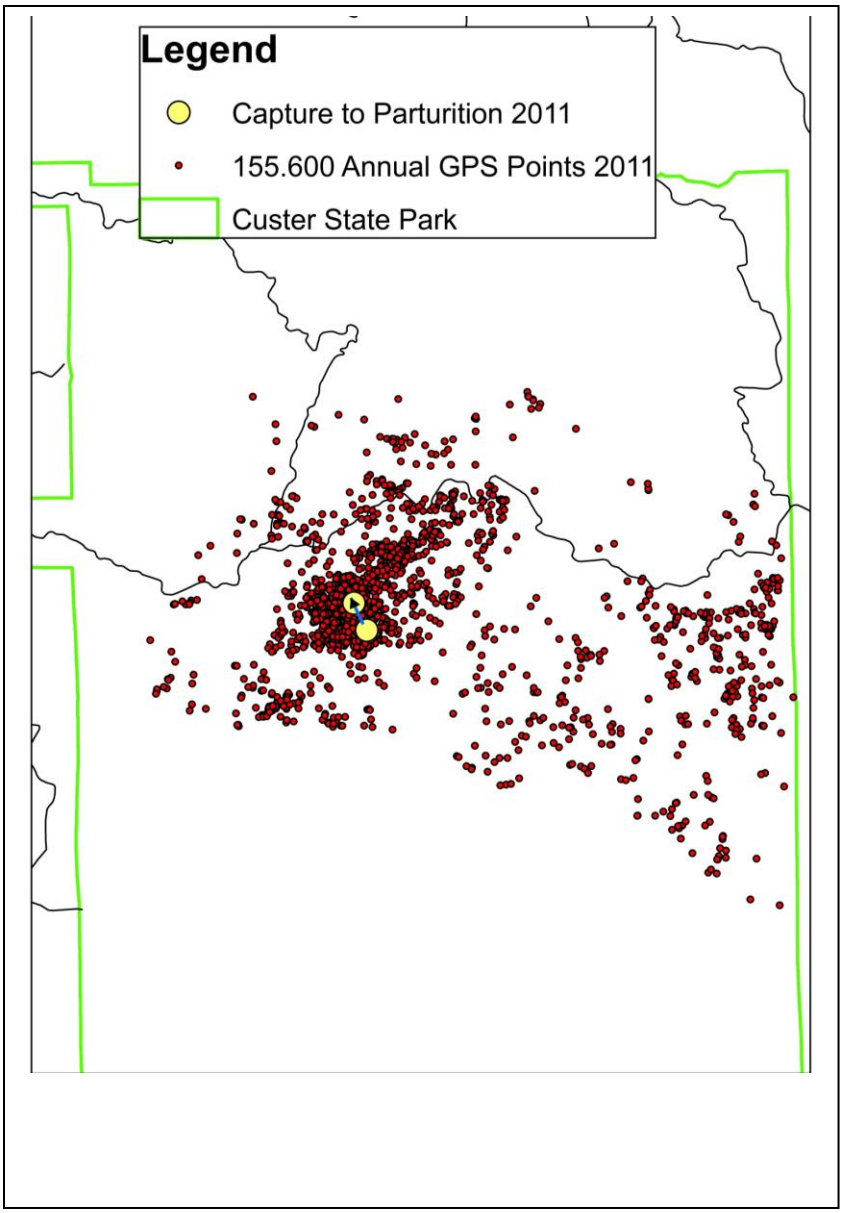
Capture to Parturition 2013
155.500 Annual GPS Points 2013
Custer State Park
Hill City


Legend
Capture to Parturition 2011
155.550 Annual GPS Points 2011
Custer State Park
Legend
Capture to Parturition 2012
155.550 Annual GPS Points 2012
Custer State Park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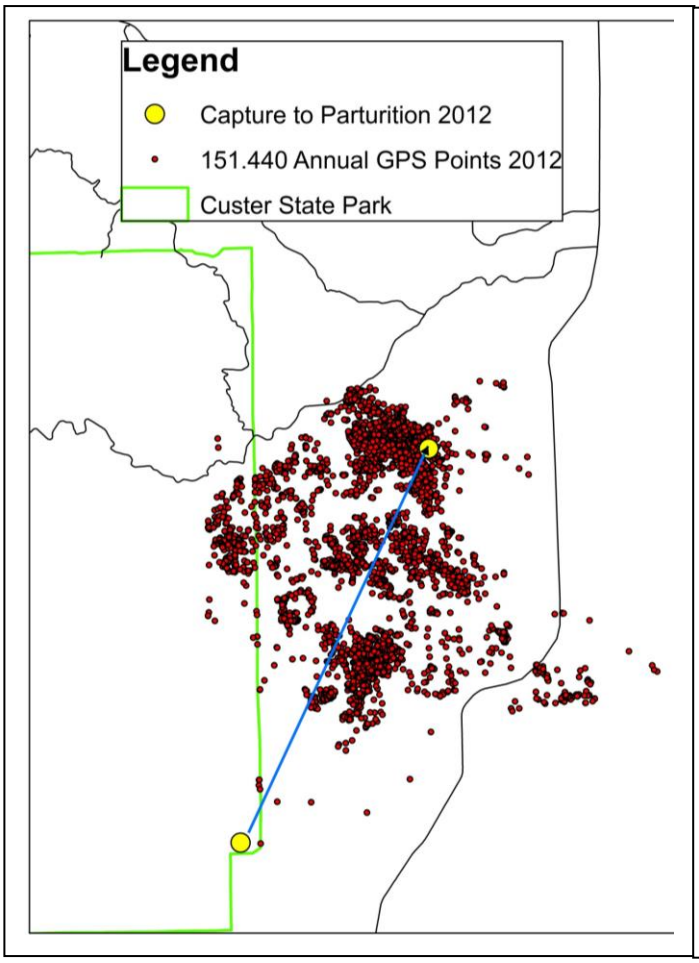
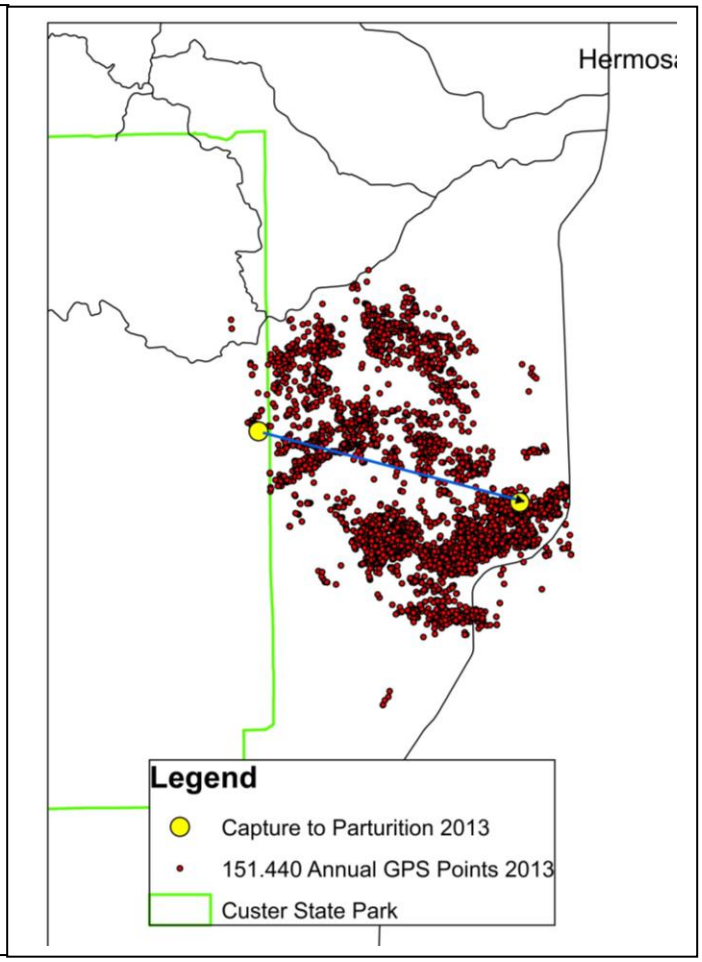
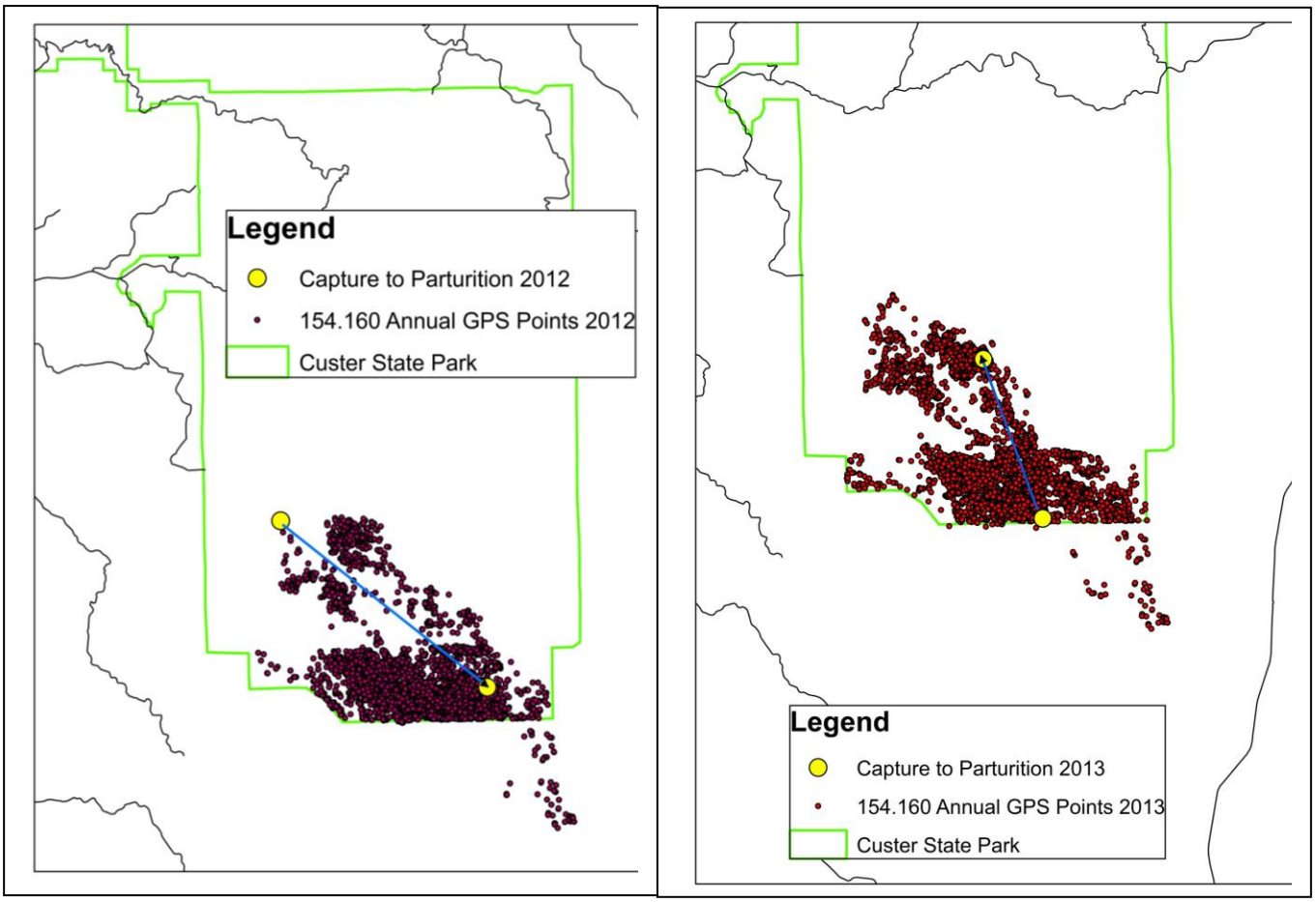
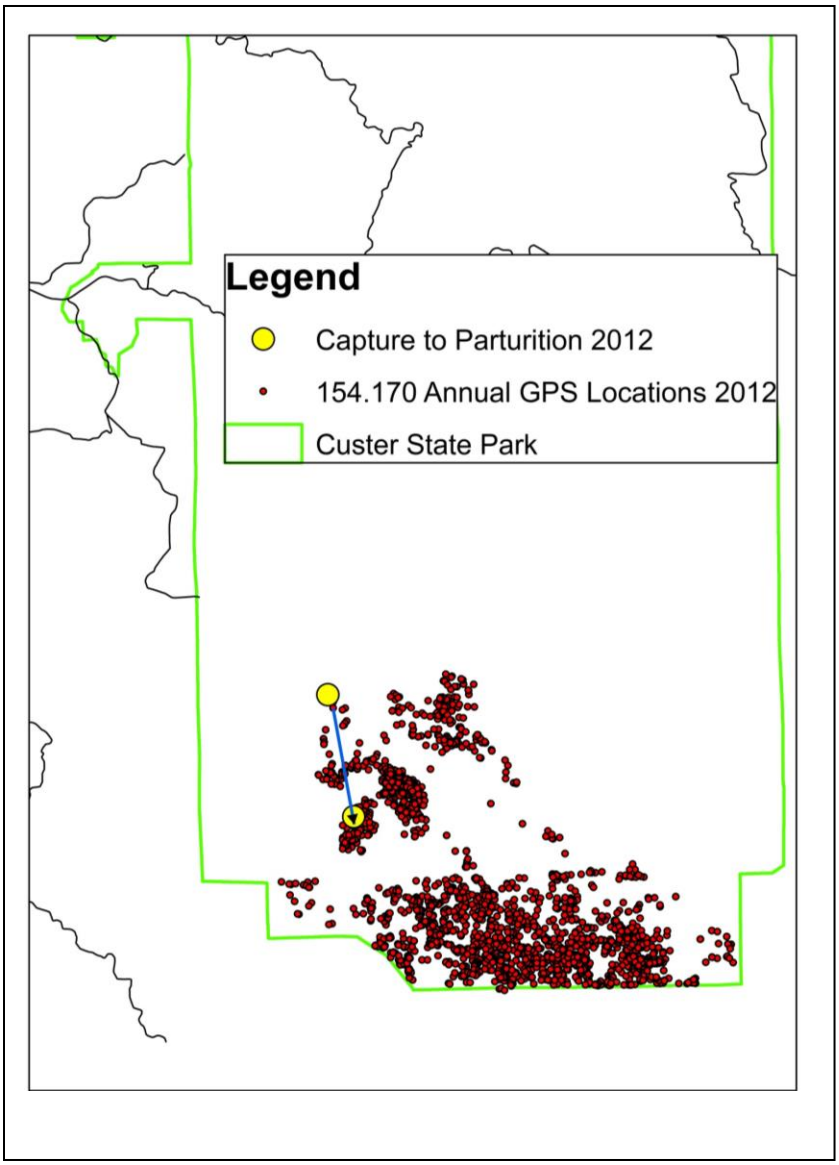
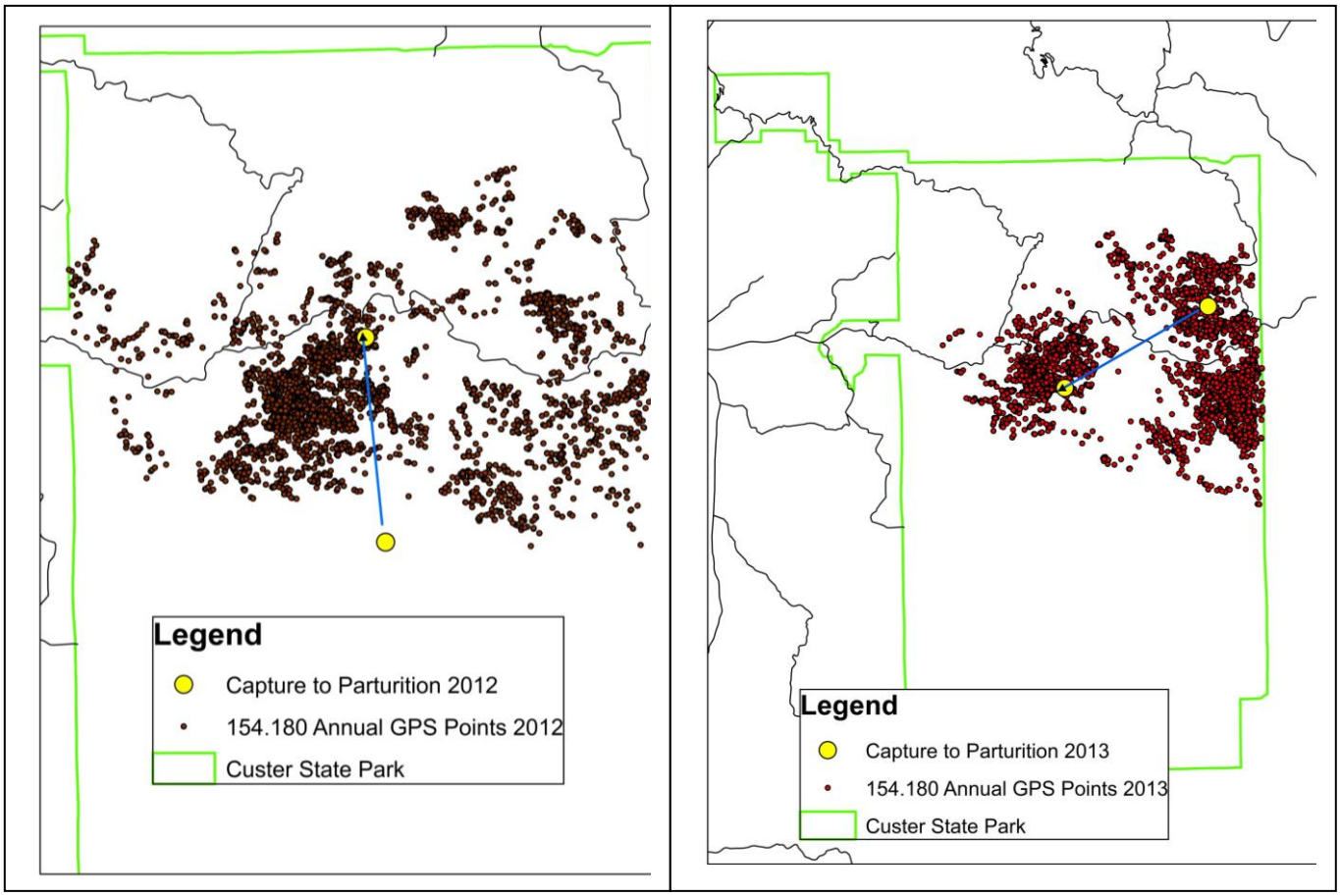
Capture to Parturition 2011
155.600 Annual GPS Points 2011
Custer State Park

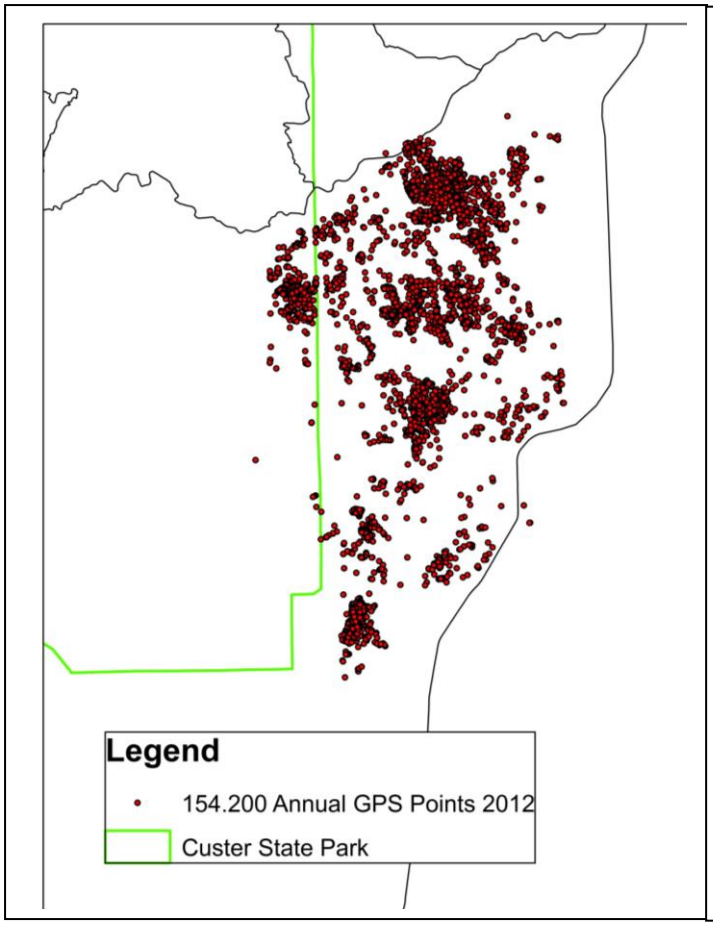

Legend
Capture to Parturition 2012
151.440 Annual GPS Points 2012
Custer State Park

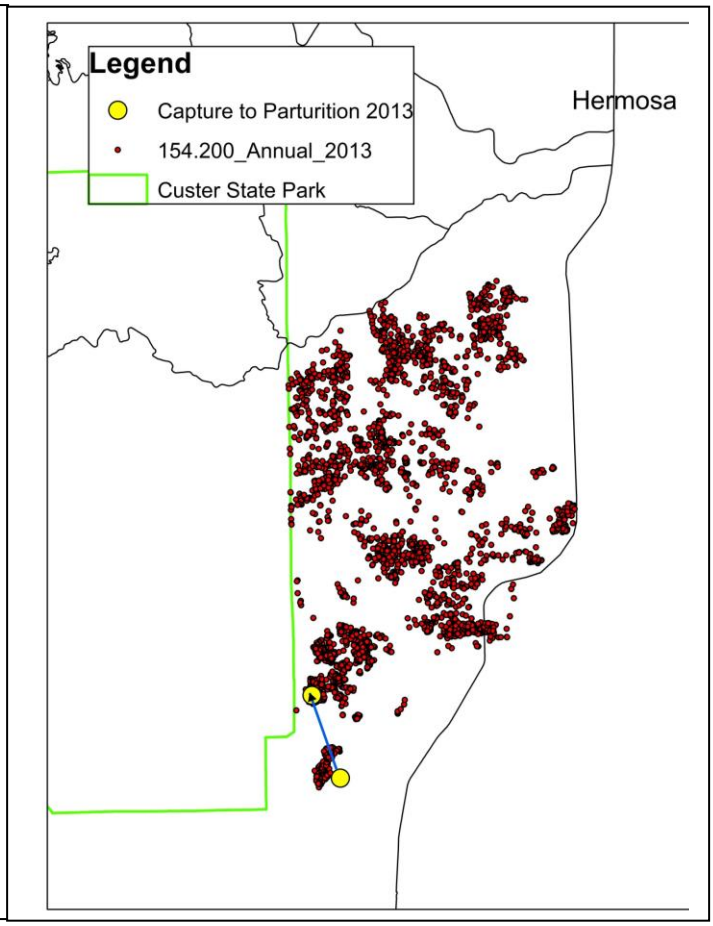

Hermosa
Legend
Capture to Parturition 2013
151.440 Annual GPS Points 2013
Custer State Park

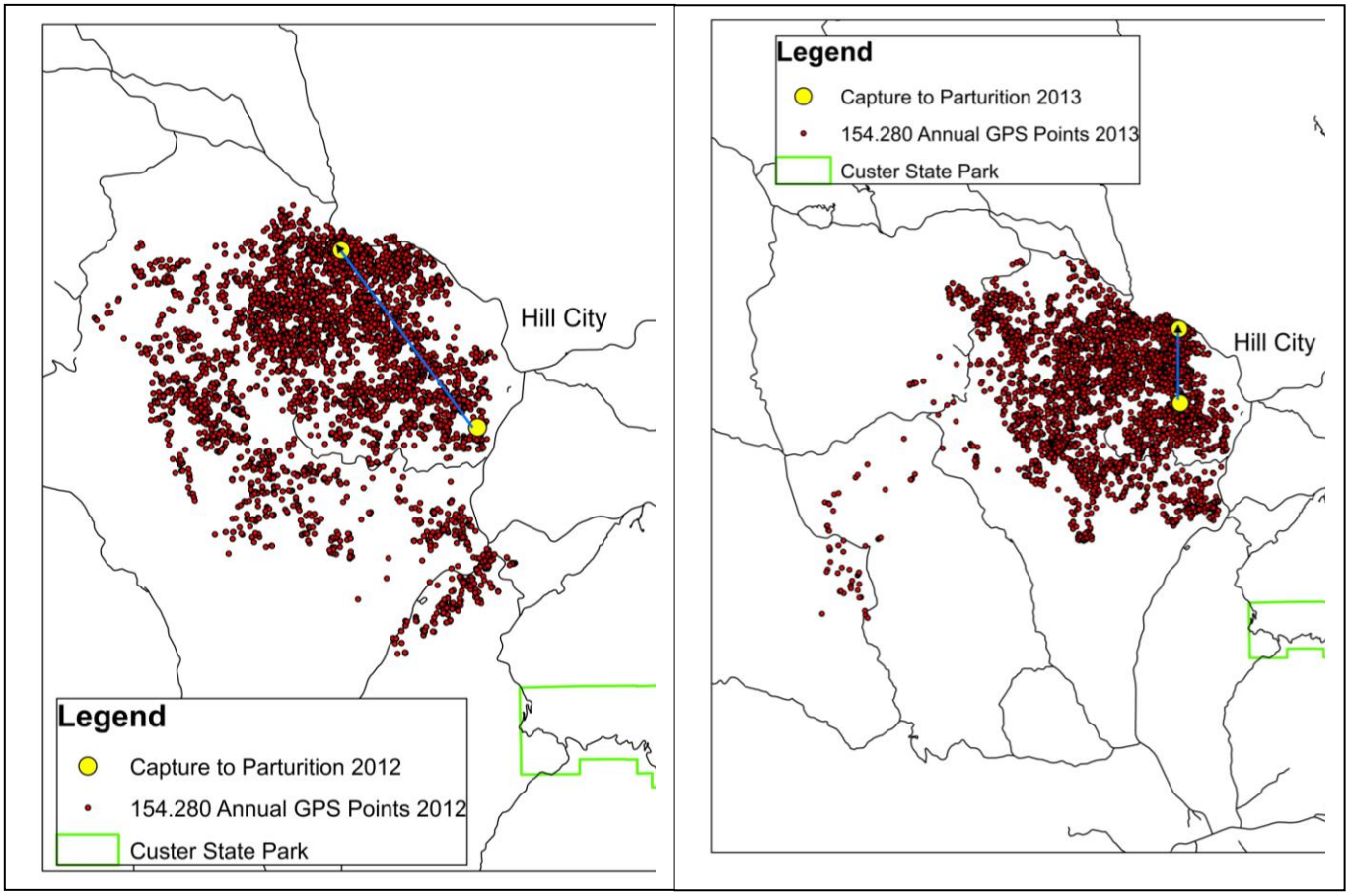

Legend
Capture to Parturition 2012
154.160 Annual GPS Points 2012
Custer State Park
Legend
Capture to Parturition 2013
154.160 Annual GPS Points 2013
Custer State Park

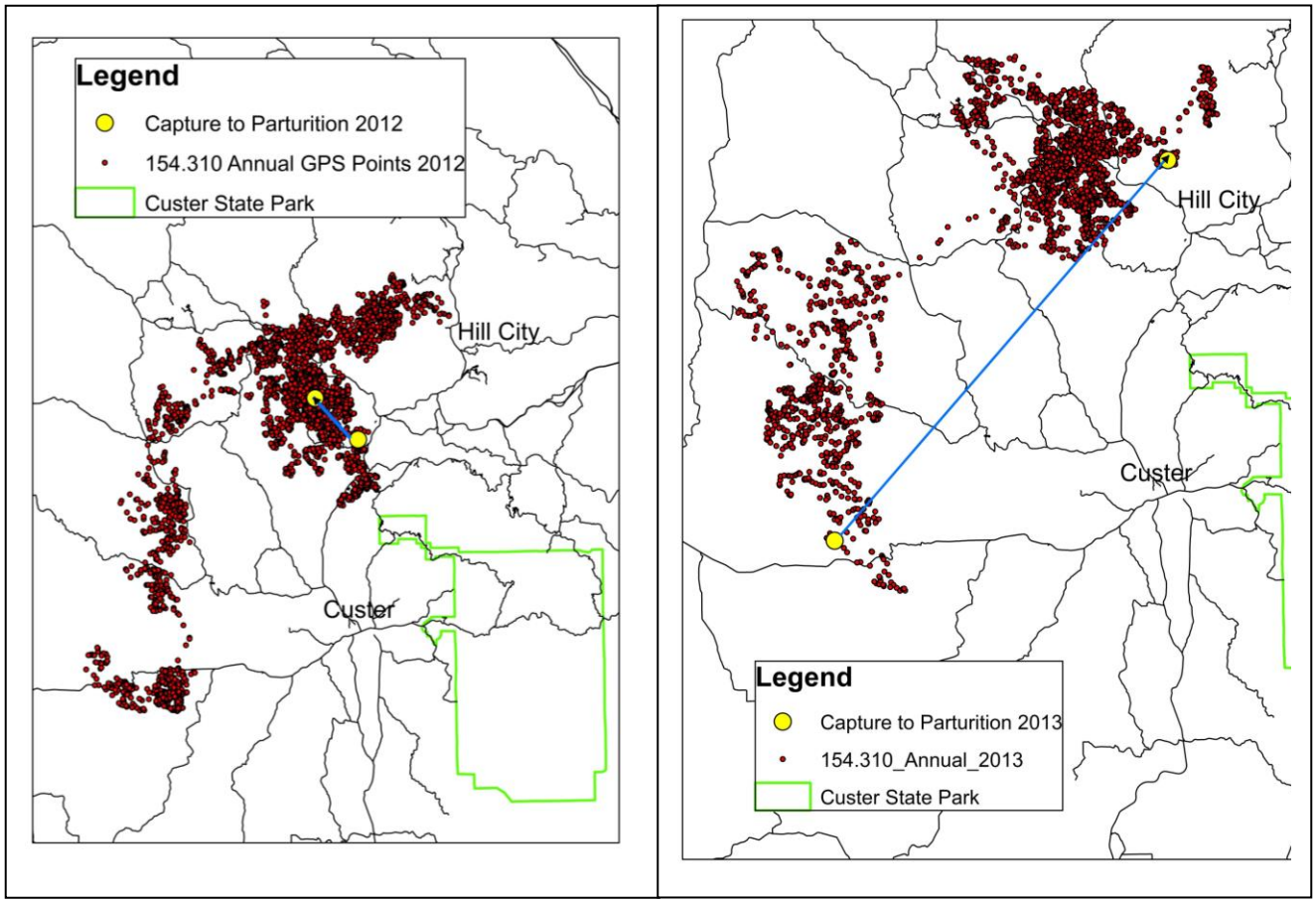

Legend
Capture to Parturition 2012
154.170 Annual GPS Locations 2012
Custer State Park

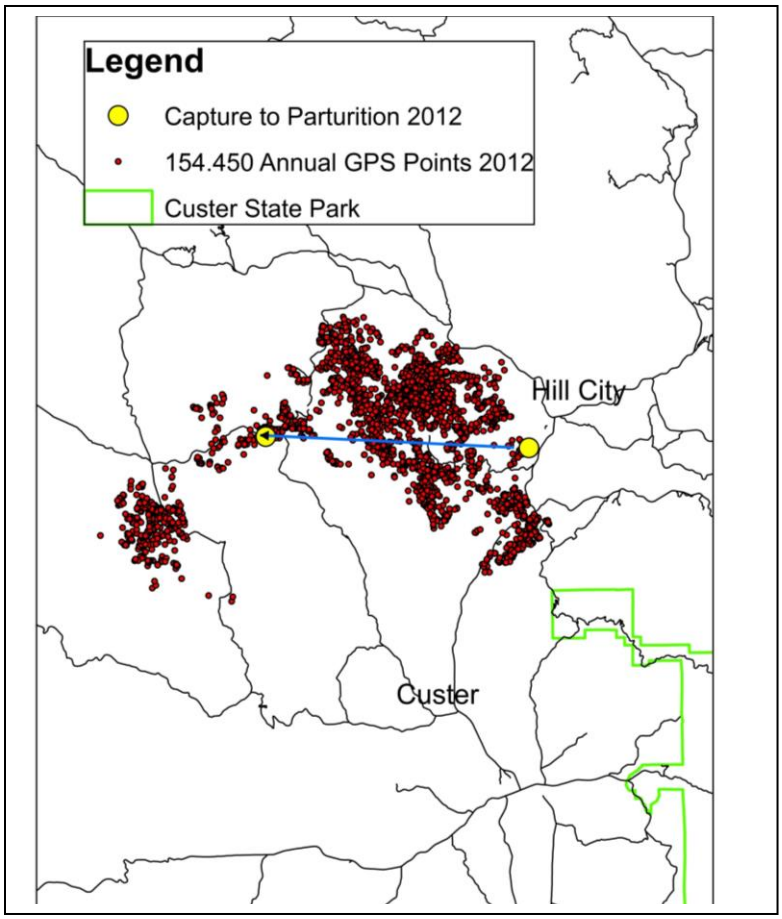

Legend
Capture to Parturition 2012
154.180 Annual GPS Points 2012
Custer State Park
Legend
Capture to Parturition 2013
154.180 Annual GPS Points 2013
Custer State Park

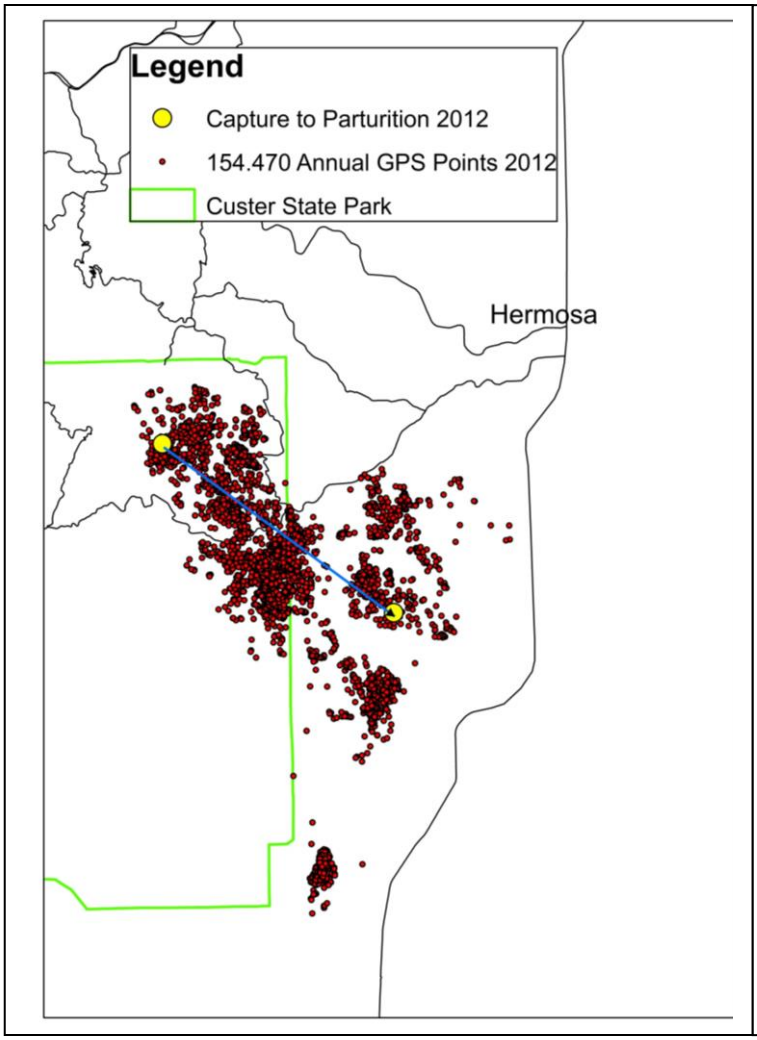

Legend
154.200 Annual GPS Points 2012
Custer State Park

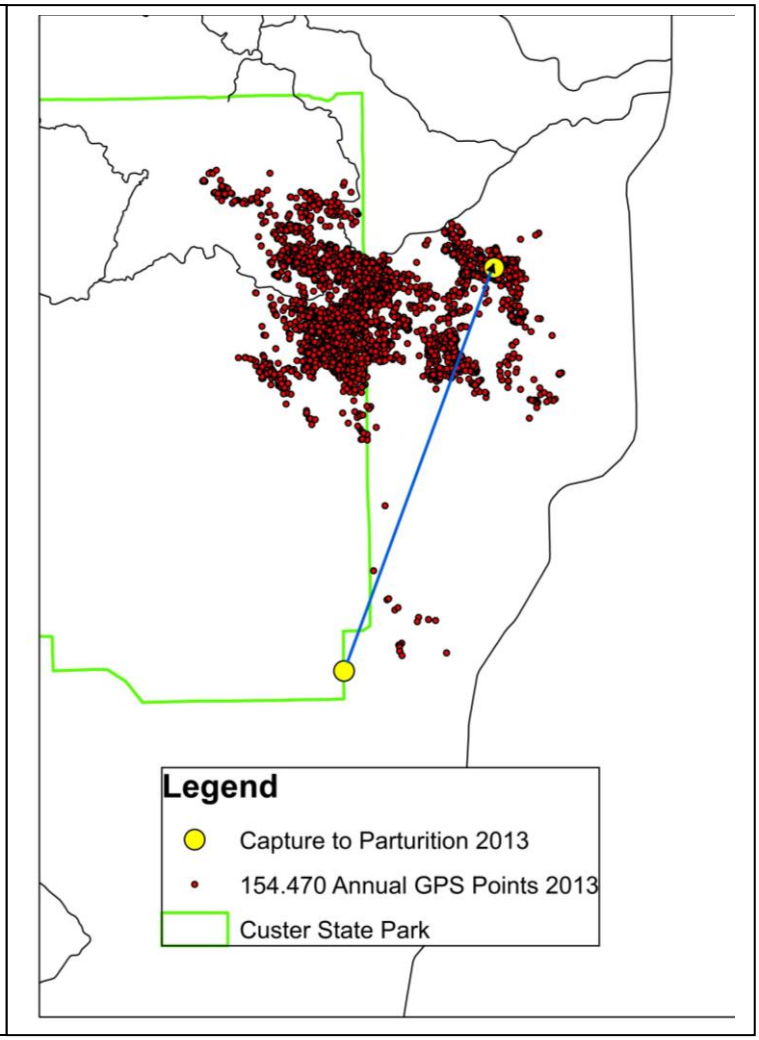

Legend
Capture to Parturition 2013
154.200_Annual_2013
Custer State Park
Hermosa


Hill City
Legend
Capture to Parturition 2012
154.280 Annual GPS Points 2012
Custer State Park
Legend
Capture to Parturition 2013
154.280 Annual GPS Points 2013
Custer State Park
Hill City


Legend
Capture to Parturition 2012
154.310 Annual GPS Points 2012
Custer State Park
Hill City
Custer
Legend
Capture to Parturition 2013
154.310_Annual_2013
Custer State Park
Hill City
Custer


Legend
Capture to Parturition 2012
154.450 Annual GPS Points 2012
Custer State Park
Hill City
Custer


Legend
Capture to Parturition 2012
154.470 Annual GPS Points 2012
Custer State Park
Hermosa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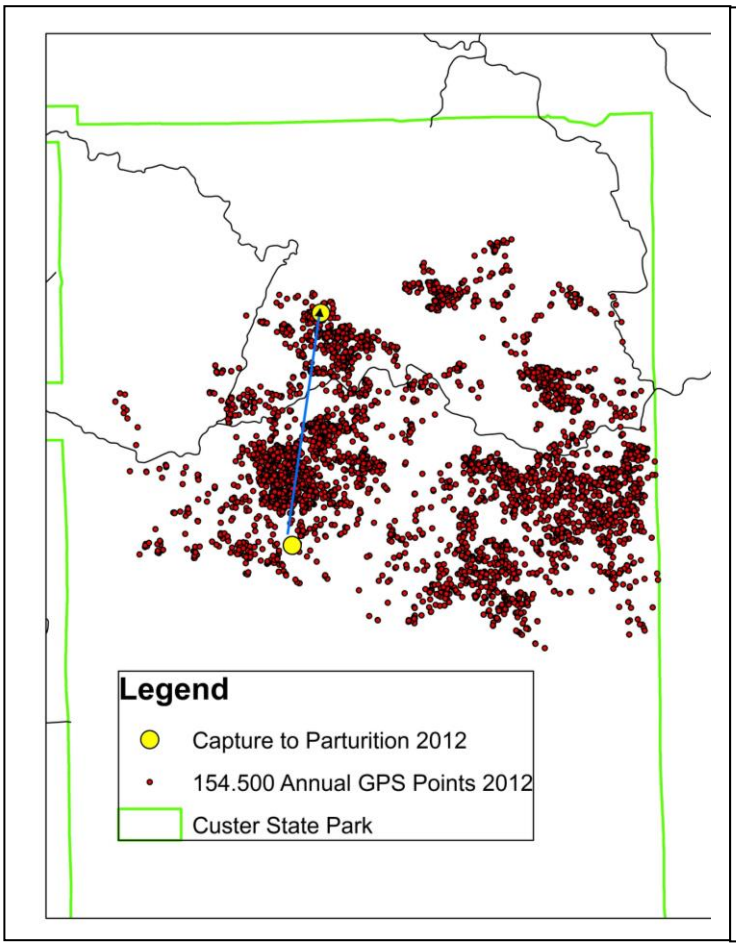
Capture to Parturition 2013
154.470 Annual GPS Points 2013
Custer State Park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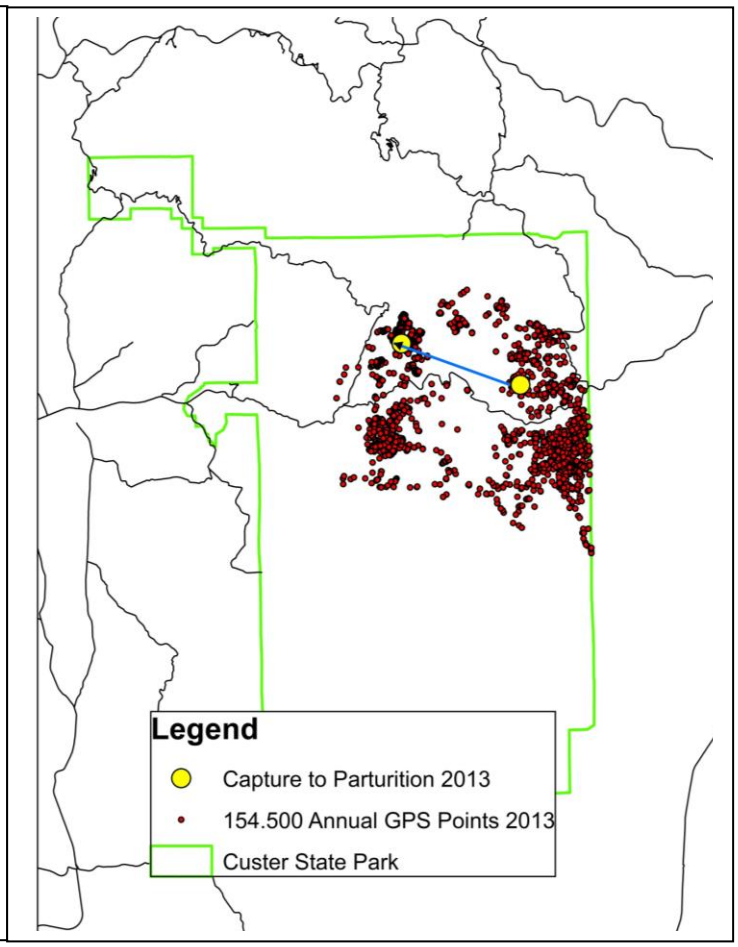
Capture to Parturition 2012
154.500 Annual GPS Points 2012
Custer State Park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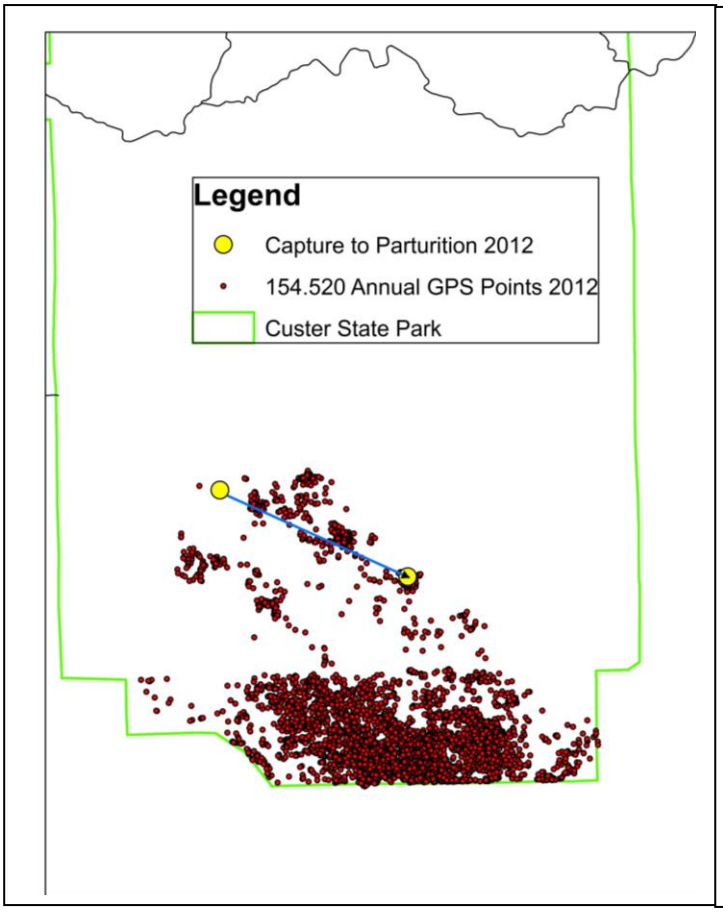
154.500 Annual GPS Points 2013
Custer State Park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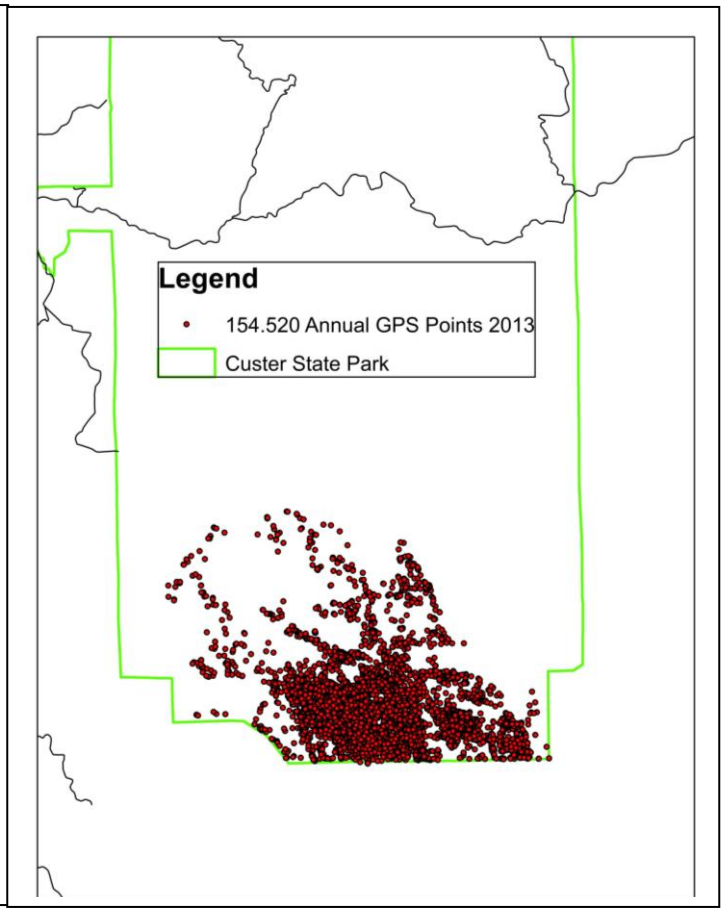
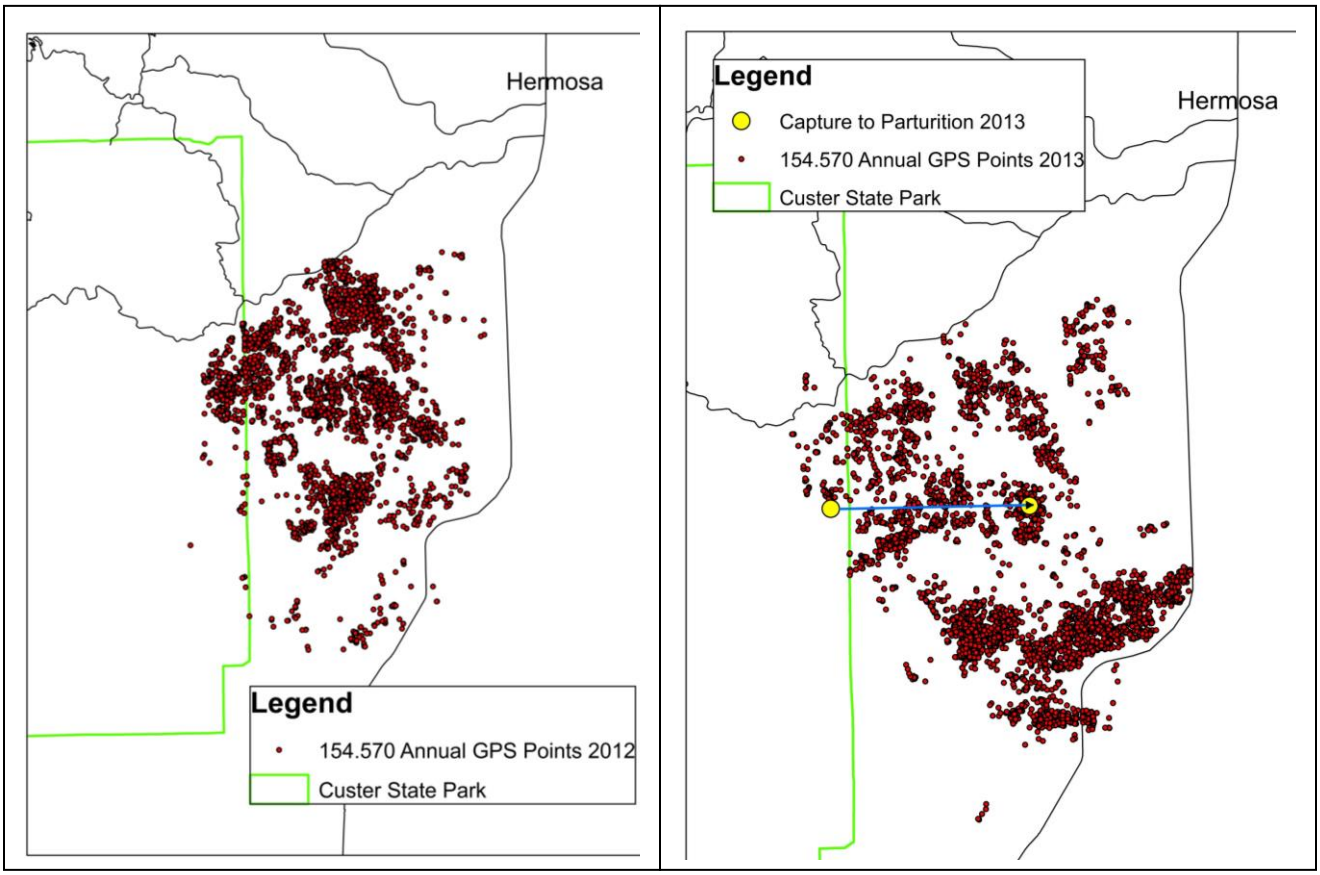
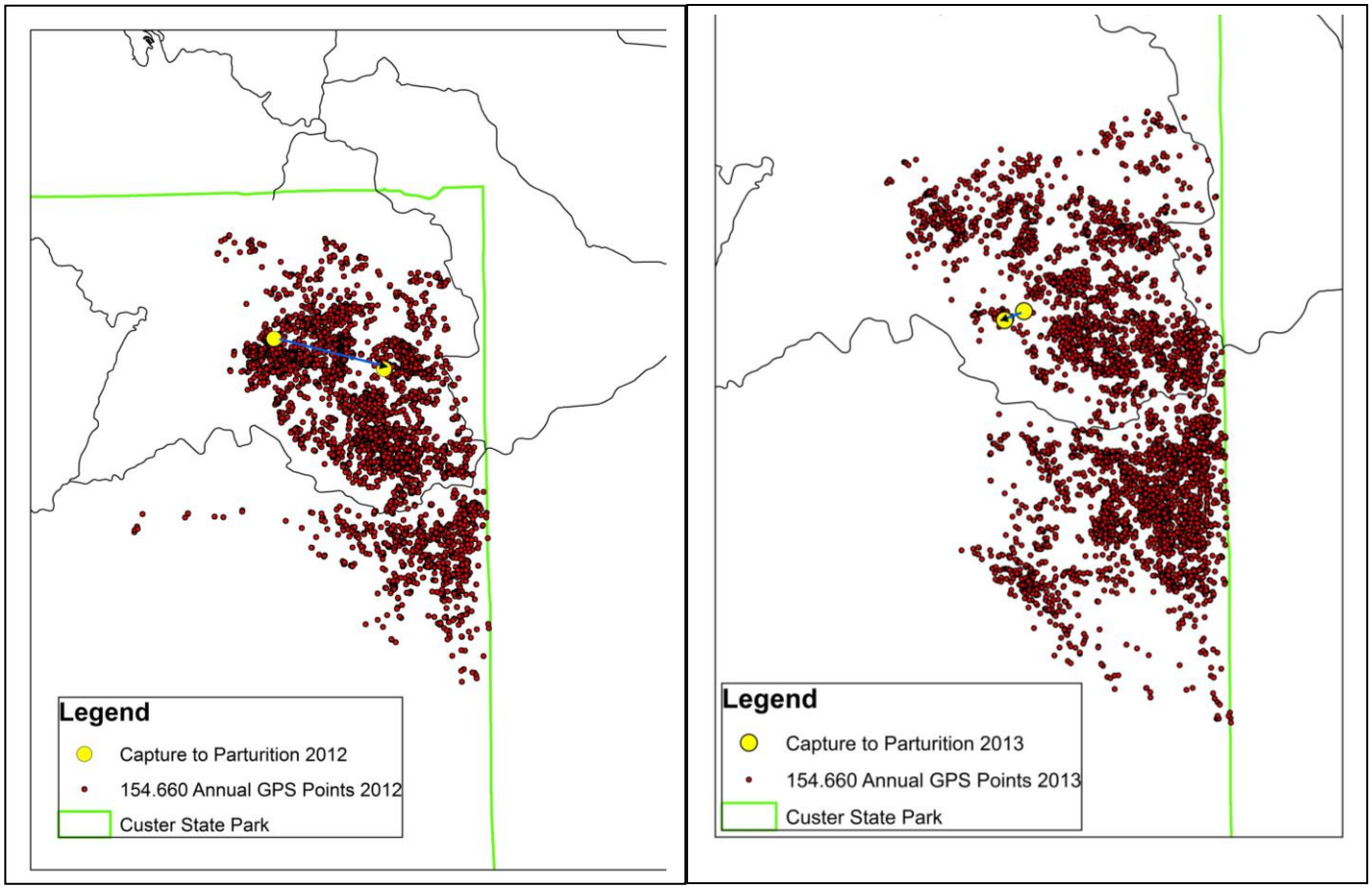
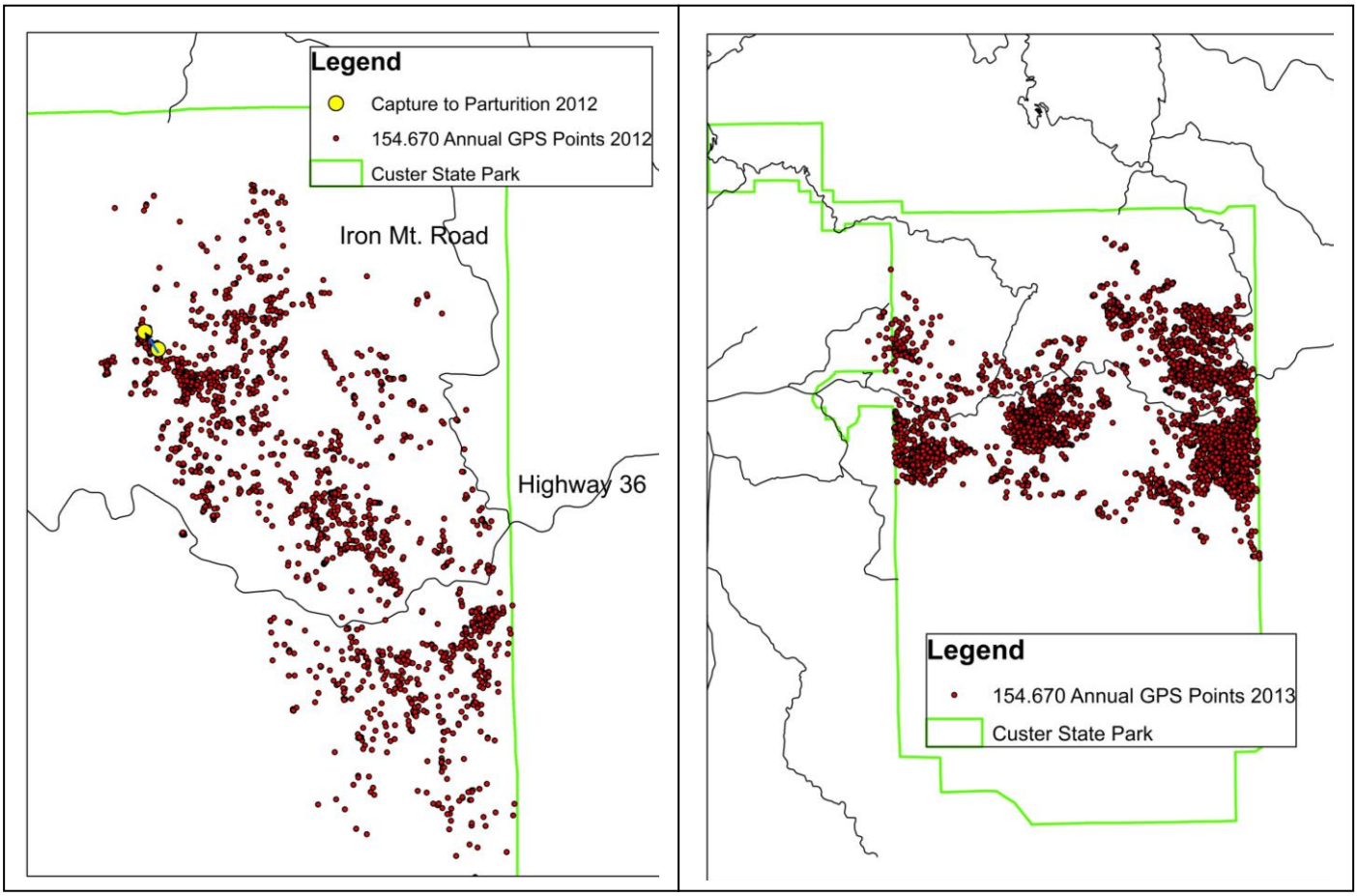
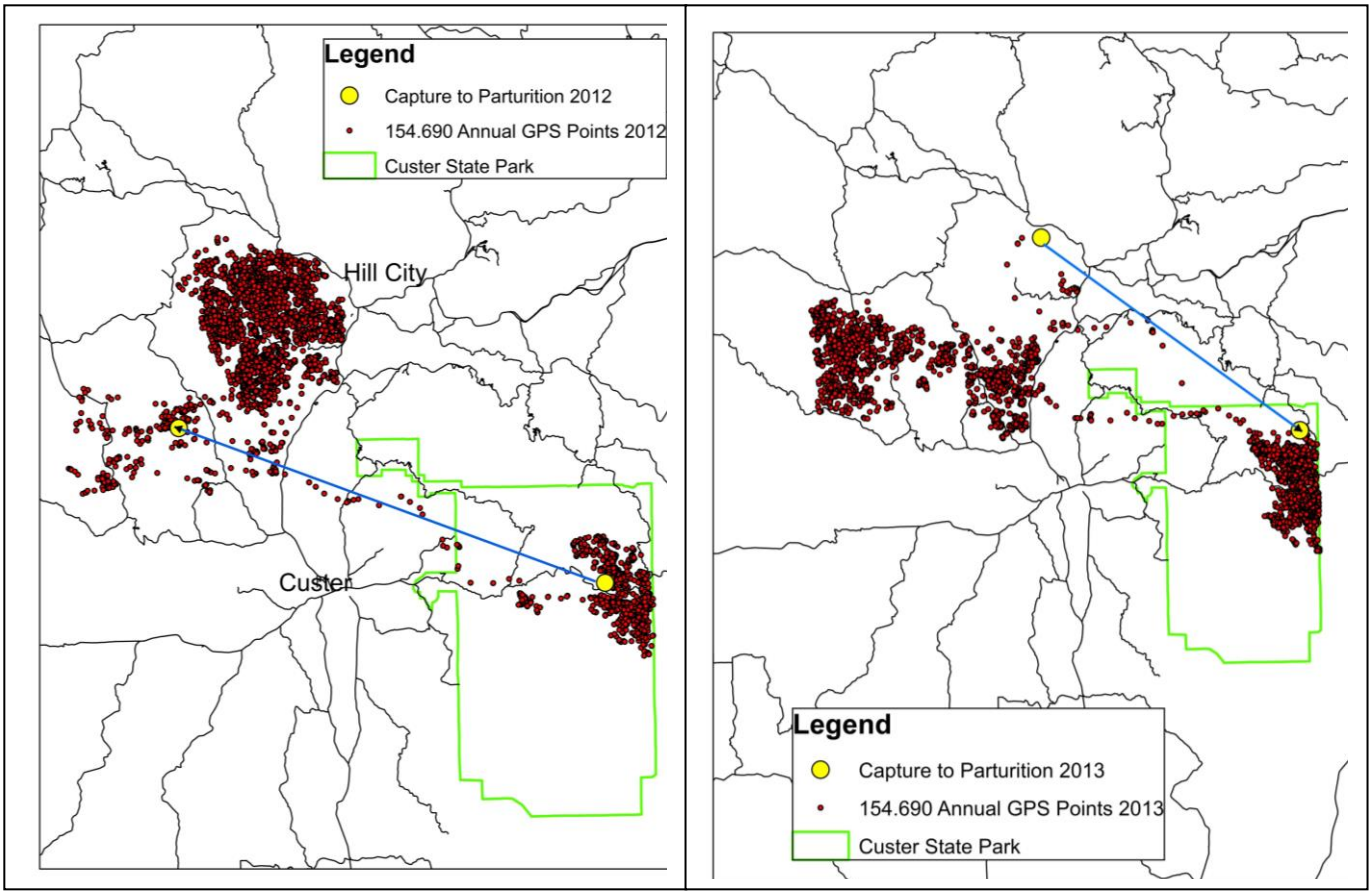
Capture to Parturition 2012
154.520 Annual GPS Points 2012
Custer State Park

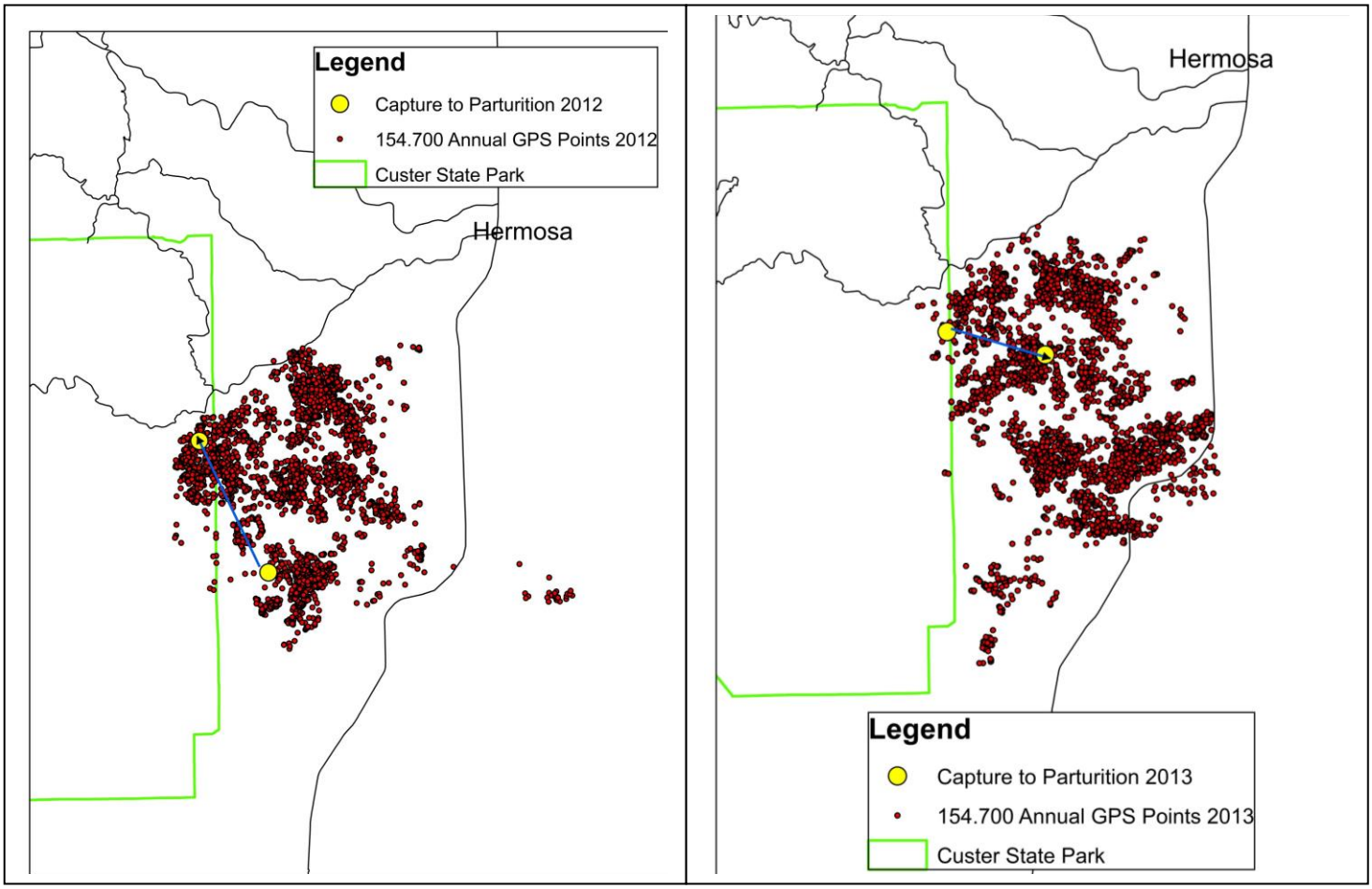

Legend
154.520 Annual GPS Points 2013
Custer State Park

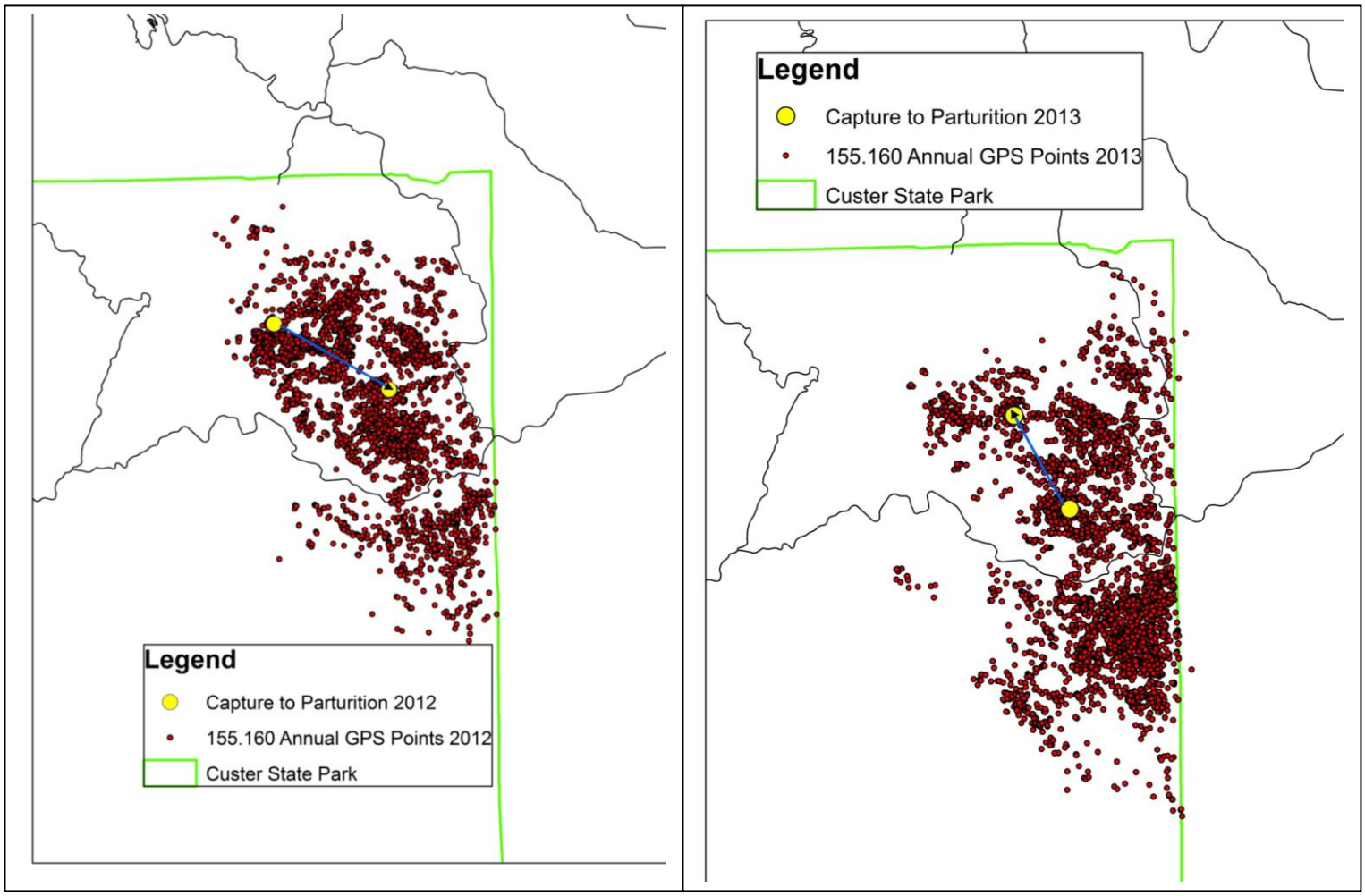

Hermosa
Legend
154.570 Annual GPS Points 2012
Custer State Park
Hermosa
Legend
Capture to Parturition 2013
154.570 Annual GPS Points 2013
Custer State Park


Legend
Capture to Parturition 2012
154.660 Annual GPS Points 2012
Custer State Park
Legend
Capture to Parturition 2013
154.660 Annual GPS Points 2013
Custer State Park


Legend
Capture to Parturition 2012
154.670 Annual GPS Points 2012
Custer State Park
Iron Mt. Road
Highway 36
Legend
154.670 Annual GPS Points 2013
Custer State Park


Legend
Capture to Parturition 2012
154.690 Annual GPS Points 2012
Custer State Park
Hill City
Custer
Legend
Capture to Parturition 2013
154.690 Annual GPS Points 2013
Custer State Park


Legend
Capture to Parturition 2012
154.700 Annual GPS Points 2012
Custer State Park
Hermosa
Hermosa
Legend
Capture to Parturition 2013
154.700 Annual GPS Points 2013
Custer State Park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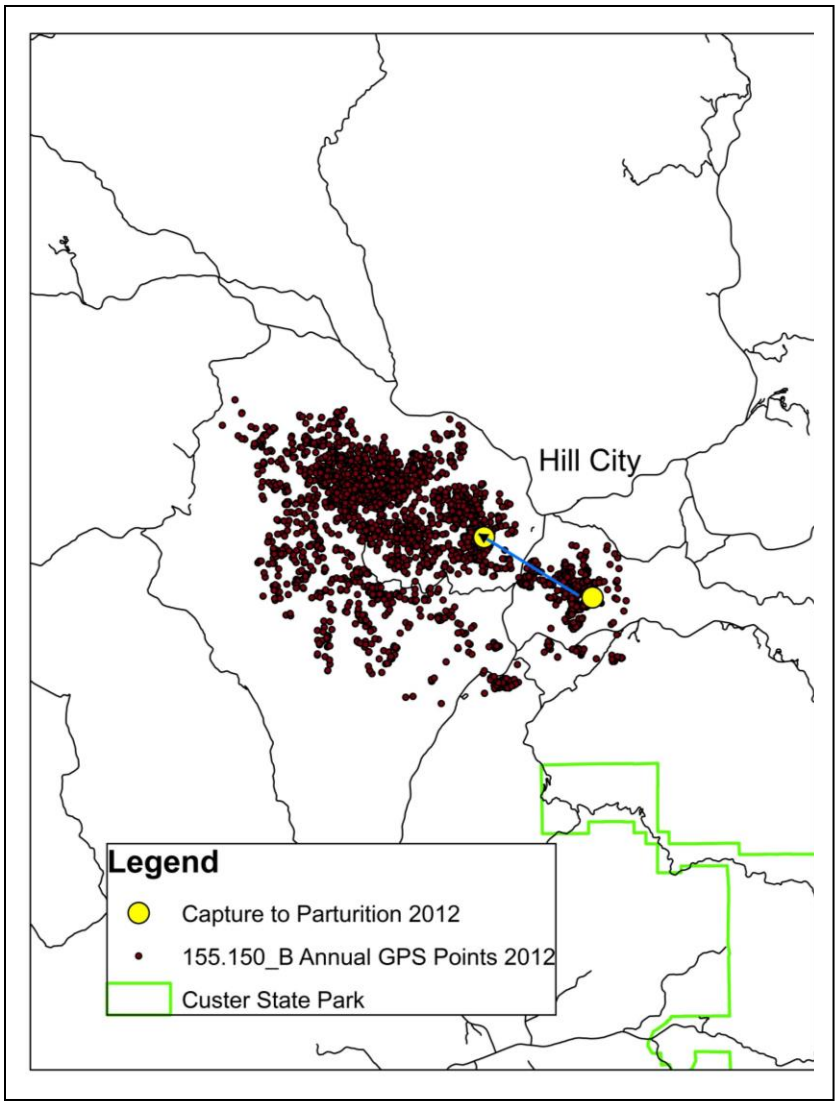
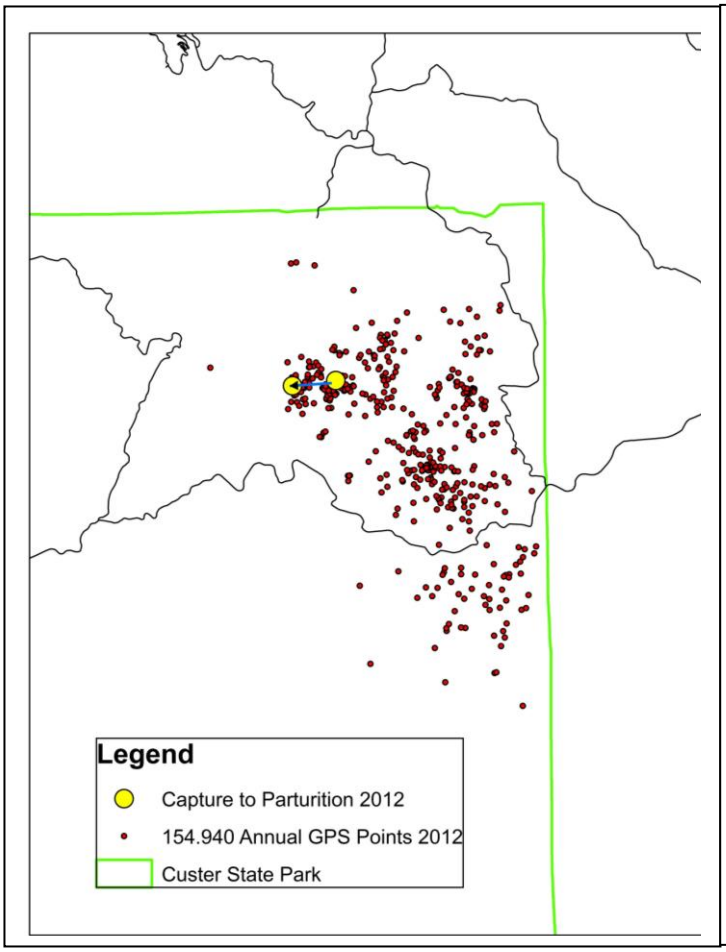
Capture to Parturition 2012
155.160 Annual GPS Points 2012
Custer State Park
Legend
Capture to Parturition 2013
155.160 Annual GPS Points 2013
Custer State Park


Hill City
Legend
Capture to Parturition 2012
155.150_B Annual GPS Points 2012
Custer State Park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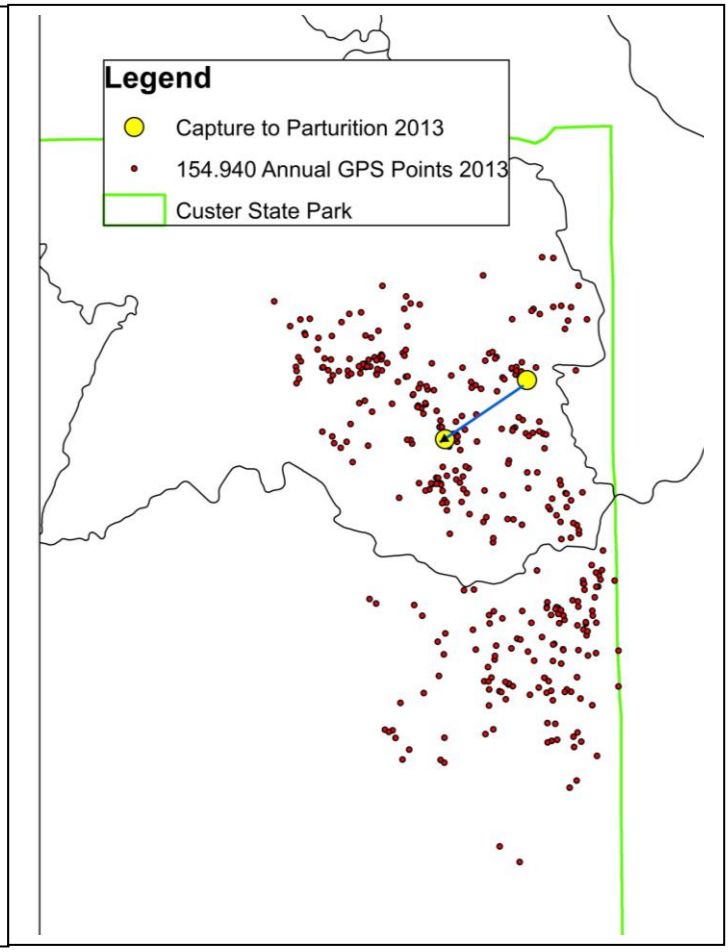
Capture to Parturition 2012
154.940 Annual GPS Points 2012
Custer State Park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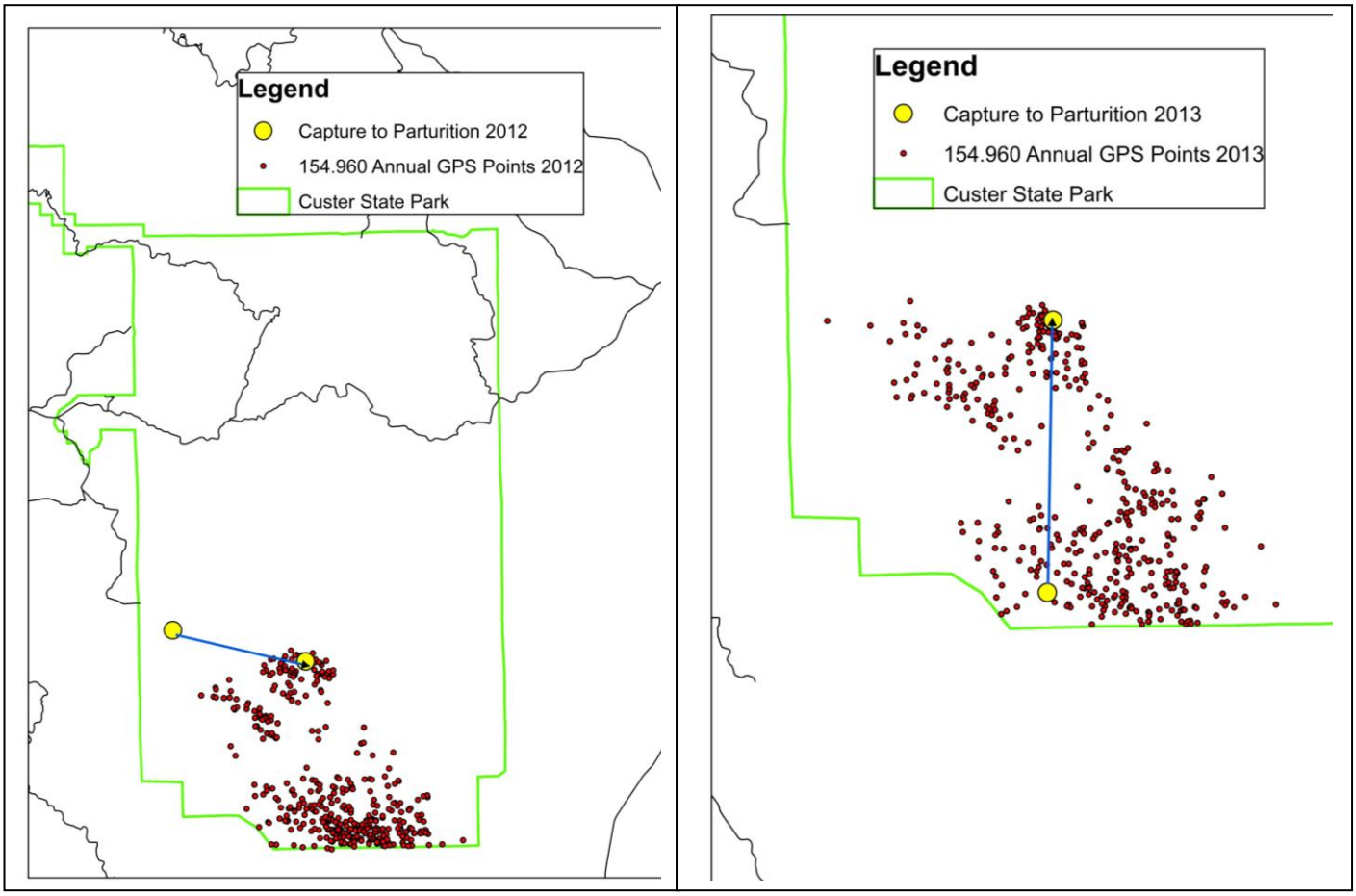
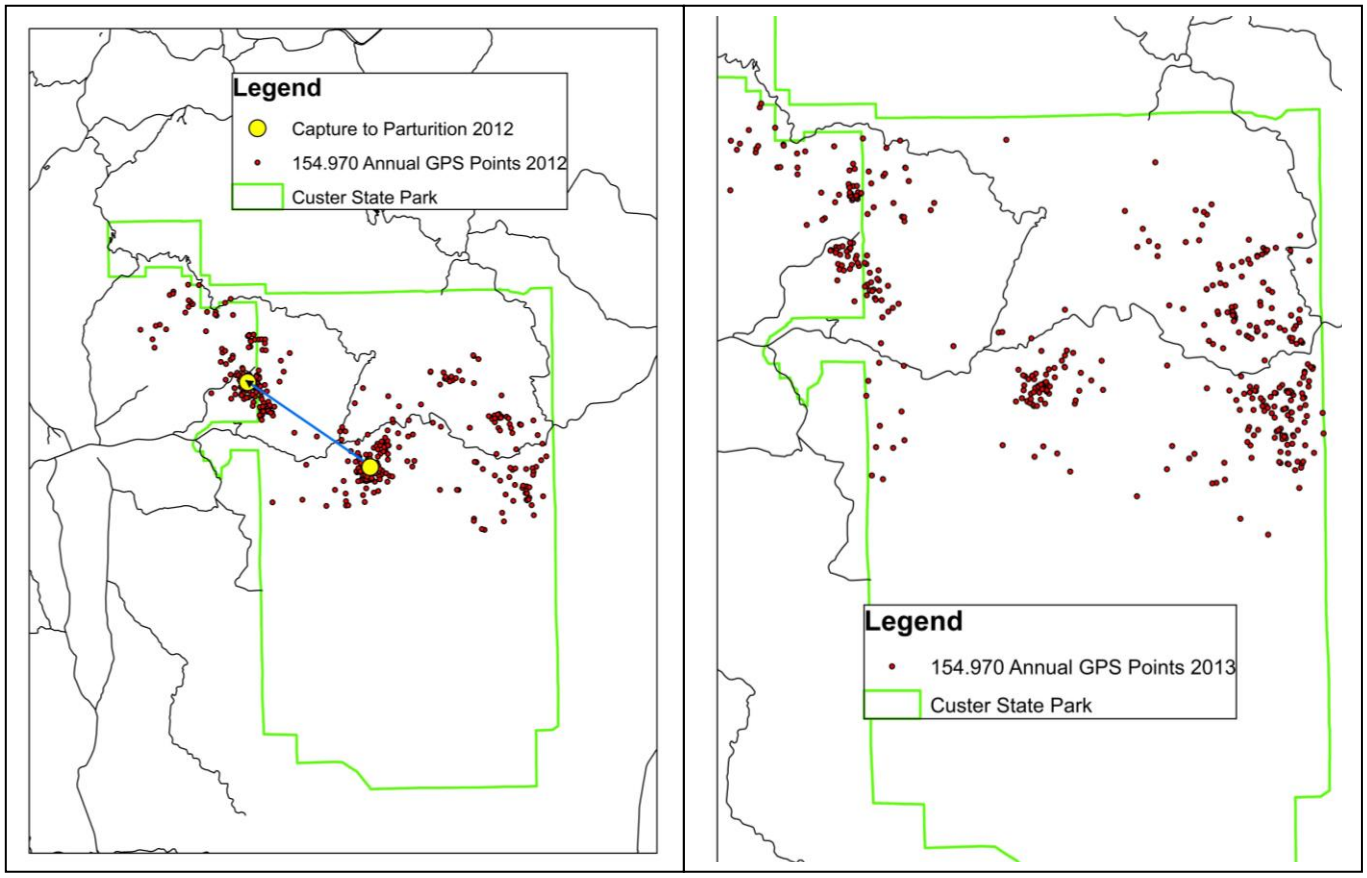
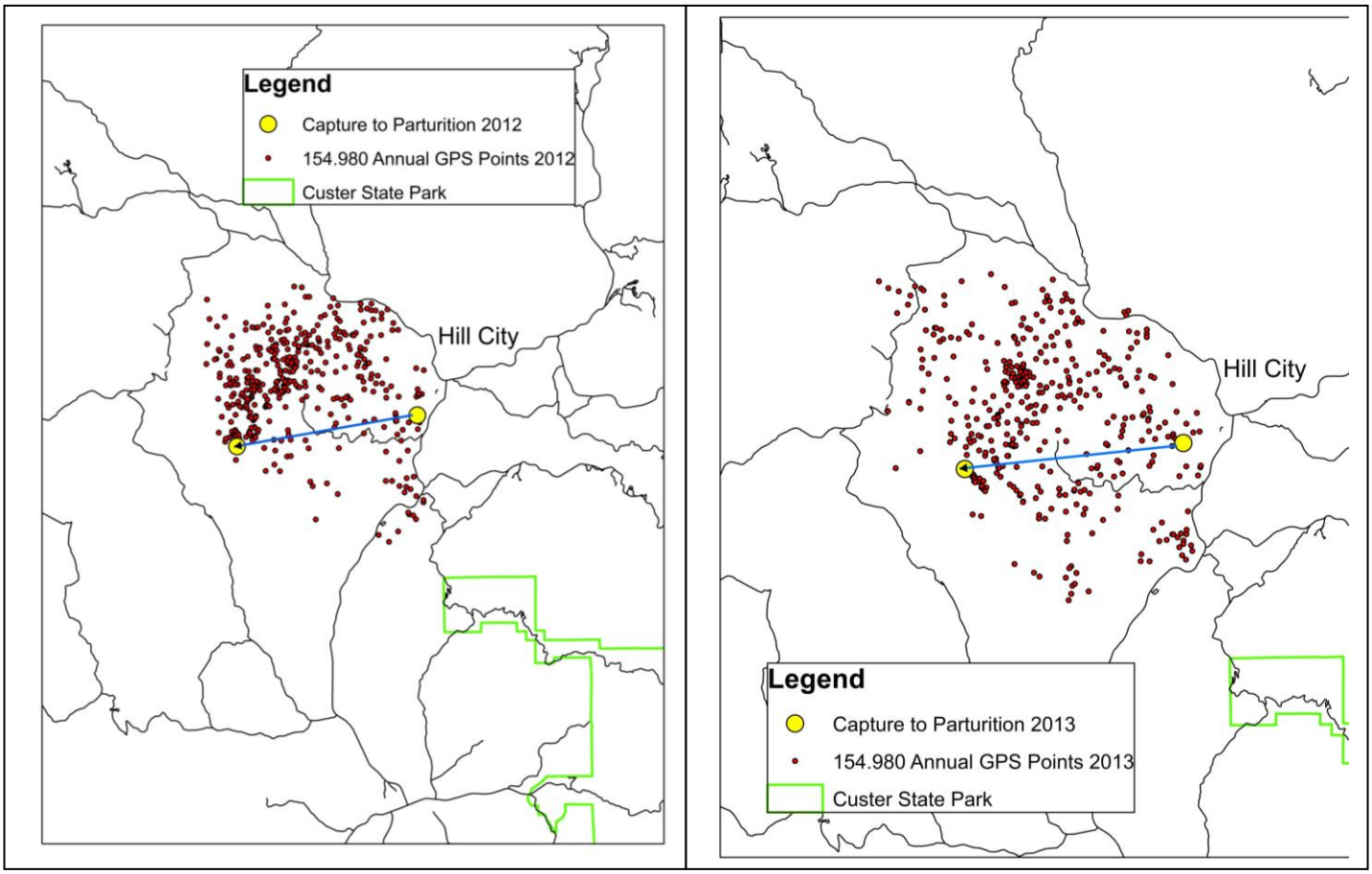
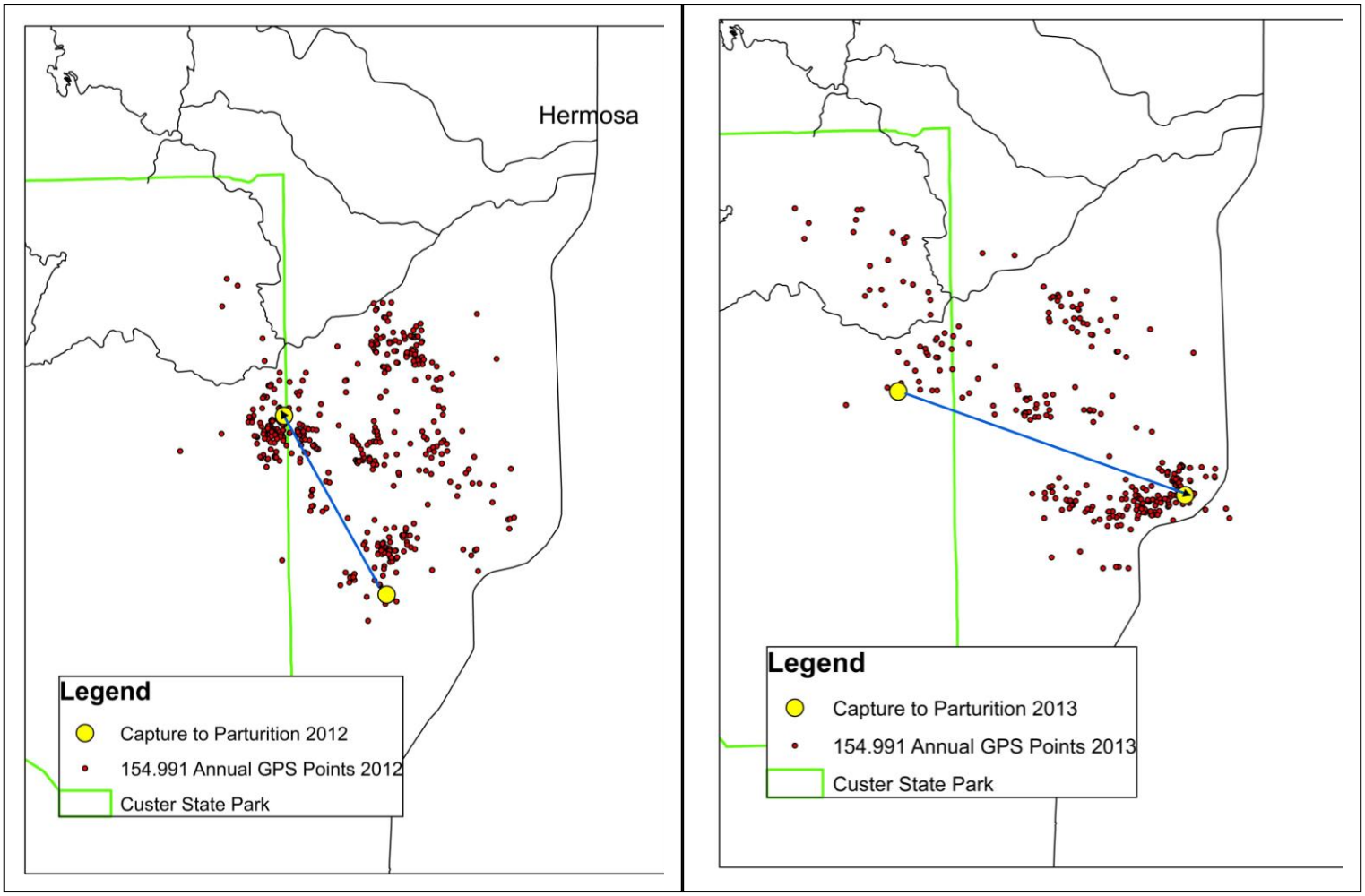
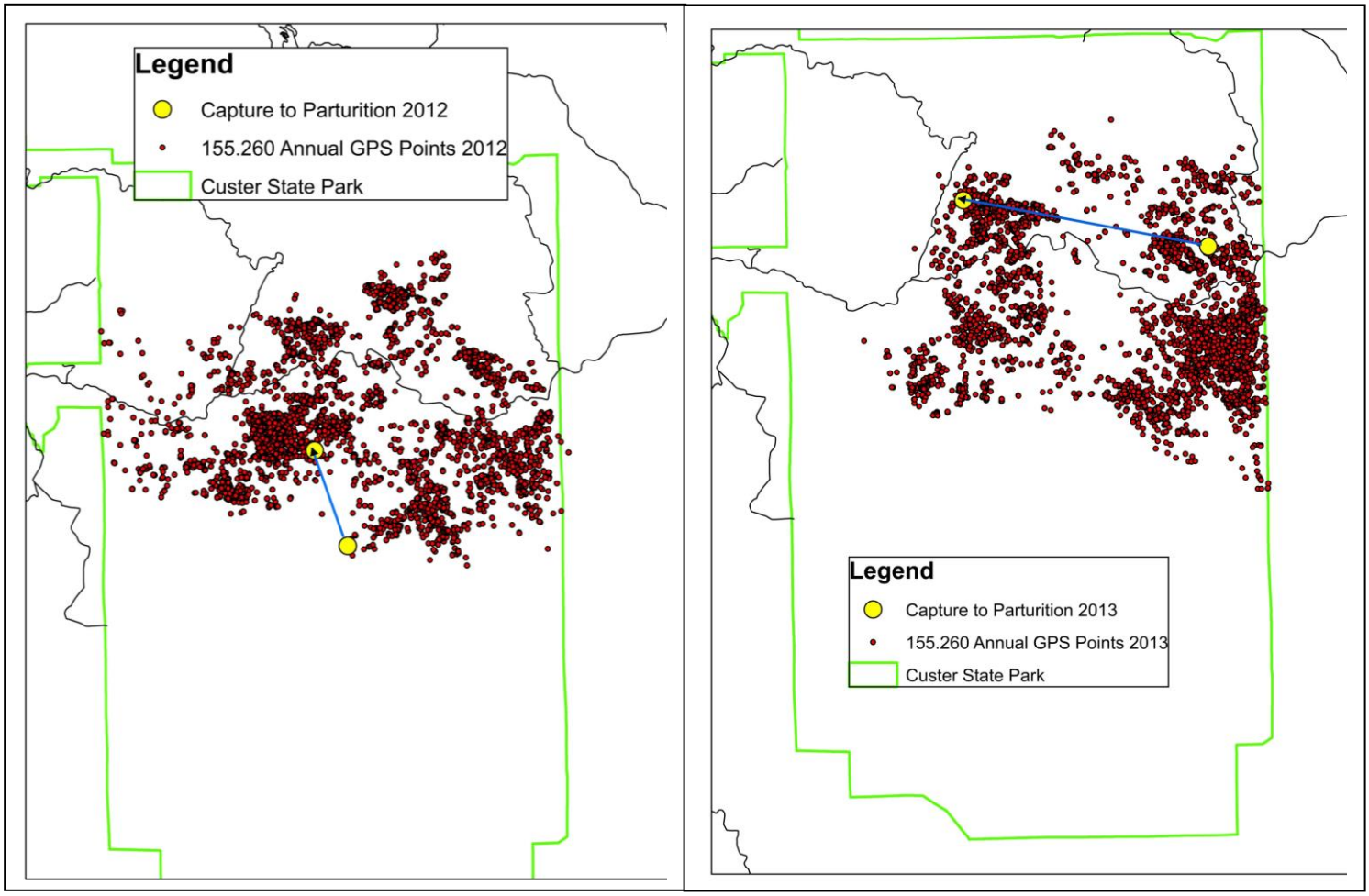
Capture to Parturition 2013
154.940 Annual GPS Points 2013
Custer State Park

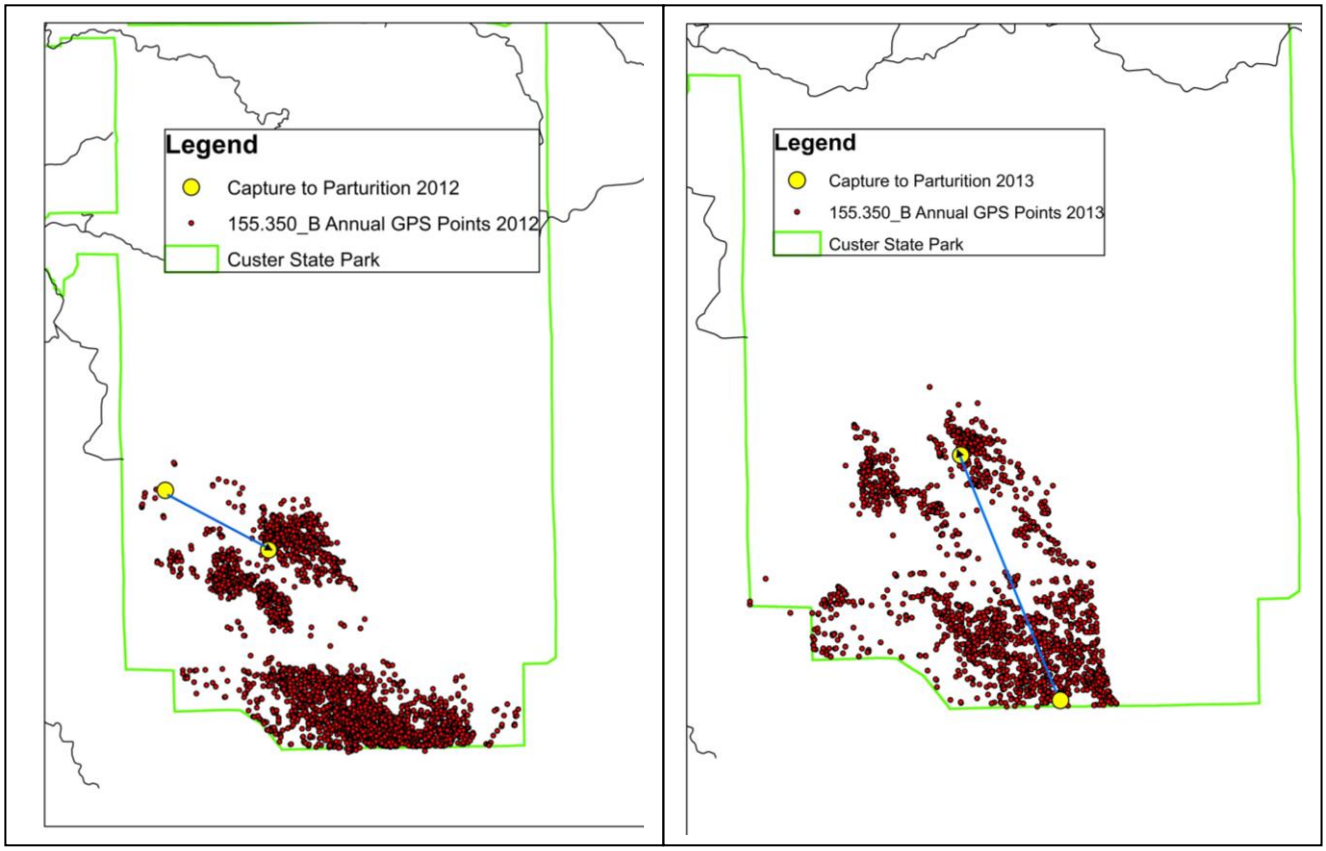

Legend
Capture to Parturition 2012
154.960 Annual GPS Points 2012
Custer State Park
Legend
Capture to Parturition 2013
154.960 Annual GPS Points 2013
Custer State Park

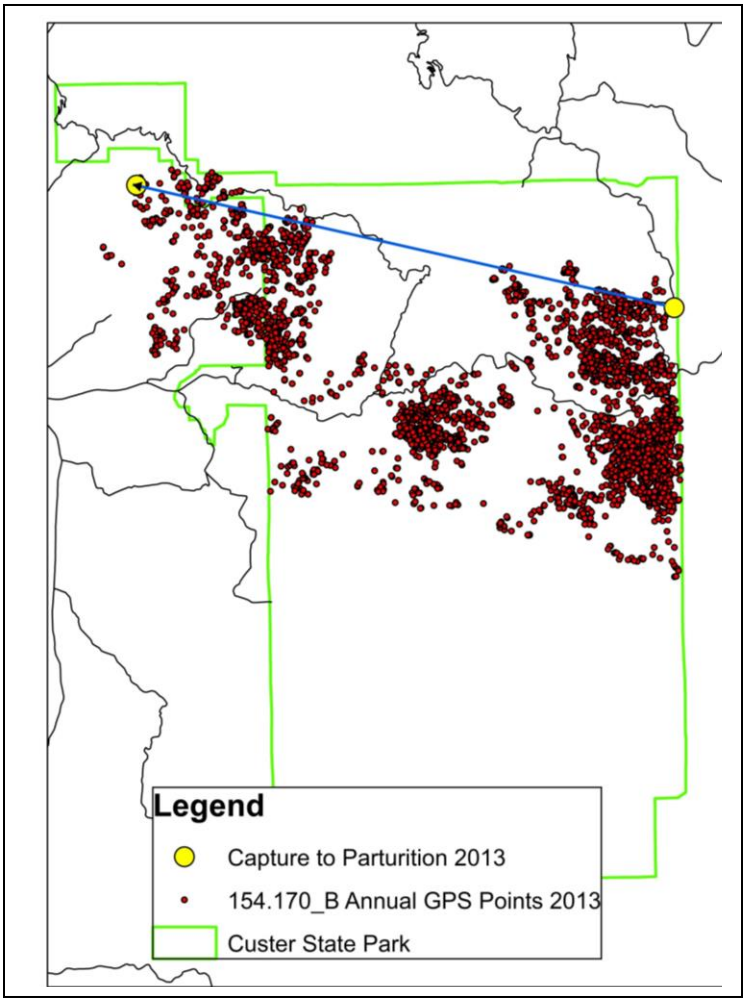

Legend
Capture to Parturition 2012
154.970 Annual GPS Points 2012
Custer State Park
Legend
154.970 Annual GPS Points 2013
Custer State Park

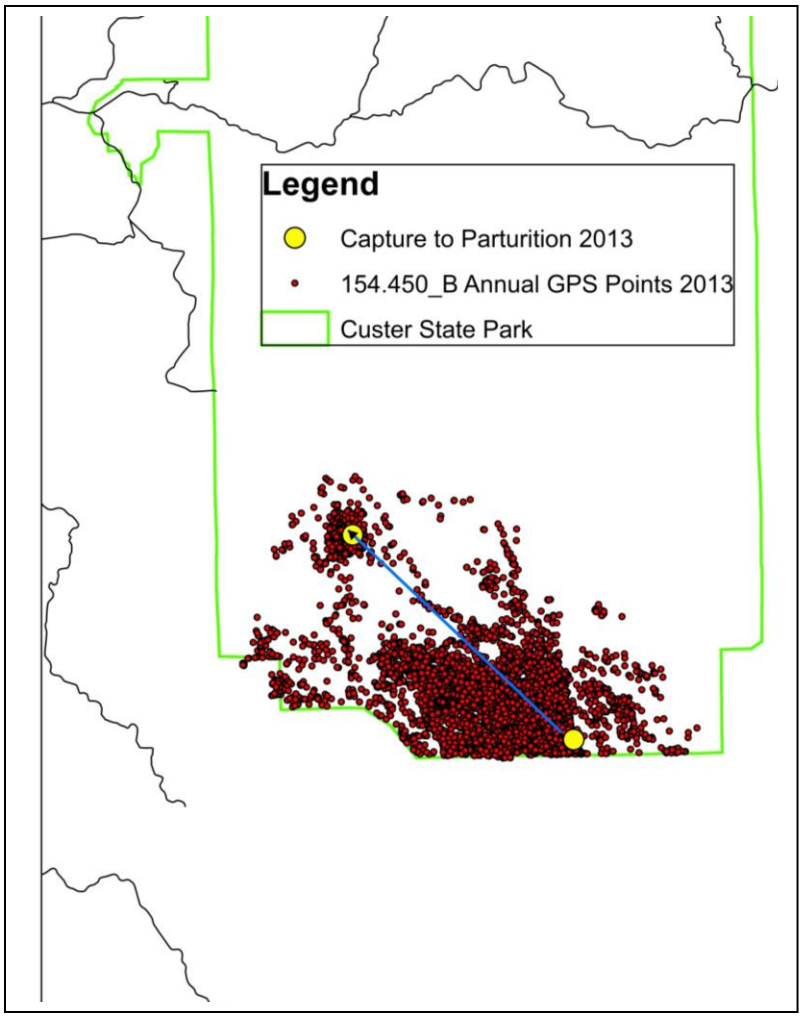

Legend
Capture to Parturition 2012
154.980 Annual GPS Points 2012
Custer State Park
Hill City
Legend
Capture to Parturition 2013
154.980 Annual GPS Points 2013
Custer State Park
Hill City


Hermosa
Legend
Capture to Parturition 2012
154.991 Annual GPS Points 2012
Custer State Park
Legend
Capture to Parturition 2013
154.991 Annual GPS Points 2013
Custer State Park


Legend
Capture to Parturition 2012
155.260 Annual GPS Points 2012
Custer State Park
Legend
Capture to Parturition 2013
155.260 Annual GPS Points 2013
Custer State Park


Legend
Capture to Parturition 2012
155.350_B Annual GPS Points 2012
Custer State Park
Legend
Capture to Parturition 2013
155.350_B Annual GPS Points 2013
Custer State Park


Legend
Capture to Parturition 2013
154.170_B Annual GPS Points 2013
Custer State Park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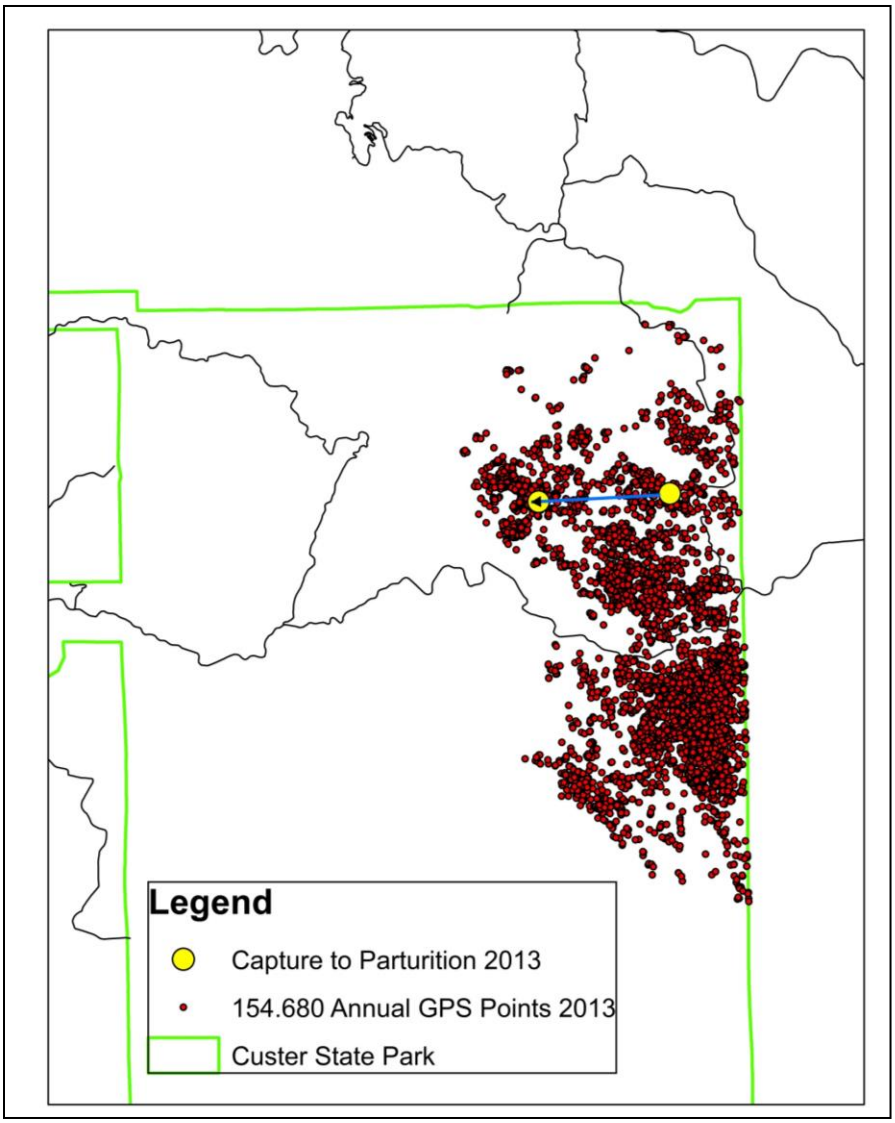
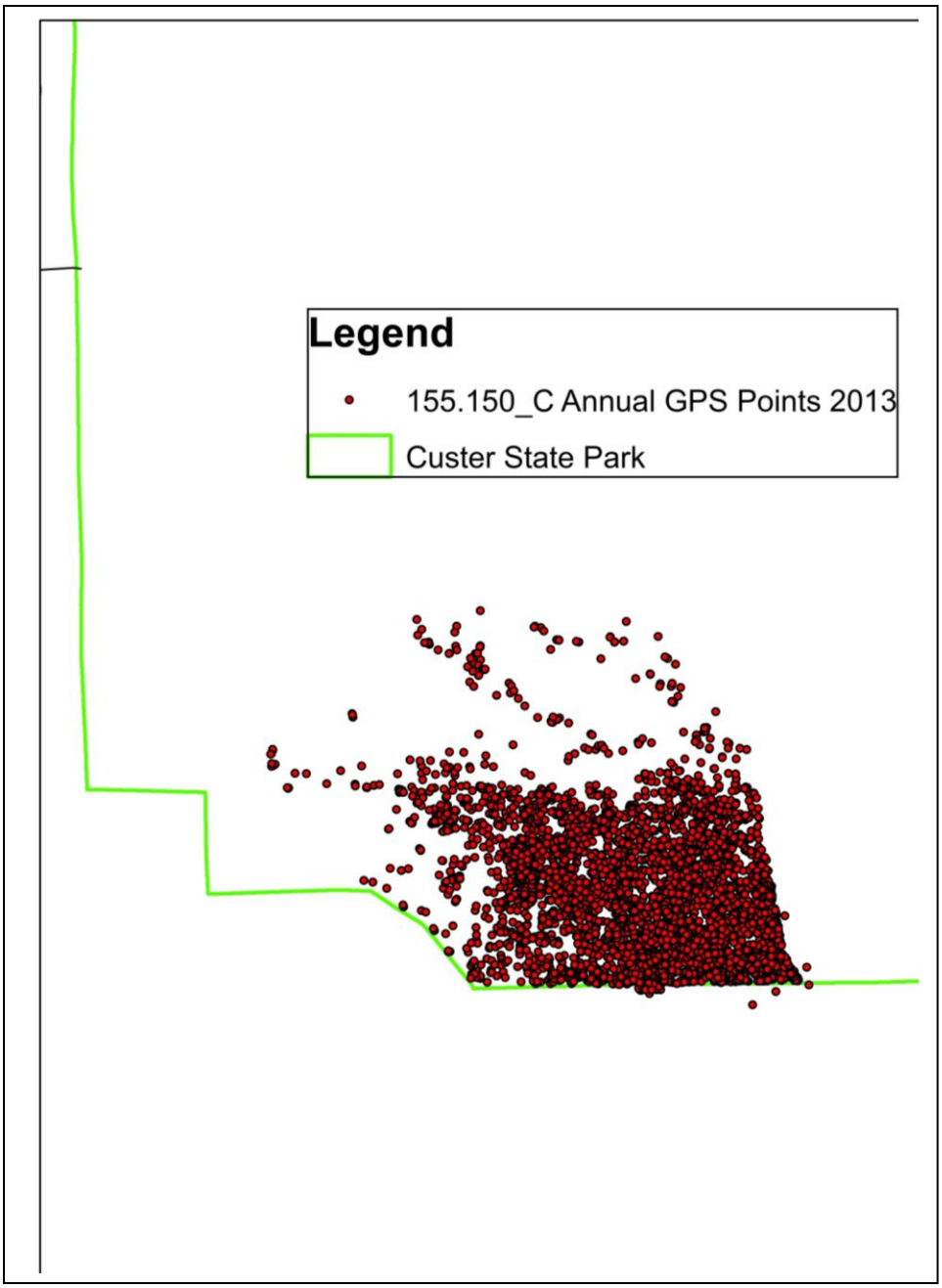
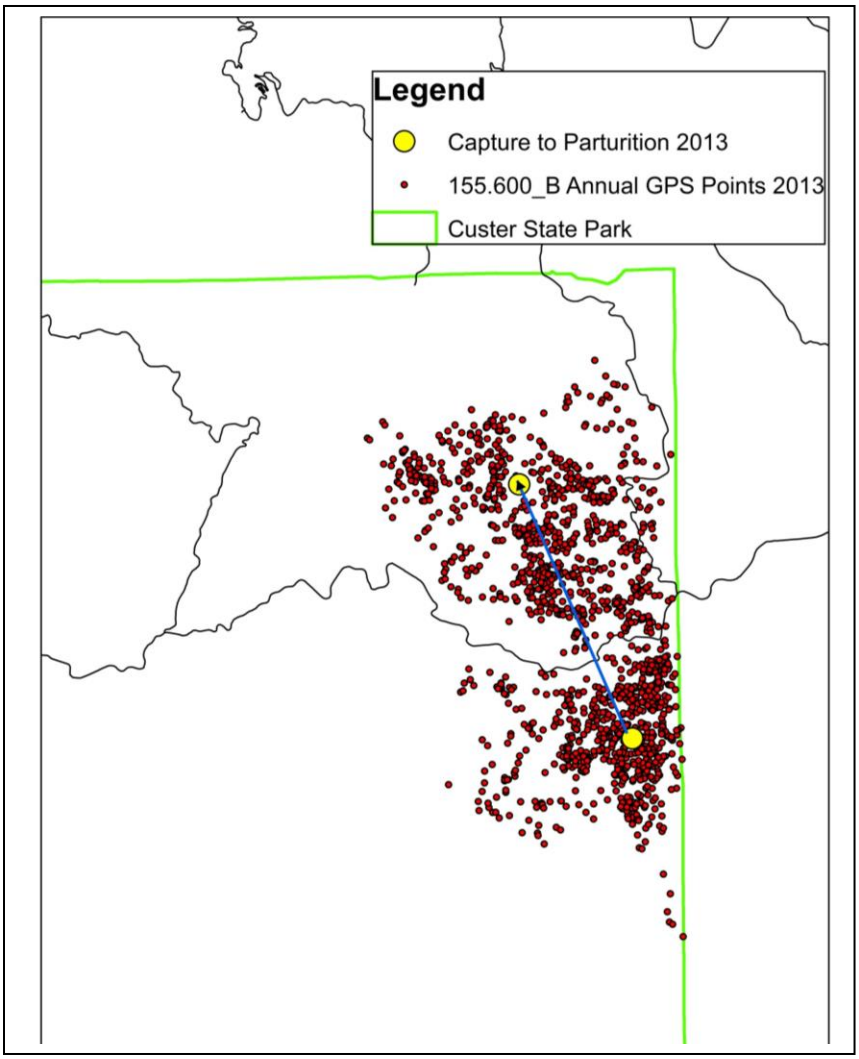
Capture to Parturition 2013
154.450_B Annual GPS Points 2013
Custer State Park


Legend
Capture to Parturition 2013
154.680 Annual GPS Points 2013
Custer State Park


Legend
155.150_C Annual GPS Points 2013
Custer State Park


Legend
Capture to Parturition 2013
155.600_B Annual GPS Points 2013
Custer State Park