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Research Article

Reproductive Characteristics of a Coyote Population Before and During Exploitation

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ABSTRACT The eastward expansion of coyotes (*Canis latrans*) has brought the species into ecosystems and landscapes different from those it historically occupied, yet little is known about the reproductive biology of coyotes in the southeastern United States or the effects of exploitation on reproduction in coyotes. Our objective was to quantify litter size, pregnancy rate, and fecundity in an essentially unexploited coyote population in South Carolina, USA and to evaluate the effect of exploitation on these parameters. We examined reproductive tracts from 235 female coyotes trapped during 2010–2012. Placental scars from coyotes trapped during 2010 indicated that prior to trapping (2009), pregnancy rates were zero for juveniles, 0.25 for yearlings, and 0.389 for adults. Litter size for adults during 2009 averaged 5.4 pups/female, resulting in fecundity of 2.1 pups/female. The number of coyotes trapped was similar among years, indicating that the population recovered following trapping each year, but it shifted toward a younger age structure during trapping. However, although pregnancy rate, litter size, and fecundity of adults all tended to increase from pre-trapping (2009) through the last trapping period (2011–2012), differences were not significant for this or any other age class. Fecundity of the population did not significantly increase during the first year of trapping (2010) but was lower during the last trapping period (2011–2012; 0.56 ± 0.15 [95% CL]) than prior to trapping (0.90 ± 0.15 [95% CL]). Thus, we observed only weak evidence for compensatory reproduction in response to trapping pressure and conclude that the increase in the juvenile component of the population was attributable primarily to immigration from neighboring areas rather than *in situ* reproduction. This increased representation of juveniles in the population, which rarely bred, coupled with a concurrent decrease in adults, which accounted for 59.2% of breeding, explains the reduction in population fecundity. High immigration rates as indicated herein render coyote populations extremely difficult to control.

KEY WORDS *Canis latrans*, coyote, exploitation, fecundity, litter size, parturition date, pregnancy rate, reproduction, South Carolina, trapping.

The rapid eastward range expansion by coyotes (*Canis latrans*) during the latter half of the twentieth and early twenty-first centuries has resulted in the species occurring in landscapes and ecosystems different from those in which it occurred at the time of European settlement. In contrast to relatively dry western plains and mountains, coyotes now occupy the fragmented but rich hardwood and coniferous forests of the northeastern and mid-Atlantic regions of North America and the dense humid subtropical forests of the southeastern states. Coyotes are adaptable to the different habitat conditions and foods available in eastern forests, sometimes reaching population densities that equal or surpass those in western portions of their range (Knowlton et al. 1999, Schrecengost 2007), suggesting that the high reproductive potential of the species apparently has not been compromised in the East. Although there has been extensive research on the reproductive biology of coyotes in the West, less is known about coyote reproduction in more recently occupied portions of eastern North America. In a heavily forested area of eastern New Brunswick, Canada parturition rates were low (Dumond and Villard 2000), but in the largely forested landscapes of southern Quebec, Canada and West Virginia, USA litter sizes were comparable to those reported from the western United States (Jean and Bergeron 1984, Albers et al. 2016). Also working in southern Quebec, Richer et al. (2002) documented greater coyote abundance in an open than forested landscape, despite the availability of comparable or greater

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food resources in the forested landscape, and suggested that coyotes may be poorly adapted to exploiting foods in dense forest vegetation. Thus, it remains unclear whether reproductive characteristics of eastern coyotes differ in accordance with the different resource conditions they experience in this largely forested region.

Coyote productivity is governed largely by available food resources (Kennelly 1978, Knowlton et al. 1999, Bekoff and Gese 2003). Reproductive output in coyotes varies with the abundance of their primary prey. For example, litter size and pregnancy rates were correlated with the abundance of snowshoe hares (*Lepus americanus*) in Alberta, Canada (Todd and Keith 1983) and with the abundance of black-tailed jackrabbits (*Lepus californicus*) in Utah and Idaho, USA (Clark 1972). In such environments, coyote reproduction may be more strongly limited than elsewhere by the abundance of a primary prey species because of a paucity of alternative prey (Todd and Keith 1983). Although the generalist nature of coyote diets is well known throughout the species' range (Bekoff 1977, Hilton 1978, Bekoff and Gese 2003), the greater diversity of food types in more southerly systems may release coyote reproduction from dependence on the abundance of one or a few prey types (Schrecengost et al. 2008, Swingen et al. 2015, Cherry et al. 2016).

Reproductive characteristics of coyote populations may also relate to population density through the effects of density on available food supply (Knowlton et al. 1999). Litter size and pregnancy rates vary among populations of different densities and levels of human exploitation pressure, with greater productivity occurring where density is low because of exploitation pressure (Knowlton 1972). Most modeling studies of coyote populations have assumed such compensatory reproduction (Connolly and Longhurst 1975, Connolly 1978, Sterling et al. 1983). More recent modeling efforts have assumed litter size was dependent on pack size as the determinant of food availability (Pitt et al 2003, Conner et al. 2008), with smaller packs resulting in more food available to the alpha female. However, as Gese (2005) noted, few field studies have evaluated the response of previously unexploited populations to density reduction, and some unexploited populations with abundant food resources already exhibit high reproductive output. Thus, the degree to which any given coyote population may increase its reproductive output remains unclear.

Predator control is ethically and biologically controversial, but it continues to be practiced commonly to benefit livestock, game, and sometimes endangered species. In the southeastern United States where coyotes did not historically occur, coyote predation can have significant depressing effects on recruitment in white-tailed deer (*Odocoileus virginianus*; Kilgo et al. 2012, Chitwood et al. 2015, Nelson et al. 2015). Consequently, considerable interest in coyote control exists among hunters and wildlife managers, despite evidence that control confers inconsistent benefits to fawn survival and recruitment (VanGilder et al. 2009, Kilgo et al. 2014, Gulsby et al. 2015). Thus, more information is needed on the reproductive response to exploitation in coyote populations, particularly in forested systems of eastern North America.

Our objectives were to quantify reproductive characteristics of an unexploited coyote population in South Carolina, USA and to evaluate the effect of an intensive control program on reproduction in this population. We hypothesized that age-specific litter sizes and pregnancy rates would increase in response to reduced abundance associated with the control program, and that these increases would translate into greater age-specific and population-level fecundity.

STUDY AREA

We conducted the study on the United States Department of Energy's Savannah River Site (SRS), a 78,000-ha National Environmental Research Park situated in the Upper Coastal Plain physiographic region in Aiken, Barnwell, and Allendale counties, South Carolina. Topography was gently rolling to flat, with elevations ranging from 20 m to 130 m. The climate was humid subtropical, with a mean annual temperature of 18°C and mean annual rainfall of 122.5 cm. Summers were hot and humid and winters mild. Greatest monthly rainfall occurred during March and July–August and least occurred during April and November. Approximately 90% of the area was forested, with uplands dominated primarily by loblolly (*Pinus taeda*) or longleaf pine (*P. palustris*) and floodplains of the Savannah River and major tributaries dominated by bottomland hardwood or cypress (*Taxodium distichum*)–tupelo (*Nyssa* spp.) associations. Pine forests were managed on 50–120-year rotations depending on species and stand-specific management goals and were prescribe-burned on 3–10-year intervals. Early successional habitat occurred in approximately 12% of forest stands that were <10 years old and >2,600 km of road, railroad, and utility rights-of-way. White-tailed deer and feral pigs (*Sus scrofa*) were the dominant large herbivores and coyotes and bobcats (*Lynx rufus*) were the dominant predators.

Coyotes were first reported on SRS in 1986 and the population grew rapidly during the 1990s, apparently stabilizing during the early 2000s (Mayer et al. 2005, Kilgo et al. 2016). Density during 2006 was estimated at 0.8–1.5 coyotes/km^2 (Schrecengost 2007). Beginning in 2007, coyotes were permitted to be shot incidental to white-tailed deer hunting at SRS, which resulted in the harvest of 20–30 coyotes/year (T. T. Mims, U.S. Forest Service [USFS] Savannah River, personal communication), but prior to 2010 (this study) no trapping occurred. Given that the estimated coyote population size on SRS was approximately 620–1,165 (Schrecengost 2007), we feel that the number of coyotes killed during deer hunts was sufficiently minimal as to warrant characterizing the population as essentially unexploited.

METHODS

We sampled coyotes killed by trappers for research examining the effects of coyote control on survival of deer fawns (Kilgo et al. 2014). Trapping occurred between 18 January and 6 April 2010–2012 on 96 km^2 distributed evenly among 3 units separated by ≥6.4 km. Contract trappers used No. 1.75 or No. 2 foot-hold traps and killed coyotes using a

0.22 caliber rifle. Trapping was conducted under South Carolina Department of Natural Resources Research Collection Permit No. 010610-01, and taxon-specific guidelines for the use of wild vertebrates in research were followed to ensure animals were treated ethically and humanely (Sikes et al. 2011).

We extracted a lower canine tooth from each coyote to estimate age at parturition. We examined radiographs of teeth for root tip closure to separate animals <1 year old from those >1 year old at time of death (Linhart and Knowlton 1967). We then submitted all teeth for cementum annuli aging to the nearest year (Matson's Laboratory, Milltown, MT, USA). However, for most analyses, we used 3 age classes: juvenile (<1 yr old), yearling (1–2 yr old), and adult (≥2 yr old). Discrepancies between aging methods in assigning juvenile versus yearling ages occurred for 6 animals, and in these cases, we assigned the age determined by cementum annuli aging. Only 2 of these were females and neither was reproductively active. To assess changes in population age structure, we analyzed age class frequency data via multinomial logits models, where we modeled the response (frequency of coyotes trapped by age class) by year, sex, year + sex, year × sex, and null (intercept only) models.

We used corpora lutea, placental scars, fetuses, and localized uterine swellings (swellings) to assess parturition date, pregnancy rate, litter size, and age-specific and population-level fecundity in female coyotes. We removed reproductive tracts from all females and recorded number of swellings or fetuses and measured crown-rump length of fetuses at necropsy. We fixed reproductive tracts in 10% buffered formalin for later examination in the lab. We counted prior year placental scars but were unable to differentiate resorption scars with confidence so estimates of litter size from scars represent maximum possible litter size. We counted corpora lutea by slicing ovaries into 1-mm sections.

We calculated conception and parturition dates from average fetal crown-rump lengths within a litter using the regression equation from Kennelly (1978) for fresh fetuses and assumed a 63-day gestation period. We determined parturition date for coyotes with corpora lutea present but no swellings or fetuses by adding 50 days to date of death and for coyotes with swellings by adding 40 days (Sacks 2005). We assessed the relationship between parturition date and age of the female using simple linear regression. To estimate pregnancy rate (i.e., the proportion of females that bred) within a year or age class, we combined evidence from placental scars, fetuses, and swellings. Presence or absence of placental scars indicated breeding status in the prior year. For the current year, we included only individuals captured after February 28 and the presence or absence of fetuses or swellings indicated breeding status because most breeding occurred by that date, whereas before then evidence of breeding may not have been visible. For estimates of litter size, we used counts of placental scars (corrected for the year and age class in which the pregnancy occurred), swellings, and fetuses, regardless of capture date. Thus, sample sizes differed among variables calculated, and for pregnancy, rate did not equate to the total number trapped. We computed variance for pregnancy rate using the binomial distribution and for litter size using the Poisson distribution. We computed year and age-specific fecundity as the product of mean litter size and pregnancy rate for each year-age combination, with variance approximated by the Delta method (Williams et al. 2002:736) assuming independence between litter size and pregnancy rate. To estimate overall population fecundity, we weighted age-specific fecundity estimates by the proportion of coyotes in each age class, based on trapping frequencies, and summed the weighted age-specific fecundity estimates. We recognize that the age distribution of the trapped sample does not necessarily reflect the true age distribution of the population, because older classes may be less susceptible to trapping. Thus, our estimates of fecundity may be conservative (i.e., biased low).

We evaluated the effect of trapping by comparing reproductive parameters among 3 periods: 2009 (prior to trapping), 2010 (during first year of trapping), and 2011–2012 combined (during established trapping). Because trapping began in 2010, we lacked fetus and swelling data for 2009, but placental scar data from 2010 reflected reproduction in 2009. We assumed that the age distribution of coyotes trapped during 2010 represented that of the untrapped population. We compared reproductive parameters among periods using 2 approaches. First, we used an information-theoretic approach to evaluate relative support among 5 generalized linear models predicting litter size (lognormal distribution), pregnancy rate (binomial error distribution), and age-specific fecundity (lognormal error distribution). Models included a null (intercept only) model, under which the parameter did not vary and models for age, period, age + period, and age × period. Age and trapping period were categorical variables. We considered the juvenile age class and the pre-trapping year (2009) as reference categories for the 2 variables, respectively, so estimated effects were for the yearling and adult classes and for the 2010 and 2011–2012 periods added to the reference value on the logit scale (pregnancy rate) or log scale (litter size and fecundity). We compared models using Akaike's Information Criterion adjusted for small sample size (AIC_c) and considered models ≤2 ΔAIC_c units as the most supported. Second, we calculated 95% confidence limits for litter size, pregnancy rate, and age-specific and population fecundity, and assessed strength of any apparent differences by confidence interval width and degree of separation among periods. We performed all analyses in R (R Core Team 2014).

RESULTS

The number of coyotes trapped was similar among years: 169 in 2010 (91 F, 78 M); 135 in 2011 (72 F, 63 M); and 167 in 2012 (82 F, 85 M). The best model describing age class frequencies included sex and year (Table 1), indicating that age distributions differed between sexes but that the age distributions of both sexes changed over time. Among females, the proportion of juveniles increased from 0.604 in 2010 to 0.764 and 0.744 in 2011 and 2012, respectively,

Table 1. Model selection results, ranked by change in Akaike's Information Criterion adjusted for small sample (ΔAIC_c) and Akaike weight (w_i), used to evaluate differences in age frequencies among coyotes at the Savannah River Site, South Carolina, USA, 2010–2012.

Model	K[a]	AIC_c	ΔAIC_c	w_i
Sex + year	5	821.335	0.000	0.859
Sex × year	9	825.043	3.708	0.134
Sex	3	831.753	10.417	0.005
Null	1	833.980	12.645	0.002
Year	3	837.719	16.387	0.000

[a] Number of parameters.

whereas the proportion of adults declined from 0.242 in 2010 to 0.073 in 2012 (Fig. 1).

We examined reproductive tracts from 245 female coyotes: 171 juveniles, 39 yearlings, and 35 adults. We detected placental scars in 17 individuals and corpora lutea in 32 individuals, 4 of which had uterine swellings and 9 of which had fetuses. Mean conception date ($n = 32$) was 10 February (range = 11 Jan to 11 Mar) and mean parturition date was 14 April (range = 15 Mar to 13 May). Parturition date was correlated negatively with female age, with older females tending to conceive and whelp somewhat earlier than younger females ($F_{1,30} = 3.62$, $P = 0.067$; Fig. 2). Overall pregnancy rate was 0.051 ± 0.022 (SE) for juveniles ($n = 98$), 0.286 ± 0.099 for yearlings ($n = 21$), and 0.485 ± 0.087 for adults ($n = 33$). Overall litter size averaged 2.80 ± 0.75 for juveniles ($n = 5$; Table 2), 4.71 ± 0.82 for yearlings ($n = 7$), and 6.00 ± 0.58 for adults ($n = 18$). Fecundity (pups/F) was 0.14 ± 0.07 for juveniles, 1.35 ± 0.53 for yearlings, and 2.91 ± 0.59 for adults.

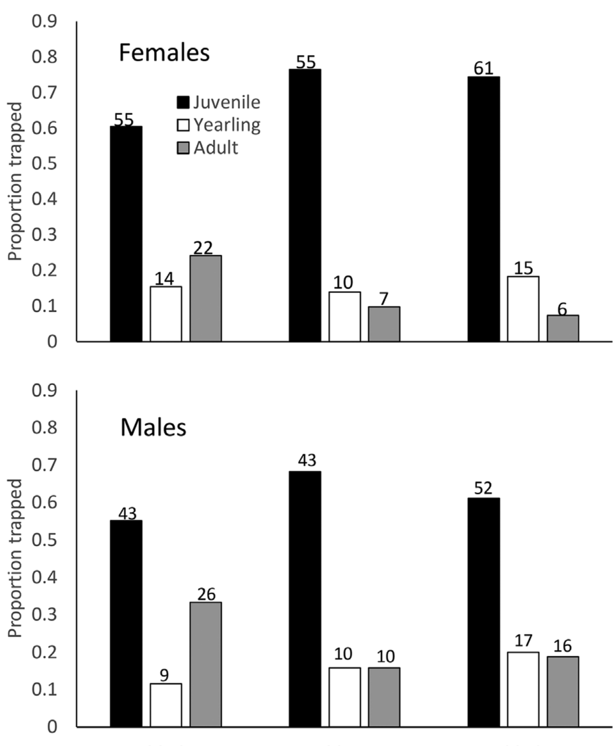

Figure 1. Age distributions of 245 female (top) and 226 male (bottom) coyotes trapped during 2010–2012 at the Savannah River Site, South Carolina, USA. Numbers of individuals are indicated above each bar.

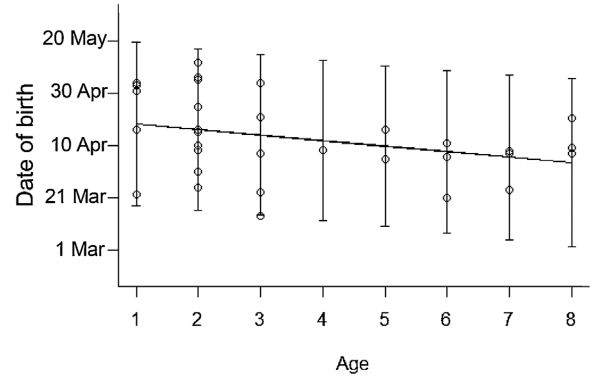

Figure 2. Mean parturition dates (solid circles; ±95% prediction intervals) estimated from fetal lengths, the presence of uterine swellings, and detection of corpora lutea from 32 female coyotes, by age (yr) at the Savannah River Site, South Carolina, USA, 2009–2012. Open circles indicate individual observations.

The best-supported model predicting both pregnancy rate and litter size was age + period (Table 3), with both parameters generally increasing with age (Table 4). Although the more parsimonious models including only age were competitive (Table 3), we evaluated the age + period models because these provided the most direct evaluation of the trapping effect. Pregnancy rate of adults was greater than of juveniles in all periods but did not differ from that of yearlings (Fig. 3). The greatest increase among periods occurred from pre-trapping (2009) to the first trapping period (2010) for yearlings (0.25 to 0.44) and adults (0.39 to 0.63), but 95% confidence intervals overlapped among periods (Fig. 3). We detected no litters among juveniles and only 1 among yearlings prior to trapping, but during the last trapping period, litter size for these age classes averaged 4.00

Table 2. Number of individuals used to assess reproductive parameters of female coyotes at the Savannah River Site, South Carolina, USA, 2009–2012.

Parameter	Juvenile	Yearling	Adult	Total
Parturition date[a]	5	10	17	32
Litter size[b]				
2009	0	1	7	8
2010	3	4	6	13
2011–2012	2	2	5	9
Pregnancy rate[c]				
2009	14	4	18	36
2010	35	9	8	52
2011–2012	49	8	7	64

[a] Includes females with corpora lutea, uterine swellings, or fetuses.
[b] Includes females with placental scars in the subsequent year and uterine swellings or fetuses in the current year, except 2009 which is represented only by placental scars detected in 2010.
[c] Includes females captured on 1 March or later during current year and all females from subsequent years in which placental scars could have been detected, as they would manifest current-year pregnancy. Thus, totals do not necessarily equate to total number of individuals captured in a year.

Table 3. Model selection results, ranked by change in Akaike's Information Criterion adjusted for small sample (ΔAIC_c) and Akaike weight (w_i), used to evaluate differences in reproductive parameters among female coyotes at the Savannah River Site, South Carolina, USA, 2009–2012.

Parameter	Model[a]	K[b]	AIC_c	ΔAIC_c	w_i
Pregnancy rate	Age + period	5	31.932	0.000	0.512
	Age	3	32.126	0.195	0.464
	Age × period	9	38.068	6.137	0.024
	Null	1	59.992	28.060	0.000
	Period	3	60.292	28.361	0.000
Litter size[c]	Age + period	5	9.742	0.000	0.606
	Age	3	11.289	1.545	0.280
	Period	3	14.459	4.717	0.057
	Null	1	14.460	4.718	0.057
Fecundity[c]	Age	3	11.322	0.000	0.817
	Age + period	5	14.309	2.988	0.183
	Period	3	32.489	21.167	0.000
	Null	1	33.910	22.589	0.000

[a] For models containing age, the reference category was juveniles. For models containing period, the reference category was the pre-treatment year, 2009.
[b] Number of parameters.
[c] Fit for the age × period model was poor because of sparse data, so AIC_c values were unreliable for comparison.

(95% CI = 1.23–6.78) and 5.00 (95% CI = 1.90–8.10), respectively. Adult litter size averaged 5.43 (95% CI = 3.70–7.15) prior to trapping and 7.00 (95% CI = 4.68–9.32) during the last trapping period. Although litter size tended to increase during the trapping periods, 95% confidence intervals overlapped among periods (Fig. 3). The best-supported model predicting fecundity included only age (Table 3). The age + period model received some support (Table 3). Fecundity of adults was greater than that of juveniles for all periods (Fig. 3). Adult fecundity increased from 2.11 pups/female prior to trapping to 4.00 during the last trapping period (Fig. 3).

Table 4. Parameter estimates and 95% confidence intervals for variables in the age + period model predicting pregnancy rate, litter size, and fecundity for female coyotes at the Savannah River Site, South Carolina, USA, 2009–2012. The age + period model was not necessarily the best-supported model for each reproductive parameter but provided the most direct evaluation of the trapping effect. Ages included juvenile (<1 yr; reference), yearling (1–2 yr), and adult (≥3 yr), and periods included pre-trapping (2009; reference), first trapping period (2010), and last trapping period (2011–2012).

Reproductive parameter	Scale	Model parameter	Estimate	95% CI
Pregnancy rate	Logit	Intercept	−3.68	−5.11 to −2.25
		Yearling	2.01	0.68–3.34
		Adult	3.23	1.95–4.52
		2010	1.26	−0.06 to 2.58
		2011–2012	0.41	−0.94 to 1.76
Litter size	Log	Intercept	1.13	0.38–1.88
		Yearling	0.51	−0.10 to 1.12
		Adult	0.75	0.14–1.35
		2010	−0.35	−1.00 to 0.31
		2011–2012	0.10	−0.58 to 0.79
Fecundity	Log	Intercept	−1.85	−2.98 to −0.72
		Yearling	1.85	1.16–2.54
		Adult	2.87	1.97–3.76
		2010	0.14	−0.97 to 1.25
		2011–2012	−0.02	−1.14 to 1.10

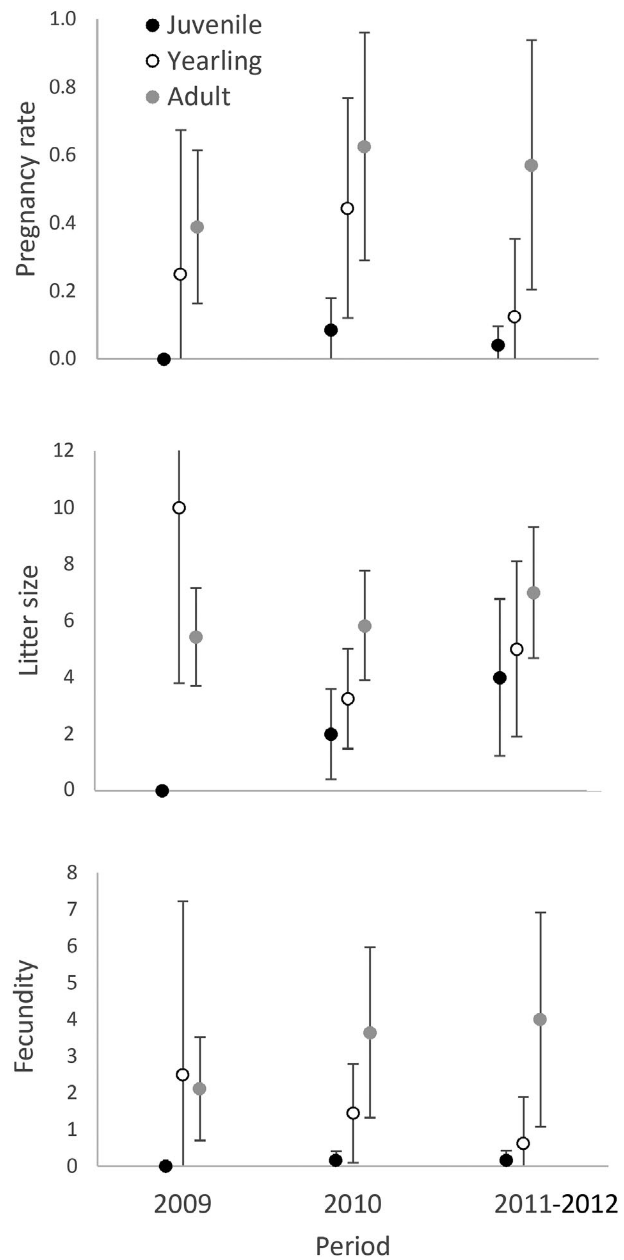

Figure 3. Estimated reproductive parameters (±95% CLs) of female coyotes, by age class, during 2009–2012 at the Savannah River Site, South Carolina, USA.

Fecundity of the population increased from 0.90 pups/female prior to trapping to 1.21 during the first year of trapping, but 95% confidence intervals overlapped (2009: 0.74–1.05; 2010: 1.02–1.39). During the last trapping period, population fecundity was lower than prior to trapping (Fig. 4).

DISCUSSION

Breeding chronology of this southeastern coyote population was generally similar to that reported for the species (Gier 1968, Kennelly 1978), but reproductive output prior to trapping was relatively low, even compared with other lightly or unexploited populations. Litter size for adults in 2009 was 5.4 with 39% of adults breeding, resulting in 2.1 pups

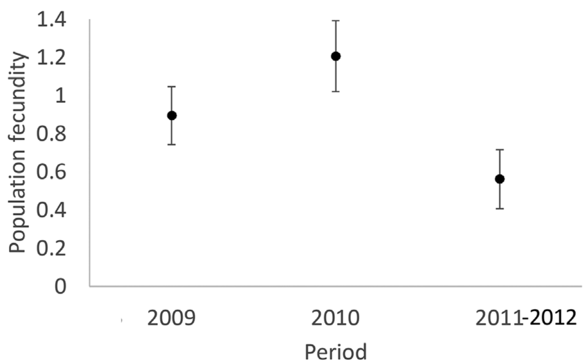

Figure 4. Population fecundity (±95% CLs) of female coyotes during 2009–2012 at the Savannah River Site, South Carolina, USA. Population fecundity was the sum of the products of age-specific fecundity and age-specific proportions in the population.

produced per adult female. This litter size was similar to that reported from a lightly exploited population in Texas, USA (5.7; Windberg 1995) and greater than from a lightly exploited population in Colorado, USA (3.4; Gese et al. 1989). However, the pregnancy rates of adults in those studies were 0.65 and 1.00, respectively, resulting in 3.7 and 3.4 pups/adult female. Similar to Gese et al. (1989), we did not detect breeding among juveniles in 2009. Low productivity, particularly among juveniles, is expected for unexploited populations, which also tend to reach greater densities and older age structures (Knowlton et al. 1999). Density of our study population, estimated 3 years prior to our study, was 0.8–1.5 coyotes/km^2 (Schrecengost 2007), and an annual population index during the intervening period did not indicate a change (T. T. Mims, unpublished data). Coyote densities for populations across western North America typically are $<1/km^2$ (Andelt 1985) but can reach $\geq 2.0/km^2$ (Knowlton et al. 1999). Thus, the density of our study population apparently was above average but did not approach the maximum reported for the species. Whether the low productivity of this population prior to trapping was attributable to its high density or a combination of other factors (e.g., habitat quality, prey abundance) remains unclear.

Following the initiation of trapping, some indication of compensatory reproduction appeared to occur. Our best-supported models for pregnancy rate and litter size indicated a period effect and for fecundity, a model containing period received some support. However, these models may have been overfit, and within age classes, 95% confidence intervals overlapped among periods for all reproductive parameters, suggesting that the effect of trapping was weak. Nevertheless, values of reproductive parameters during trapping generally were greater and were more similar to those from exploited populations across the species' range. Mean litter size of adults increased from 5.4 during the pre-trapping period to 7.0 during the last trapping period, and the pregnancy rate among adults increased from 0.39 prior to trapping to 0.63 in 2010 and 0.57 in 2011–2012. In exploited populations, adult litter sizes may range from 4.0 to 7.7 (Clark 1972, Knowlton 1972, Todd and Keith 1983, Jean and Bergeron 1984), averaging around 6 (Bekoff and Gese 2003), and adult pregnancy rates range from 37% to 94% (Nellis and Keith 1976, Todd and Keith 1983), though the typical range is 60–90% (Bekoff and Gese 2003). Variation in coyote reproduction among populations has been attributed to variation in density (and its effect on food supply) caused by exploitation level (Knowlton 1972, Knowlton et al. 1999). Similarly, jackals (*Canis mesomelas*) in South Africa that were subjected to hunting exhibited greater pregnancy rates and larger litter sizes among young age classes than those not hunted (Minnie et al. 2016). Models predicting the response of coyote populations to exploitation over time indicate that they demonstrate compensatory reproduction (Connolly and Longhurst 1975, Connolly 1978, Sterling et al. 1983). Yet these models were necessarily based on among-population data because of a paucity of research on how particular populations respond to exploitation level; little field data exist to validate these models. We are aware of only 2 studies that monitored the response of a previously unexploited coyote population to exploitation. Gese (2005) reported an increase in litter size and a slight increase in yearling reproduction after initiation of control in a Colorado population. However, Cypher and Scrivner (1992) reported no evidence of compensatory reproduction following control efforts in California, USA. Our data suggest a modest but non-significant increase in reproduction following the initiation of control in South Carolina.

Any increase in reproduction that may have occurred in response to trapping was not realized in population fecundity, which actually was lower during 2011–2012 than prior to trapping, contrary to our expectations. This reduction was attributable to the reduced portion of the population in the adult age class. Across all years, adults had greater pregnancy rates and larger litters than juveniles and yearlings (excepting the single outlier point representing yearling litter size in 2009), accounting for nearly 60% (16 of 27) of all breeding. However, adults accounted for only 22% (33 of 152) of potential breeders, and their representation in the population declined throughout the trapping period. During 2010, 24% of the female population were adults, but by 2012, adults comprised only 7% (Fig. 1). Because of this, the modest increase in litter size and pregnancy rates likely was, at best, sufficient only to replace those individuals lost to trapping, rather than to contribute to population recovery from trapping and other mortality.

This shift toward a younger age structure during trapping likely was due to mortality of adults from trapping and to an influx of immigrants vying for the vacated territories. Increasing trap-shyness among adults naïve to trapping at the beginning of the study may have been a factor during the last 2 years of study (2011–2012). However, such trap-shyness should not be evident among coyotes harvested opportunistically by deer hunters. The average age of 31 coyotes taken during 2011 deer hunts on SRS (1–2 months prior to the 2012 trapping season) actually was lower (1.52 yr) than that of our trapped coyotes (1.57 yr; J. C. Kilgo, USFS, unpublished data). Therefore, we believe any bias in our sample from trap-shyness likely was minimal. Genetic structure of the coyotes in our sample indicated that immigration was important in the recovery of the population from trapping (Kierepka et al. 2017). Transients are often (though not always) juvenile coyotes that roam over large areas seeking vacant territories in which to settle, and they frequently comprise ≥30% of coyote populations (Windberg and Knowlton 1988). Chamberlain et al. (2000) suggested that this percentage may be even greater in coyote populations in the southeastern United States, and recent studies of radio-collared coyotes corroborate this possibility. Half of studied coyotes in eastern North Carolina (Hinton et al. 2015) and up to 75% of coyotes in Virginia (D. J. Morin, Virginia Tech University, unpublished data) were considered transient. High immigration rates would be expected if such a large pool of transients existed in the vicinity of our study area. Whatever the cause of this shift toward a younger age structure, during trapping it, overwhelmed any compensatory reproductive response among remaining adults at the population level.

Increased pregnancy rates among juvenile and yearling coyotes have been associated with heavy exploitation pressure (Knowlton et al. 1999). Although we observed greater pregnancy rates among these age classes during the first year of trapping than before or after, the effects were not significant. We did not detect breeding among juveniles prior to trapping but did during trapping, albeit at rates <0.10. Pregnancy among yearlings increased from 0.25 prior to trapping to 0.44 during the first year of trapping but then declined to 0.13 during 2011–2012. Our small sample size for this age class likely contributed to such high variability. However, the mean pregnancy rate among yearlings during the last trapping period (0.29) was similar to that reported from exploited populations in Texas (35%; Knowlton 1972), West Virginia (30%; Albers et al. 2016), and Alberta (23–25%; Todd 1985).

Despite sampling nearly 250 individuals, sample sizes for certain age classes and years were small, limiting our ability to discern statistical differences. Nevertheless, we feel that our data support the conclusion that coyotes in the southeastern United States are capable of reproducing at rates comparable to those from the species' historical range. Although levels of reproductive parameters for this population prior to trapping may have tended toward the low end of reported values, during the last trapping period, these values were much more typical. Considering the high variability in reproductive parameters that coyotes exhibit across their range, it should not be surprising that the values reported herein fall within reported ranges. Thus, our study suggests that the reproductive potential of coyotes is not compromised by the forested nature of the southeastern landscape.

MANAGEMENT IMPLICATIONS

Trapping returns were similar during the 3 years of control, indicating that although temporary seasonal reduction in population size occurred (Kilgo et al. 2014), the population recovered to approximate pre-trapping levels each year in <1 year. Marginal increases in reproductive output of the population in response to trapping pressure likely contributed somewhat to recovery, but these increases were unlikely sufficient for complete recovery of pre-trapping population size. Instead, population recovery was achieved largely through immigration from surrounding areas. Thus, given the impossibility of implementing a trapping program over hundreds of km^2, which would be necessary to limit the regional pool of immigrants, control efforts are unlikely to reduce coyote populations in the Southeast for longer than a few months. Managers should be aware of this limitation when considering coyote control.

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LITERATURE CITED

Albers, G., J. W. Edwards, R. E. Rogers, and L. L. Mastro. 2016. Natality of yearling coyotes in West Virginia. Journal of Fish and Wildlife Management 7:192–197.

Andelt, W. F. 1985. Behavioral ecology of coyotes in south Texas. Wildlife Monographs 94:1–45.

Bekoff, M. 1977. *Canis latrans*. Mammalian Species 79:1–9.

Bekoff, M., and E. M. Gese. 2003. Coyote (*Canis latrans*). Pages 467–481 *in* G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild mammals of North America: biology, management, and conservation. Second edition. Johns Hopkins University Press, Baltimore, Maryland, USA.

Chamberlain, M. J., C. D. Lovell, and B. D. Leopold. 2000. Spatial-use patterns, movements, and interactions among adult coyotes in central Mississippi. Canadian Journal of Zoology 78:2087–2095.

Cherry, M. J., K. L. Turner, M. B. Howze, B. S. Cohen, L. M. Conner, and R. J. Warren. 2016. Coyote diets in a longleaf pine ecosystem. Wildlife Biology 22:64–74.

Chitwood, M. C., M. A. Lashley, J. C. Kilgo, K. H. Pollock, C. E. Moorman, and C. S. DePerno. 2015. Do biological and bedsite characteristics influence survival of neonatal white-tailed deer? PLoS ONE 10:e0119070.

Clark, F. W. 1972. Influence of jackrabbit density on coyote population change. Journal of Wildlife Management 36:343–356.

Conner, M. M., M. R. Ebinger, and F. F. Knowlton. 2008. Evaluating coyote management strategies using a spatially explicit, individual-based, socially structured population model. Ecological Modelling 219:234–247.

Connolly, G. E. 1978. Predator control and coyote populations: a review of simulation models. Pages 327–345 *in* M. Bekoff, editor. Coyotes: biology, behavior, and management. Academic Press, New York, New York, USA.

Connolly, G. E., and W. M. Longhurst. 1975. The effects of control on coyote populations: a simulation model. Division of Agricultural Science Bulletin 1872, University of California, Davis, USA.

Cypher, B. L., and J. H. Scrivner. 1992. Coyote control to protect endangered San Joaquin kit foxes at the Naval Petroleum Reserves, California. Proceedings of the Vertebrate Pest Conference 15:42–47.

Dumond, M., and M. A. Villard. 2000. Demography and body condition of coyotes (*Canis latrans*) in eastern New Brunswick. Canadian Journal of Zoology 78:399–406.

Gese, E. M. 2005. Demographic and spatial responses of coyotes to changes in food and exploitation. Proceedings of the Wildlife Damage Management Conference 11:271–285.

Gese, E. M., O. J. Rongstad, and W. R. Mytton. 1989. Population dynamics of coyotes in southeastern Colorado. Journal of Wildlife Management 53:174–181.

Gier, H. T. 1968. Coyotes in Kansas. Bulletin 393, Kansas Agricultural Experiment Station, Manhattan, USA.

Gulsby, W. D., C. H. Kilmaster, J. W. Bowers, J. D. Kelly, B. N. Sacks, M. J. Statham, and K. V. Miller. 2015. White-tailed deer fawn recruitment before and after experimental coyote removals in central Georgia. Wildlife Society Bulletin 39:248–255.

Hilton, H. 1978. Systematics and ecology of the eastern coyote. Pages 210–228 *in* M. Bekoff, editor. Coyotes: biology, behavior, and management. Academic Press, New York, New York, USA.

Hinton, J. W., F. T. van Manen, and M. J. Chamberlain. 2015. Space use and habitat selection by resident and transient coyotes (*Canis latrans*). PLoS ONE 10:e0132203.

Jean, Y., and J.-M. Bergeron. 1984. Productivity of coyotes (*Canis latrans*) from southern Quebec. Canadian Journal of Zoology 62:2240–2243.

Kennelly, J. J. 1978. Coyote reproduction. Pages 73–93 *in* M. Bekoff, editor. Coyotes: biology, behavior, and management. Academic Press, New York, New York, USA.

Kierepka, E. M., J. C. Kilgo, and O. E. Rhodes Jr. 2017. Effect of compensatory immigration on the genetic structure of coyotes. Journal of Wildlife Management 81:1394–1407.

Kilgo, J. C., H. S. Ray, M. Vukovich, M. J. Goode, and C. Ruth. 2012. Predation by coyotes on white-tailed deer neonates in South Carolina. Journal of Wildlife Management 76:1420–1430.

Kilgo, J. C., M. Vukovich, H. S. Ray, C. E. Shaw, and C. Ruth. 2014. Coyote removal, understory cover, and survival of white-tailed deer neonates. Journal of Wildlife Management 78:1261–1271.

Kilgo, J. C., M. Vukovich, M. J. Conroy, H. S. Ray, and C. Ruth. 2016. Factors affecting survival of adult female white-tailed deer after coyote establishment in South Carolina. Wildlife Society Bulletin 40:747–753.

Knowlton, F. F. 1972. Preliminary interpretations of coyote population mechanics with some management implications. Journal of Wildlife Management 36:369–382.

Knowlton, F. F., E. M. Gese, and M. M. Jaeger. 1999. Coyote depredation control: an interface between biology and management. Journal of Range Management 52:398–412.

Linhart, S. B., and F. F. Knowlton. 1967. Determining age of coyotes by tooth cementum layers. Journal of Wildlife Management 31:362–365.

Mayer, J. J., L. D. Wike, and M. B. Caudell. 2005. Furbearers. Pages 366–373 *in* J. C. Kilgo and J. I. Blake, editors. Ecology and management of a forested landscape: fifty years on the Savannah River Site. Island Press, Covelo, California, USA.

Minnie, L., A. Gaylard, and G. I. H. Kerley. 2016. Compensatory life-history responses of a mesopredator may undermine carnivore management efforts. Journal of Applied Ecology 53:379–387.

Nellis, C. H., and L. B. Keith. 1976. Population dynamics of coyotes in central Alberta, 1964–68. Journal of Wildlife Management 40:389–399.

Nelson, M. A., M. J. Cherry, M. B. Howze, R. J. Warren, and L. M. Conner. 2015. Coyote and bobcat predation on white-tailed deer fawns in a longleaf pine ecosystem in south western Georgia. Journal of the Southeastern Association of Fish and Wildlife Agencies 2:208–213.

Pitt, W. C., P. W. Box, and F. F. Knowlton. 2003. An individual-based model of canid populations: modelling territoriality and social structure. Ecological Modelling 166:109–121.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Richer, M.-C., M. Crete, and J.-P. Ouellet. 2002. The low performance of forest versus rural coyotes in northeastern North America: inequality between presence and availability of prey. Ecoscience 9:44–54.

Sacks, B. N. 2005. Reproduction and body condition of California coyotes (*Canis latrans*). Journal of Mammalogy 86:1036–1041.

Schrecengost, J. D. 2007. Home range and food habits of the coyote (*Canis latrans*) at the Savannah River Site, South Carolina. Thesis, University of Georgia, Athens, USA.

Schrecengost, J. D., J. C. Kilgo, D. Mallard, H. S. Ray, and K. V. Miller. 2008. Seasonal food habits of the coyote in the South Carolina Coastal Plain. Southeastern Naturalist 7:135–144.

Sikes, R. S., W. L. Gannon, D. S. Carroll, B. J. Danielson, J. W. Dragoo, M. R. Gannon, D. W. Hale, C. McCain, D. K. Odell, L. E. Olson, S. Ressing, R. M. Timm, S. A. Trewhitt, and J. E. Whaley. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

Sterling, B., W. Conley, and M. R. Conley. 1983. Simulations of demographic compensation in coyote populations. Journal of Wildlife Management 47:1177–1181.

Swingen, M. B., C. S. DePerno, and C. E. Moorman. 2015. Seasonal coyote diet composition at a low-productivity site. Southeastern Naturalist 14:397–404.

Todd, A. W. 1985. Demography and dietary comparisons of forest and farmland coyote, *Canis latrans*, populations in Alberta. Canadian Field Naturalist 99:163–171.

Todd, A. W., and L. B. Keith. 1983. Coyote demography during a showshoe hare decline in Alberta. Journal of Wildlife Management 47:394–404.

VanGilder, C. L., G. R. Woods, and K. V. Miller. 2009. Effects of an intensive predator removal on white-tailed deer recruitment in northeastern Alabama. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 63:11–16.

Williams, B. K, J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, California, USA.

Windberg, L. A. 1995. Demography of a high-density coyote population. Canadian Journal of Zoology 73:942–954.

Windberg, L. A., and F. F. Knowlton. 1988. Management implications of coyote spacing patterns in southern Texas. Journal of Wildlife Management 52:632–640.

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