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Reevaluating fox squirrel (*Sciurus niger*) population declines in the southeastern United States

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We used southeastern fox squirrels (*Sciurus niger*) in the southeastern United States as an example of how modern approaches to estimate density coupled with a reevaluation of previous estimates can provide important new insights into the management and conservation of mammals. There are few rigorous density estimates of southeastern fox squirrels, which hinders our ability to manage and conserve their populations. Based on an initial estimate from 1957 of 38 squirrels/km^2 and subsequent decreases in estimates of population densities, noted decreases in hunter harvest reports, and anecdotal observations, southeastern fox squirrels are believed to be declining. To assess the extent of this decline, we first estimated the density of a subspecies of southeastern fox squirrel, Sherman's fox squirrel (*S. n. shermani*), using live trapping and camera trapping and modern analytical approaches for mark–recapture analysis. Then, to compare our densities to previous work, we calculated a standardized effective survey area correction factor for past studies and recalculated their population densities. Once standardized, we found little temporal or geographic variation in densities of southeastern fox squirrels (2.4–8.5 squirrels/km^2) spanning nearly 70 years of research. Past densities were substantially lower than initially reported with corrected survey areas, suggesting that densities may have always been naturally low but were incorrectly inflated due to study designs and statistical approaches. Moreover, corrected densities from all studies were correlated with the bounded survey area, suggesting that researches aiming to estimate population densities of southeastern fox squirrels were frequently conducted at scales too small relative to the size of their home ranges. The use of methodological and analytical approaches such as those used in this study may help to avoid misdirected conservation designations or management actions and misuse of conservation funding.

Key words: abundance, camera surveys, camera trapping, density estimation, live trapping, mark–recapture, photo identification, robust design, Sherman's fox squirrel

Understanding spatial and temporal changes in the size of populations is critical for the management of game species and recovery of imperiled wildlife (Gibbs et al. 1999). To address this need, there have been considerable advancements during the past several decades in survey methods and statistical approaches used to estimate densities of animal populations. Traditional methods to estimate population densities have been constrained by their inability to account for uncertainty and heterogeneous detections (Royle and Dorazio 2008). Additionally, traditional estimates of density often failed to account for the effective survey area (Dice 1938; Bondrup-Nielsen 1983; Wilson and Anderson 1985) even though it has long been recognized that individuals move into or out of a study area, thereby making the effective survey area larger than the boundaries of the area trapped. These issues lead to estimates of density that are biased upwards and have been especially problematic for estimating population sizes of rare and elusive species (McDonald 2004).

Ecologists now have a suite of tools to estimate population sizes of rare species and improve the rigor and precision of abundance and density estimates. Advances in statistical applications allow researchers to account for uncertainties such as individual heterogeneity and variation in detectability, and the influences of animal movements such as temporary emigration and immigration (e.g., Otis et al. 1978; Pollock 1982; Seber 1982; Pollock et al. 1990; Efford and Fewster 2013). Modern survey techniques, such as remote photographic sampling (hereafter, camera trapping) have also improved our ability to account for uncertainty in a species' presence, making them increasingly popular in wildlife monitoring (Karanth and Nichols 1998; Karanth et al. 2004). These advancements have greatly benefited recent studies investigating wildlife demographics, but for many mammal species where our state of knowledge stems from earlier approaches, information may be less reliable (Skalski et al. 2005). To better understand the dynamics of many wildlife species, there is a need to use modern estimation methodologies to generate rigorous estimates of density and to adjust previous estimates to ensure these approaches are comparable.

The need to generate rigorous estimates of current population parameters and to revisit historical estimates that shaped management and conservation decisions is particularly true for 4 of the 6 subspecies of fox squirrel (*Sciurus niger vulpinus*, *S. n. niger*, *S. n. shermani*, and *S. n. bachmani*) in the southeastern United States (hereafter, southeastern fox squirrels). Unlike midwestern fox squirrels, ecologically and morphologically distinct southeastern fox squirrels appear to have declining populations (Loeb and Lennartz 1989; Humphrey and Jodice 1992; Kantola 1992). Southeastern fox squirrels are ecologically important as dispersers and predators of ectomycorrhizal fungi (Johnson 1996) and seeds, and prey for many avian and mammalian predators (Steele and Koprowski 2001). Declines in southeastern fox squirrel populations and densities have clear ecological implications, thereby increasing the need to monitor their population trends for conservation purposes.

Generating precise estimates of density and population size for southeastern fox squirrels has been hindered by their sparse distribution, low densities, and low detectability (Loeb and Lennartz 1989; Weigl et al. 1989; Loeb and Moncrief 1993; Wooding 1997). The 1st estimate of population density for southeastern fox squirrels was at 38 squirrels/km^2 (reported as 1 squirrel per 6 acres) for Sherman's fox squirrel (*S. n. shermani*—Moore 1957). Most subsequent authors have reported substantially lower estimates and used the original estimate from Moore (1957) as evidence of a decline in densities of southeastern fox squirrels (Weigl et al. 1989; Loeb and Moncrief 1993; Conner et al. 1999). This apparent decline, combined with habitat loss, decreases noted in hunter harvest reports, and declines in visual observations from wildlife professionals, has led to the protection of several southeastern fox squirrel subspecies. In Florida, Sherman's fox squirrel (*S. n. shermani*) is designated as a Species of Special Concern (Kantola 1992). In South Carolina, the southern fox squirrel (*S. n. niger*) is a Species of Special Concern and although considered a small game species, it is protected in > 61% of Wildlife Management Areas (South Carolina DNR 2015). Two other subspecies of southeastern fox squirrels also have a special conservation status: the Big Cypress fox squirrel (*S. n. avicennia*) is Threatened in Florida (Humphrey and Jodice 1992) and the Delmarva fox squirrel (*S. n. cinereus*) was recently (16 November 2015) delisted as federally endangered under the United States Endangered Species Act (1973 [as amended]; United States Fish and Wildlife Service 1993), but remains state-listed in Delaware, Maryland, and Virginia (United States Fish and Wildlife Service 2015). Although the latter 2 subspecies are considered southeastern fox squirrels in the literature, we did not include them in this study because of their relatively low densities and unique habitat preferences (Lustig and Flyger 1976; Williams and Humphrey 1979; Flyger and Smith 1980; Ditgen et al. 2007).

Survey methods traditionally used to estimate densities of southeastern fox squirrels have had varying degrees of success. Live trapping has been the most common method (Tappe et al. 1993; Wooding 1997; Conner et al. 1999) but has been hindered by low capture success (< 1%—Steele and Koprowski 2001). Other methods used to estimate densities of southeastern fox squirrels have included line-transects (Humphrey et al. 1985), nest counts (Moore 1957; Wooding 1997), and nest box surveys (Weigl et al. 1989). The reliability of these estimates, however, is unknown. Authors using visually based methods (e.g., line-transects, nest surveys) estimated densities either by assuming perfect detectability (Moore 1957; Wooding 1997) or rounding estimates up (Weigl et al. 1989) to account for potentially missed squirrels. Only in 2 studies on southeastern fox squirrels (Tappe et al. 1993; Conner et al. 1999) did the authors not assume that detected animals were confined to their study area.

Here, we use the southeastern fox squirrel as an example of how modern approaches to estimate density, coupled with a reevaluation of previous estimates, can provide important new insights for management and conservation. Our specific objectives for this study were to: 1) estimate the population densities of southeastern fox squirrels using a traditional (live trapping) and modern survey technique (camera trapping) combined with modern statistical methods; 2) recommend the best sampling approach for estimating densities based on precision; 3) add effective survey areas to previous studies and generate revised density estimates; and 4) use current and revised estimates of density to reevaluate population trends in southeastern fox squirrels.

Materials and Methods

Study area.—Our study was conducted in Florida at Camp Blanding Wildlife Management Area in Clay County and Ordway-Swisher Biological Station in Putnam County. The linear distance between our study sites was 34.1 km. The mean annual high temperature for Starke, Florida (near Camp Blanding) is 26.2°C, with a mean low of 13.3°C, and a mean low-high range of 4.6–18.6°C in January and 20.9–32.3°C in August; annual average rainfall is 1,280 mm (United States Climate Data 2016). The land cover types at Camp Blanding were classified as a mixture of sandhill and mesic flatwoods, and Ordway was classified as sandhill (Florida Natural Areas Inventory 2010). At Camp Blanding, longleaf pine (*Pinus palustris*), slash pine (*P. elliottii*), and turkey oaks (*Quercus laevis*) were the common tree species, and the understory vegetation was primarily saw-palmetto (*Serenoa repens*), gallberry (*Ilex glabra*), and swamp bay (*Persea palustris*). At Ordway, longleaf pine, turkey oak, and live oak (*Q. virginiana*) were the common tree species, and the ground cover was primarily wiregrass (*Aristida stricta*).

Trapping surveys.—At each study area, we randomly established two 75-ha grids in areas occupied by Sherman's fox squirrels. Grids were 4 × 5 in arrangement, with 20 survey points at each grid spaced 250 m apart (Fig. 1). Grids were separated by 510 m at Ordway and 645 m at Camp Blanding to minimize movements between grids. The distance at Camp Blanding was greater because of the presence of a dense riparian zone which, although used by southeastern fox squirrels (e.g., for nesting—Prince et al., 2016), is atypical habitat. We conducted live-trapping and camera-trapping sessions seasonally on each grid, with seasons (for 4-day sessions) defined as: fall = 7 October–5 December 2011, winter = 18 February–26 March 2012, spring = 29 April–26 May 2012, and summer = 16 August–18 September 2012. Seasons were selected following those defined previously (Moore 1957; Weigl et al. 1989) with the goal of capturing annual variation in activity patterns due to weather and the availability of food. The fall session extended into a third month because of constraints on site access due to military exercises.

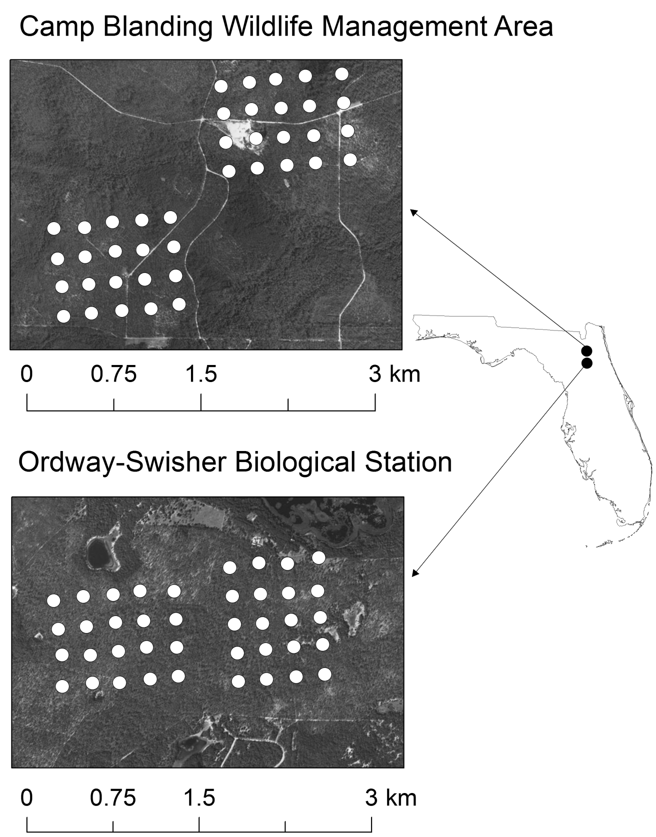

Fig. 1.—Distribution of the 4 trapping grids used in a study to estimate densities of Sherman's fox squirrels (*Sciurus niger shermani*). Grids were located at Camp Blanding Wildlife Management Area in Starke, Florida, and the Ordway-Swisher Biological Station in Melrose, Florida from 2011 to 2012.

To live trap, we placed a wooden box trap (63 × 18 × 22 cm—Baumgartner 1940) on the ground at the base of a tree nearest to the survey point and strapped a Tomahawk wire-cage trap (Model No. 103; Tomahawk Live Trap, Hazelhurst, Wisconsin) on a wooden platform (Huggins and Gee 1995) attached to the trunk of the same tree 1.5 m above the ground. Live traps were prebaited with pecans and cracked corn every other day for 6 days, then set from sunrise until sunset for 4 consecutive days; traps were checked every 2–3 h to avoid heat-related stress or trap mortality. Captured fox squirrels were transferred to a handling bag to determine sex and body mass before marking them with an ear tag (Monel #1005-3; National Band and Tag Company, Newport, Kentucky). All methods were in accordance with guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2011) and a Florida Fish and Wildlife Conservation Commission Scientific Collecting Permit (LSSC-11-00026) and were approved by the University of Florida's Non-Regulatory Animal Research Committee (021–10WEC).

To camera trap, we placed a camera (Bushnell Trophy Cam model 119436c, Bushnell Outdoor Products, Overland Park, Kansas) at each survey point for 6 consecutive days. We equipped cameras with a 2 GB SanDisk memory card (SanDisk Corporation, Milpitas, California) and set them to take 3 photos every 10 s at the "normal sensitivity" setting. We placed a camera at each survey point 70 cm above the ground and angled it towards a bait pile of pecans and cracked corn (Baumgartner 1940; McCleery and Parker 2011) placed at the base of a tree 1.5 m from the camera. Camera stations were baited on the 1st and 4th days. Because we expected low live-capture success (Steele and Koprowski 2001), we camera trapped before live trapping as additional baiting periods except for 2 sessions (spring at Blanding; fall at Ordway) when live trapping had to occur first because of limited site access. We used the variable coloration and unique patterns among fox squirrels to identify individuals (Tye et al. 2015) for capture–recapture analysis. All identifications were conducted by one of the authors (DUG) for consistency. To avoid biasing our results, we limited our ability to identify individuals from camera-trap photos to using only morphological features. We did not use visible ear tags on marked fox squirrels as an additional feature. After plotting the time difference between successive photographs ($n = 2{,}940$) for each individual at a survey point, we found that < 6% ($n = 163$) of the encounters included an individual that returned to a survey point after a 20-min interval. Therefore, we defined a detection of an individual to be independent if ≥ 20 min elapsed since its last observation at a survey point.

Data analysis.—To generate estimates of abundance and their 95% confidence intervals, we used Pollock's robust design analysis (Pollock 1982) with the Huggins' heterogeneity p and c (Huggins 1989, 1991) model type in Program MARK 8.0 (White and Burnham 1999). We pooled encounter histories of daily captures for both sites to improve parameter estimates but derived abundance estimates separately for each site and season. We developed 5 candidate models for our 4-day live-trapping sessions (Supplementary Data SD1) and 9 models for our 4-day

(Supplementary Data SD2) and 6-day (Supplementary Data SD3) camera-trapping sessions. We developed global models that included survival, emigration, immigration, capture, and recapture parameters as site-, day-, and season-specific. Other candidate models were modeled the same but were independent of daily time effects (i.e., constant across days) to avoid over-parameterization so models would converge (Cooch and White 2014). Models were evaluated using Akaike's Information Criterion (AIC—Akaike 1973). We model-averaged all models to account for model selection uncertainty (Anderson 2008; Cooch and White 2014) but excluded those that did not estimate all parameters to maintain reliability in the parameter estimates.

Individual animals often move inside and outside of the bounded area where they are trapped (Otis et al. 1978). To calculate unbiased estimates of density from abundance, it is therefore necessary to determine the actual extent of the area that was trapped (Dice 1938; Bondrup-Nielsen 1983). This "effective survey area" has typically been calculated using the movements of animals between capture locations. We used the full mean maximum distance moved (MMDM), a proxy for the diameter of a home range (Stickel 1954; Tanaka 1972; Wilson and Anderson 1985) as a buffer to our study grids to estimate our effective survey area. This buffer approach has performed better in field (Parmenter et al. 2003; Soisalo and Cavalcanti 2006; Sharma et al. 2010) and in simulation studies (Ivan 2011; Tobler and Powell 2013) compared to the alternative ½ MMDM method. We generated our MMDM by including the distances between capture and detection locations of individuals with ≥ 2 captures per season for a survey method but excluded distances of 0 m if an individual was recaptured at the same survey point. Then, we determined the maximum distance moved for each individual and averaged maximum distances across all individuals. To increase the accuracy of our maximum distance estimate (Williams et al. 2002), we pooled the movement measurements from live trapping and camera trapping. We then added the MMDM as a buffer to the periphery of our study grids to define our effective survey area. We divided our abundance estimates by the effective survey area to calculate fox squirrel densities (squirrels/1 km^2) for each site and survey method. We used the delta method to recalculate the *SE*s on our density estimates (Seber 1982; Nichols and Karanth 2002). To determine which survey method was more precise, we used the density estimates with the MMDM correction and calculated the coefficient of variation for each season.

To compare our density estimates with previous studies and to account for possible seasonal and site-specific variation in space use, we calculated a standardized effective survey area correction factor (hereafter, standardized correction factor) by taking the average of published movement data for southeastern fox squirrels (excluding *S. n. avicennia* and *S. n. cinereus*). Small numbers of capture locations can underestimate home-range size and movement distances and thereby underestimate the "true" effective area; however, movements estimated from radiotelemetry can serve as an alternative (Parmenter et al. 2003). Therefore, we pooled full MMDM values ($n = 101$) from individuals that were live captured (Tappe and Guynn 1990; this study) and home-range diameters from individuals that were radiocollared ($n = 108$—Hilliard 1979; Edwards 1986; Weigl et al. 1989; Kantola and Humphrey 1990; Conner et al. 1999). To minimize biases in home-range estimates, we used the minimum convex polygon (MCP) estimates for all studies, except Conner (2000) who published composite estimates and Kantola and Humphrey (1990) who presented harmonic means of 95% of their locations as MCPs. We applied this buffer to most studies that estimated the densities of southeastern fox squirrels (Table 1) but excluded 1 study on a rare, high-density island population (Lee et al. 2008), 1 study with an insufficient description of the size of the study area (Humphrey et al. 1985), and some estimates from Weigl et al. (1989) with multiple study areas (some sparsely occupied); for the latter, we used their 3 highest estimates. We considered density estimates derived from different survey methods to be comparable when detection was assumed to be perfect (Moore 1957; Wooding 1997) or nearly perfect (Weigl et al. 1989) from census-type approaches to those that accounted for detectability (Tappe et al. 1993; Conner et al. 1999). Revised estimates of densities were calculated from the authors' naive density estimates (Tappe et al. 1993; Conner et al. 1999) when a detection probability was considered, or the total number of individuals captured if detection was assumed to be nearly perfect (Weigl et al. 1989) or perfect (Moore 1957; Wooding 1997; Table 1).

Results

We live captured 42 individuals among 82 total captures at 43 survey points; 20 of these individuals were male, 19 female, and 3 were undetermined sex. No live-captured fox squirrels were documented moving between grids. Of the 42 live-captured individuals, 50.0% had 1 capture, 26.2% had 2 captures, 9.5% had 3 and 4 captures, and 2.4% had 5 and 6 total captures across all seasons. Our live-capture success exceeded the expected < 1% (Steele and Koprowski 2001); for the 1,280 trap days across seasons, our capture success was 6%. For the camera surveys, we photographed 56 individuals at 58 survey points during the 4-day sessions, with a range of 1–17 detections per individual (average = 4) across all seasons. During the 6-day session, 60 individuals were detected at 64 survey points with camera traps. We were unable to quantify our success rate in identifying individuals from camera-trap photos. Although we did not use visible ear tags for individual identification, a post hoc review of all camera-trap photos did not reveal any individuals with ear tags that we classified as camera trapped but never live trapped, suggesting misidentification was uncommon. Four individuals moved between grids in our camera surveys, all occurring at Ordway; 3 moved within a season and 1 between seasons. All relocations were indicative of dispersal events (i.e., none of the individuals returned to the grid where they previously were detected); therefore, we excluded their dispersal distances from MMDM calculations.

The minimum number known alive (MKNA) each season from live captures increased across seasons: fall ($n = 11$),

Table 1.—Density estimates (squirrels/km^2) for southeastern fox squirrels (*Sciurus niger* spp.). Data are categorized as from this study (Camp Blanding Wildlife Management Area [CB] and Ordway-Swisher Biological Station [OS]) in Florida or the literature (Source), by the US state where a study was conducted (State), by survey method (Method), and by when the study occurred (Period). Density estimates and their 95% confidence intervals (*CI*s) are presented for naive estimates with no effective survey area correction (Naive), an author correction (Corrected), and with our standardized correction factor for effective survey areas (Density).

Source	State	Method	Period	Naive (*CI*)	Corrected (*CI*)	Density (*CI*)
Moore (1957)	Florida	Nest counts	July–Aug. 1946	38		3.4
Weigl et al. (1989)	North Carolina	Captures, nest counts	1982–1983	22		2.9
Weigl et al. (1989)	North Carolina	Captures, nest counts	1983–1984	28		3.6
Weigl et al. (1989)	North Carolina	Captures, nest counts	1984–1985	19		2.5
Weigl et al. (1989)	North Carolina	Captures, nest counts	1984–1985	35		2.7
Tappe et al. (1993)	Georgia	Live traps	May 1989	40 (31–52)	17.7[b]	8.5
Tappe et al. (1993)	Georgia	Live traps	May 1990	34 (29–47)	10.9[b]	7.2
Wooding (1997)	Florida	Live traps[a]	Jan. 1990–Mar. 1991	7.4		2.4
Wooding (1997)	Florida	Live traps[a]	Jan. 1991–June 1994	11.7		4.1
Conner et al. (1999)	Georgia	Live traps	May–June 1993	33 (30–35)	18 (17–20)[c]	7.0
Conner et al. (1999)	Georgia	Live traps	May–June 1993	29 (26–33)	16 (14–18)[c]	6.1
Conner et al. (1999)	Georgia	Live traps	May–June 1993	30 (24–35)	17 (14–20)[c]	6.3
Conner et al. (1999)	Georgia	Live traps	May–June 1993	28 (19–37)	16 (11–21)[c]	5.9
Conner et al. (1999)	Georgia	Live traps	May–June 1993	22 (17–26)	12 (9–15)[c]	4.7
Conner et al. (1999)	Georgia	Live traps	May–June 1993	34 (22–46)	19 (12–26)[c]	7.2
This study (CB)	Florida	Camera traps	Oct.–Nov. 2011		2.1 (1.6–2.7)[d]	2.1 (1.5–2.6)
This study (CB)	Florida	Camera traps	Feb.–Mar. 2012		1.5 (1.1–1.8)[d]	1.4 (1.1–1.8)
This study (CB)	Florida	Camera traps	Apr.–May 2012		2.3 (1.8–2.7)[d]	2.2 (1.8–2.7)
This study (CB)	Florida	Camera traps	Feb.–Mar. 2012		1.6 (1.3–2.0)[d]	1.6 (1.2–2.0)
This study (Ord)	Florida	Camera traps	Oct.–Nov. 2011		3.7 (2.8–4.5)[d]	3.6 (2.7–4.4)
This study (Ord)	Florida	Camera traps	Feb.–Mar. 2012		2.5 (2.0–3.0)[d]	2.4 (1.9–2.9)
This study (Ord)	Florida	Camera traps	Apr.–May 2012		3.5 (2.9–4.1)[d]	3.4 (2.8–4.0)
This study (Ord)	Florida	Camera traps	Aug.–Sept. 2012		2.8 (2.3–3.3)[d]	2.7 (2.2–3.3)

[a] Author also sighted squirrels using radiotelemetry.
[b] Corrected with ½ mean maximum distance moved from a radiotelemetry study at their site.
[c] Corrected with radius of average home range from concurrent radiotelemetry study.
[d] Corrected with full mean maximum distance moved.

winter (n = 17), and spring (n = 17), with the most individuals captured during the summer (n = 21). The MKNA from 4-day camera-trap surveys increased from fall (n = 21) to winter (n = 26) and spring (n = 33) but decreased during the summer (n = 24). This same trend was observed with the 6-day surveys: fall (n = 25), winter (n = 36), spring (n = 39), and summer (n = 30). We detected more individuals and squirrels at more survey points with camera traps than live traps; up to 52% more individuals were detected in each season and, during some seasons, at 60% more survey points.

In our analyses, the primary difference between our best models derived from live trapping and camera trapping was how the probability of recapture was modeled. With live trapping, fox squirrels had lower recapture probabilities than capture probabilities in 3 of the 4 seasons. With camera traps, the probability of recapture did not differ from the probability of 1st capture in our 4- and 6-day sessions (Supplementary Data SD1–SD3). Estimates of emigration and immigration were similar between live trapping and camera trapping, but overall had high *SE*s and, therefore, were not informative. Model-averaged capture and recapture probabilities were higher in all seasons for camera trapping compared to live trapping (Supplementary Data SD4–SD6). For live trapping, our capture probability was 0.286 (*SE* = 0.081), which exceeded the recapture probability of 0.122 (*SE* = 0.028). For camera trapping, seasonal recapture probabilities (Supplementary Data SD4) ranged from 0.313 (*SE* = 0.052) to 0.320 (*SE* = 0.053) and were not different from recapture probabilities (Supplementary Data SD5), ranging from 0.329 (*SE* = 0.041) to 0.337 (*SE* = 0.038).

We calculated a MMDM buffer of 524 m from live trapping and camera trapping at both sites (Ordway = 619 m and Blanding = 420 m), which increased our effective survey area for each grid from 75 to 343 ha. We had 71 maximum distances from 39 individuals, represented by 37 individuals from camera trapping and 9 from live trapping. Eleven of the movements occurred in the fall, 23 in winter, 25 in spring, and 12 in summer.

Overall, density estimates from camera traps corresponded closely with those from live trapping, but those derived from camera-trapping surveys were more precise at both study sites and in all seasons (Supplementary Data SD7). At Camp Blanding, our density estimates for the 4-day camera-trap session ranged from 0.9 squirrels/km^2 (*SE* = 0.2) to 2.6 squirrels/km^2 (*SE* = 0.4), compared to live-trapping estimates of 1.0 squirrels/km^2 (*SE* = 0.3) to 1.8 squirrels/km^2 (*SE* = 0.4; Fig. 2). At Ordway, camera-trap estimates for the 4-day session ranged from 2.6 squirrels/km^2 (*SE* = 0.4) to 3.2 squirrels/km^2 (*SE* = 0.5), compared to live-trapping estimates that ranged from 0.6 squirrels/km^2 (*SE* = 0.3) to 3.2 squirrels/km^2 (*SE* = 0.7; Fig. 2). Adding 2 days of camera-trapping data resulted in marginally higher (Fig. 2; Supplementary Data SD4–SD6) and

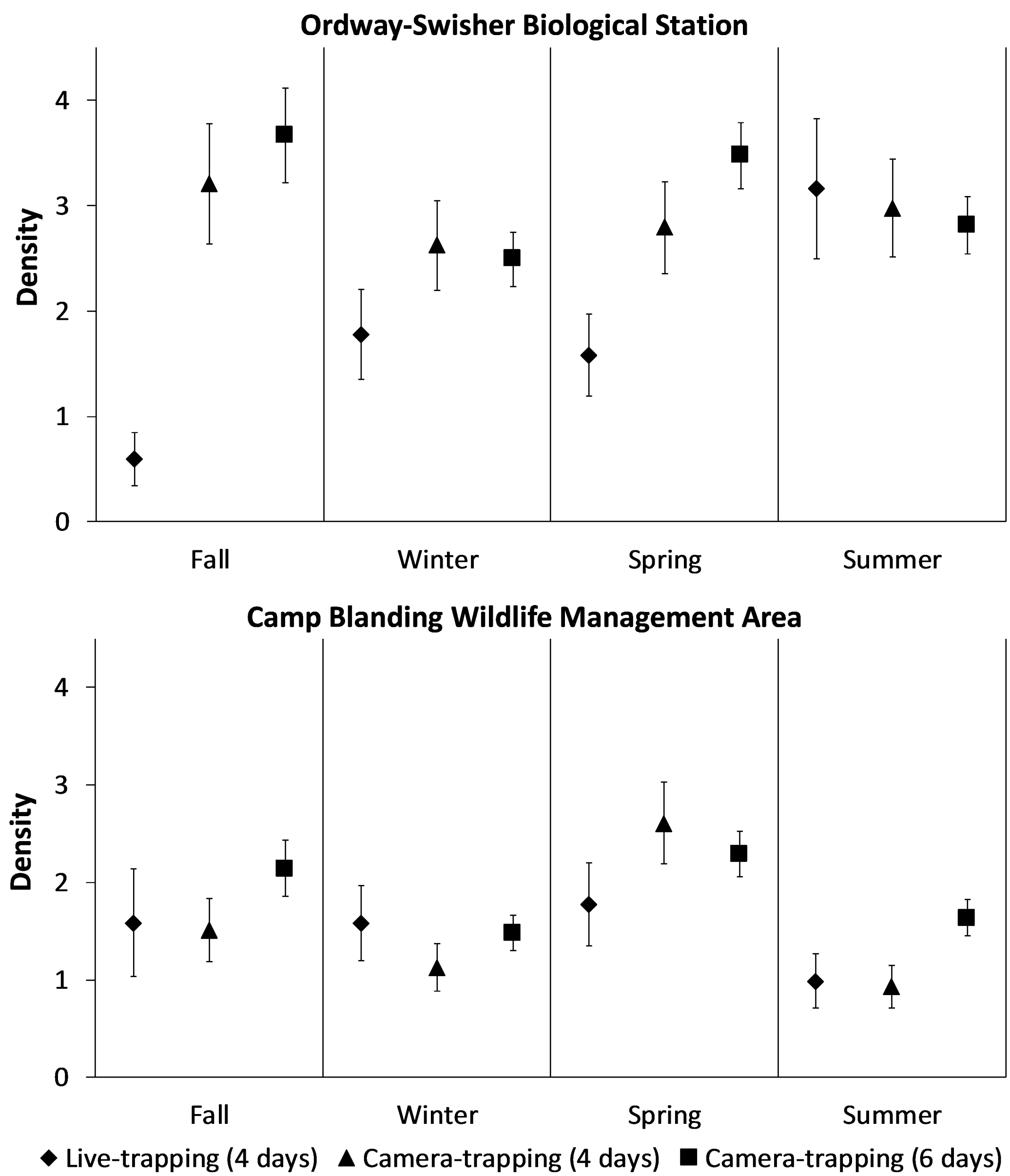

Fig. 2.—Model-averaged seasonal density estimates (squirrels/km^2) with unconditional *SE* bars from robust design analyses of Sherman's fox squirrels (*Sciurus niger shermani*) from live trapping and camera trapping at Ordway-Swisher Biological Station in Melrose, Florida (top), and Camp Blanding Wildlife Management Area in Starke, Florida (bottom) from 2011 to 2012.

more precise density estimates compared to estimates from live trapping and camera trapping from 4-day sessions (Supplementary Data SD7).

For our standardized correction factor, we calculated a buffer of 538 m (MMDM = 490 m and radiotelemetry = 581 m) to estimate the effective trapping area of previous studies on southeastern fox squirrels. Applying this buffer to past studies and our 6-day camera-trapping sessions greatly decreased previously published density estimates. Corrected estimates of densities across these studies ranged from 2.4 to 8.5 squirrels/km^2 in upland sandhill habitat (Table 1; Fig. 3).

Discussion

Advances in survey techniques and analytical tools have greatly improved our ability to estimate population densities of wildlife, but for many mammals, our current state of knowledge is derived from results obtained using traditional approaches that are prone to bias. Using the southeastern fox squirrel in Florida as an example, we found that adding an effective survey area buffer to past studies that either restricted their density estimates to the bounded survey areas or used a correction method that is known to bias estimates upward greatly decreased their density estimates (Table 1). In many cases, the original high estimates of density can be attributed to survey design and statistical oversights. For example, using nest counts to estimate a density of 38 squirrels/km^2, Moore (1957) failed to account for individuals that were not confined to his study area, despite documenting individuals with nests near the boundary of his survey area. Using our standardized correction factor, we estimated the density of fox squirrels on Moore's site to be 3.4 squirrels/km^2. Similarly, Weigl et al. (1989) used the ratio of

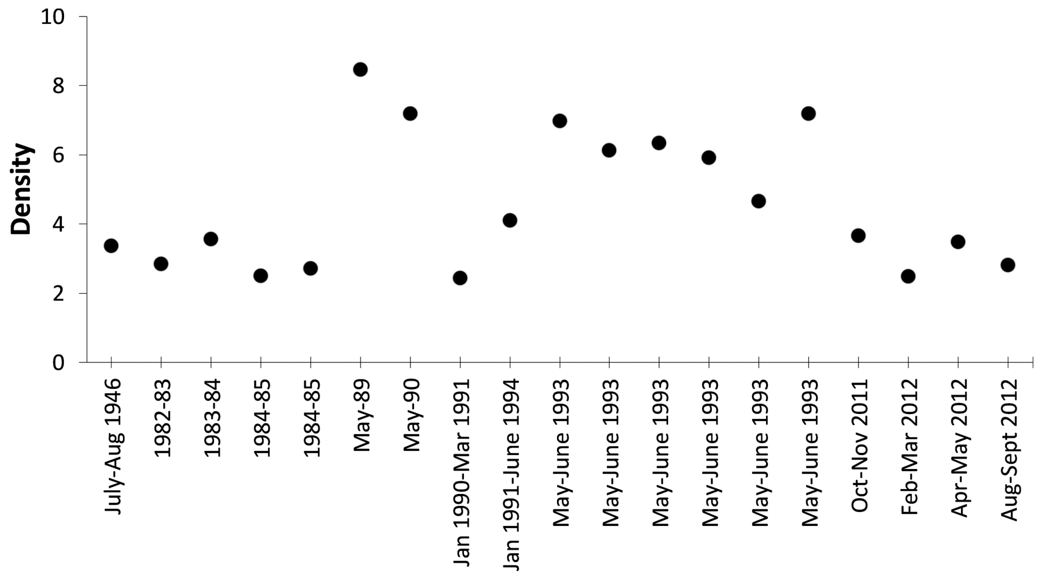

Fig. 3.—Density estimates (squirrels/km^2) for southeastern fox squirrels (*Sciurus niger* spp.) in sandhill communities from published and unpublished literature after being corrected for an effective survey area. Time periods on the x-axis are derived from this and 5 previous studies outlined in Table 1.

the number of captures and active nests to the area of each study site as a measure of density. They also estimated home ranges of males to be 43.7 ha, which was larger than the area of 4 of their 12 study sites. Using our standardized correction factor for their highest estimate of 35 squirrels/km^2 would suggest that 17-ha site more likely had a density of 2.7 squirrels/km^2.

We encountered 4 main issues that we could not account for and may have led to a bias in our corrected densities for past studies. First, densities obtained during previous studies might have been biased. We did not know how the range of methods used to calculate densities might have influenced estimates in past studies. For example, some authors assumed detectability was perfect (e.g., Moore 1957; Wooding 1997) or nearly perfect (Weigl et al. 1989), which rarely occurred given their acknowledgement of not having population closure. Second, we were unable to account for differences in habitat quality, which was mentioned as a possible barrier on the periphery of a study area (e.g., Tappe et al. 1993). Third, biases associated with estimates of MMDM from live trapping can be related to the size of the survey area, where larger survey areas reduce violations of population closure, but often use larger spacing between traps, thereby reducing the number of recaptures (Tappe and Guynn 1990). Similarly, the precision in radiotelemetered home-range estimates may have varied depending on the number of locations used for individuals, number of individuals monitored, and the telemetry technique used (e.g., homing versus triangulation). Although MMDM and radiotelemetry are 2 techniques commonly used to determine effective survey areas, the latter may be more reliable because MMDM may bias density estimates upward if trapping configuration results in short distances between consecutive detections (Parmenter et al. 2003; Soisalo and Cavalcanti 2006; Tioli et al. 2010). And fourth, for all studies, the actual area utilized by fox squirrels may have varied by weather conditions, food availability, season, and population densities (Sanderson 1966; Adams and Davis 1967; Weigl et al. 1989).

Nonetheless, these potential sources of bias may have had a limited influence on our corrected estimates. Of the potential biases, the assumption of perfect or nearly perfect detectability may not have severely affected the uncorrected density estimates given that these authors used a combination of live trapping with surveys of natural nests (Moore 1957), nest boxes (Weigl et al. 1989), or radiotelemetry (Wooding 1997). Second, southeastern fox squirrels have traditionally been studied in open pinelands where they are believed to have evolved and are most abundant (Steele and Koprowski 2001), and authors described their study areas as being high-quality habitat. Similarly, southeastern fox squirrels also use a variety of land cover types (e.g., Greene and McCleery 2016; Prince et al., 2016; Tye et al., in press) that are considered low-quality or unsuitable habitat and, therefore, a habitat barrier may not have been a great concern nor prevented movement of individuals into or out of their study area. Third, there is support from other species that densities calculated using the full MMDM and telemetry-based estimates can be similar (i.e., GPS telemetry—Soisalo and Cavalcanti 2006). In our study, the MMDM from live and camera trapping was 14 m less than our standardized correction factor. Therefore, the concern that MMDM could be unreliable from grid-based trapping for small mammals (Parmenter et al. 2003) may not have been great in our study; however, there were differences in MMDM estimates for our study sites (199 m) and survey methods (91 m), but these estimates may have been influenced by sample sizes. Previous averages of home ranges were generally consistent across studies: Edwards (1986) = 27.8 ha; Weigl et al. (1989) = 30.2 ha; Kantola and Humphrey (1990) = 30.1 ha; and Conner (2000) = 27.1 ha, although Hilliard (1979) = 21.4 ha was lower. Nonetheless, this average from Hilliard (1979) only represented 7% of all radiotelemetry estimates and 4% overall used for the standardized correction factor. If radiotelemetry home-range widths are more reliable as a buffer, our corrected densities of southeastern fox squirrels using the standardized correction factor would be biased upwards. These changes, however, would be minimal (e.g., the range of estimates of density from Weigl et al. [1989] would decrease from 2.5–3.6 to 2.3–3.2 squirrels/km^2 using only a radiotelemetry correction factor). However, it seems more likely that the corrected densities for most studies are underestimates. For example, in our study, an effective survey area 4.6 times larger than the bounded area was so large that individuals far from our grid probably did not encounter a trap during our 4- or 6-day sessions. This is supported by the few individuals detected on both grids at a site in our study. Furthermore, in past studies, authors with the largest uncorrected survey areas (Wooding 1997 = 95 and 230 ha; Tappe et al. 1993 = 121 ha; Conner et al. 1999 = 121 ha) had the highest corrected densities, suggesting that corrected estimates in our study and others, especially Moore (1957 = 21 ha) and Weigl et al. (1989 = 17 ha and 3 from 36 ha), are biased low. And fourth, Weigl et al. (1989) found that home ranges of both sexes in open pinelands were generally consistent throughout the year, and while indications of seasonal variation appeared to be related to food availability, it was activity patterns, not the areas used that were markedly different during the seasons as food conditions varied. Furthermore, because densities and home ranges were similar among studies, it is unlikely that these had a substantial influence on our recalculated density estimates.

We recommend the use of camera traps when handling live animals is not needed to accomplish other study objectives. Live-trapped individuals exhibited trap-shyness as indicated by the decrease between capture and recapture probabilities, whereas there was no apparent behavioral effect from camera traps as indicted by the similar capture and recapture probabilities. The increased number of individuals identified and overall number of detections from camera traps resulted in a more robust data set that led to more precise density estimates. Although we did not have 6 days of live trapping for comparison, nor annual replication, camera traps clearly outperform live trapping at detecting southeastern fox squirrels (Greene et al. 2016) and estimating their densities due to the higher number of recaptures. As observed in our study, southeastern fox squirrel densities vary by season, therefore, monitoring should consider temporal variation when estimating densities. Additionally, regardless of the survey method used, studies should account for the area used by fox squirrels during a survey period by including an effective area correction rather than limiting the estimates to the study boundaries to reduce biasing the results downward. However, our survey area may have still resulted in biased densities due to the effective survey area being so large relative to our bounded area that it is possible that not all animals had an equal probability of being detected; therefore, we also recommend that future studies aiming to estimate population sizes of southeastern fox squirrels should be conducted with survey grids much larger than 75 ha to avoid underestimating densities. Furthermore, surveying for > 6 days may also yield enough captures and recaptures for analyses with spatially explicit capture–recapture models that estimate density directly by modeling the effective survey area (Efford 2004; Royle and Young 2008; Efford and Fewster 2013), which we were unable to do in this study because of sparse datasets for individual seasons and survey methods.

Despite the biases associated with density estimates for southeastern fox squirrels in past studies, there appears to be a lack of distinct spatial or temporal variation in densities where they have been studied in minimally disturbed pine savannas. Comparing density estimates of southeastern fox squirrel in upland sandhill habitat from this study and our corrected density estimates from past studies over a 66-year period of field studies, densities from past studies with bounded surveys areas ≤ 75 ha ranged from 2.4 to 3.6 squirrels/km^2 and our estimates from 6 nights of camera trapping ranged from 2.5 to 3.7 squirrels/km^2. However, density estimates were higher when bounded areas were > 75 ha, ranging from 4.1 to 8.5 squirrels/km^2 (Table 1; Fig. 3). However, these comparatively consistent density estimates may be limited to relatively small areas of high-quality habitat where research efforts have been focused. Although southeastern fox squirrels use a variety of habitats, they seem to be most prolific in open pine savannas (Moore 1957; Loeb and Lennartz 1989; Tye et al., in press). Due to the loss of 97% of the historical longleaf pine ecosystem (Frost 1993) that once covered most of the southeastern United States, it has been widely reported that remaining southeastern fox squirrel populations are patchily distributed throughout the region and many are disjunct and declining (Weigl et al. 1989; Loeb and Moncrief 1993). Furthermore, there is no doubt that southeastern fox squirrels within fragments that are degraded due to changes in forest management practices, such as prescribed fire, have declined and today occur in lower densities, and depending on the severity of degradation can eventually be replaced by eastern gray squirrels (*Sciurus carolinensis*), a potential competitor that prefers closed-canopy hardwood forests (Conner et al. 1999). Future conservation and management efforts for fox squirrel populations should consider restoring and maintaining the open pine savannas that have maintained relatively consistent population densities.

As the technological and analytical tools in wildlife ecology advance, there is an opportunity to use them not only to generate reliable knowledge, but to reevaluate historical findings that have been used as baseline conditions. Using the southeastern fox squirrel as an example, we demonstrate how the use of modern approaches to estimate densities and a reevaluation of results from historical studies can change long held assumptions about population trends. The use of approaches like those outlined in this manuscript may help to avoid misdirected conservation designations, management actions, or misuse of funding that would be better applied to the conservation of other wildlife species.

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Supplementary Data

Supplementary Data SD1.—Table of candidate models used to estimate abundance of Sherman's fox squirrel (*Sciurus niger shermani*) from 4-day live-trapping sessions.

Supplementary Data SD2.—Table of candidate models used to estimate abundance of Sherman's fox squirrel (*Sciurus niger shermani*) from 4-day camera-trapping sessions.

Supplementary Data SD3.—Table of candidate models used to estimate abundance of Sherman's fox squirrel (*Sciurus niger shermani*) from 6-day camera-trapping sessions.

Supplementary Data SD4.—Table of model-averaged parameter estimates from 4-day live-trapping sessions for Sherman's fox squirrel (*Sciurus niger shermani*).

Supplementary Data SD5.—Table of model-averaged parameter estimates from 4-day camera-trapping sessions for Sherman's fox squirrel (*Sciurus niger shermani*).

Supplementary Data SD6.—Table of model-averaged parameter estimates from 6-day camera-trapping sessions for Sherman's fox squirrel (*Sciurus niger shermani*).

Supplementary Data SD7.—Table of seasonal density estimates of Sherman's fox squirrel (*Sciurus niger shermani*) corrected for effective survey areas from live trapping and camera trapping.

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