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Variations in reproduction and age structure in the North American river otter in North Carolina, USA

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Abstract

Historically, the North American river otter (*Lontra canadensis*; otter) was distributed across North Carolina, USA, but populations were decimated by the early 1900s. Otter trapping was prohibited in 1938, reopened in 1947, and gradually expanded until it was opened statewide in 2005. Between 1986 and 1992, the North Carolina Wildlife Resources Commission and Great Smoky Mountains National Park released 404 otters to restore populations in western North Carolina. Our objective was to determine if the age structure and reproductive rates of otters throughout North Carolina shifted from 1978 to 2018 between remnant and reintroduced populations. During the 1978–1980 (period 1; Coastal Plain) and the 2009–2013 and 2014–2016 (period 2; statewide) trapping seasons, we collected 1,439 otter carcasses from licensed trappers, fur buyers, and wildlife damage control agents throughout the 3 Furbearer Management Units (FMUs) and 14 river basins in North Carolina. We conducted necropsies, used cementum annuli of the lower canine for age analysis, and counted corpora lutea and fetuses for fecundity estimates. Age distributions for all otters were skewed toward the younger age classes and did not differ between collection periods. During period 1, adults in the Coastal Plain had higher corpora lutea counts than during period 2, whereas Coastal Plain yearlings and juveniles had higher numbers of corpora lutea during period 2. During period 2, corpora lutea counts differed among FMUs; counts in the Mountain FMU ($\bar{x}$ = 2.56) were higher than in the Coastal Plain FMU ($\bar{x}$ = 1.62) or the Piedmont FMU ($\bar{x}$ = 1.91). Within the Coastal Plain FMU and pooling all age classes, fecundity increased by 45% from period 1 to period 2. Adult fecundity in the Coastal Plain FMU declined 16% from period 1 to period 2, while juveniles and yearlings began reproducing between the periods, indicating that reproduction has shifted to younger age classes between 1978 and 2018.

KEYWORDS

age structure, corpora lutea, fecundity, juvenile, *Lontra canadensis*, North Carolina, reproduction, river otter, trapping, variation, yearling

The North American river otter (*Lontra canadensis*; otter) is the largest mustelid inhabiting North Carolina, USA. Poor farming and logging practices degraded streams during the late nineteenth century. Coupled with unregulated harvest, this decimated otter populations in the Piedmont and Mountain Furbearer Management Units (FMUs; Figure 1) by the early twentieth century. In the Coastal Plain FMU, large swamps and wetlands provided a refuge that buffered the surviving otter populations (Melquist and Dronkert 1987).

To protect the otter population in North Carolina, otter trapping was prohibited statewide in 1938, reopened in 1947, and gradually expanded from the Coastal Plain FMU westward until it was opened statewide in 2005 (Figure 2). Also, between 1986–1992, 137 otters (81 male, 56 female) were translocated by the National Park Service from Louisiana, North Carolina, and South Carolina, USA, into the Great Smoky Mountains National Park (Griess 1987, Raesly 2001). Between 1988 and 1996, the North Carolina Wildlife Resources Commission (NCWRC) also translocated 267 otters (160 male, 107 female) from the Coastal Plain to the Mountain FMU (Spelman 1998). Today, otters are abundant and self-sustaining in all 3 FMUs with a statewide otter trapping season and no bag limits.

River otters reproduce annually and generally begin at 2 years of age (Hamilton and Eadie 1964, Tabor and Wight 1977). Although yearling reproduction has been documented, it is considered rare (Liers 1958, Docktor et al. 1987, Crimmins et al. 2011). In recent decades, there have been increasing reports of yearlings reproducing,

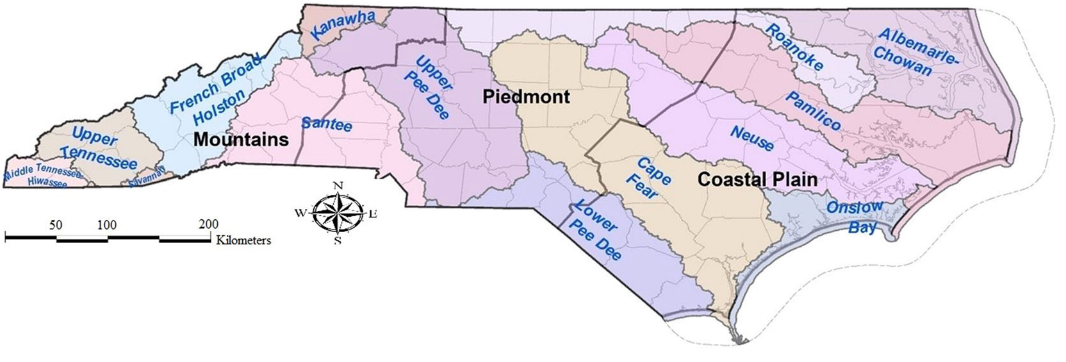

FIGURE 1 Furbearer Management Units and river basins of North Carolina, USA, 1978–2016.

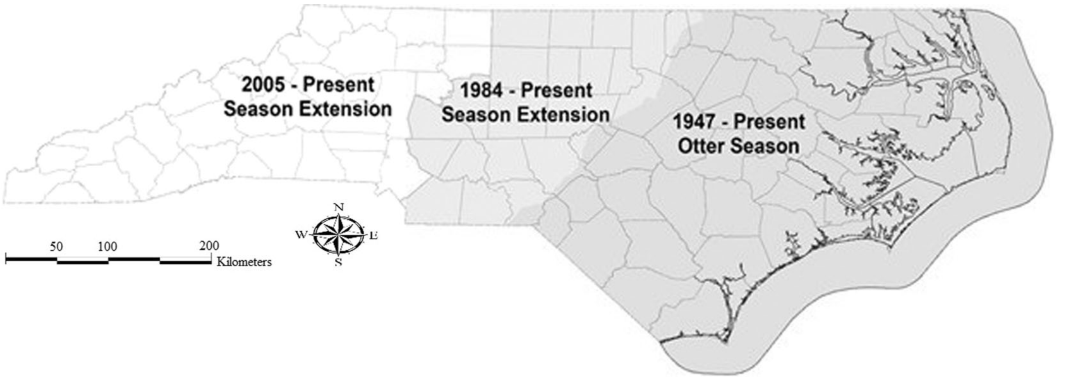

FIGURE 2 River otter trapping seasons in North Carolina, USA, 1947–2022.

especially in reintroduced populations (Johnson et al. 2007, Crimmins et al. 2011), which suggests greater species resiliency and adaptability. The International Union for Conservation Otter Specialist Group's first and third recommended conservation priorities (Foster-Turley et al. 1990) included evaluating the population status of otter populations and analyzing carcasses to increase our knowledge of otter reproduction.

Because of the historical otter reintroductions that have occurred in North Carolina, our objective was to determine if the age structure and reproductive rates of otters throughout North Carolina shifted from 1978 to 2018 and whether rates differed between remnant and reintroduced populations and among river basins, FMUs, periods, and age classes. Our analyses were facilitated by the abundance of data collected by the NCWRC through volunteer trapper surveys, fur buyer reporting, and Convention on International Trade in Endangered Species (CITES) tag sales.

STUDY AREA

We conducted our study across North Carolina, a geographically and ecologically diverse state in the southeastern United States, covering 139,391 km^2, with weather and climate appropriate for a temperate zone. We did not model weather during our study period, but it did not exceed historical limits. For furbearer management, the NCWRC established 3 FMUs (i.e., Mountain, Piedmont, and Coastal Plain), which followed physiographic regions and county boundaries (Figure 1). North Carolina has 14 different river basins ranging from mountain streams to brackish rivers. These include cold water systems in the mountains and piedmont and warmwater systems throughout the state. Within those river basins are 17 terrestrial and 11 wetland communities. Wetland communities include bogs, black and brown water systems, freshwater tidal wetlands, pocosins, swamps, natural lakes, reservoirs, impoundments, and saltwater estuaries (North Carolina Wildlife Resources Commission 2015).

METHODS

Data collection

During the 1978–1980 (period 1; Coastal Plain and Piedmont FMUs) and the 2009–2013 and 2014–2016 (period 2; statewide) trapping seasons, we collected otter carcasses from licensed trappers, fur buyers, and wildlife damage control agents. The field season was concurrent with the regular trapping season, which spanned from

November–February annually. For all otters collected, we recorded the date and location trapped, which included specific coordinates, addresses, or a general description of the trap site (i.e., county, locality, roads, and prominent landmarks).

We froze all carcasses until necropsy. During necropsy, we extracted a lower canine tooth for cementum annuli aging (Stephenson 1977). The samples from period 1 were aged at North Carolina State University, and the samples from period 2 were sent to Matson's Laboratory (Manhattan, MT, USA). Otters aged as zero were juveniles, otters aged as 1 year old were yearlings, and otters ≥2 years were considered adults. We considered otters that were unable to be aged by cementum annuli but morphologically mature to be in the adult age class. We removed female reproductive tracts and preserved them in a 10% formalin solution. We sectioned each ovary in 1-mm slices (Hamilton and Eadie 1964) and counted active corpora lutea. We dissected the uterine horns and counted visible fetuses (i.e., litter size). During period 1, we collected blastocysts by flushing each uterine horn with sterilized water and examining it under a microscope. During period 2, because blastocysts quickly degrade (Johnson et al. 2007), we did not collect blastocysts and only report corpora lutea, which is consistent with the literature (Docktor et al. 1987, Chilelli et al. 1996, Crimmins et al. 2011).

Data analysis

We conducted the statistical analysis in SAS 9.4 (SAS Institute, Cary, NC, USA) using Proc TTEST for *t*-tests, Proc ANOVA for analysis of variance (ANOVA), and Proc GENMOD for models. We used 2-sample *t*-tests and 1-way ANOVA to determine significant differences between periods and among FMUs. We used Tukey's honestly significant difference (HSD) test to examine differences within variables. We used a paired *t*-test to compare corpora lutea and fetus counts (litter size) during period 1 and period 2 and used a 1-way ANOVA to determine differences across age classes. We limited our candidate model set to a generalized linear model of corpora lutea and fetus counts with the 2 *a priori* categorical covariates including age and FMU and an additive model, to avoid including spurious effects. We did not use river basins in our models because sample sizes were not distributed across all basins. We used Akaike's Information Criterion (AIC) to assess model weights and rank candidate models (Burnham and Anderson 2002). We used model averaging across parameters for age and FMU, and calculated the unconditional variance estimates and associated 95% confidence intervals (Burnham and Anderson 2002, Anderson 2008, Gould and Andelt 2013).

RESULTS

Sample size and otter age

During period 1, we collected 617 otter carcasses (330 male, 287 female) from over 50 licensed trappers and fur dealers (Table 1). We determined ages for 330 males and 274 females via cementum annuli. No females were collected from the Piedmont FMU during period 1. During period 2, we collected 822 (524 male, 298 female) otter carcasses across North Carolina from over 50 licensed trappers, fur dealers, and wildlife damage control agents; all ages were determined via cementum annuli.

During period 1, using otters aged with cementum annuli, the average ages of males ($n = 330$) and females ($n = 274$) were 1.9 and 1.7, respectively (Table 1). During period 2, the average ages of males ($n = 524$) and females ($n = 298$) were 2.0 and 1.7, respectively, and age did not differ between collection periods ($t_{1,213} = -0.82$, $P = 0.412$). Age distributions for all otters combined across both collection periods were skewed toward the younger age classes and prevalence favored juveniles in period 1 and yearlings in period 2 (Figure 3). During period 1, Coastal Plain FMU male and female age-at-harvest distributions were similar ($t_{602} = -1.02$, $P = 0.31$). During period 2, there

TABLE 1 Average age-at-harvest via cementum annuli of river otters in 1978–1980 (period 1) and 2009–2016 (period 2) in North Carolina, USA, by sex and Furbearer Management Unit (FMU).

Sex	n_1, n_2	FMU	Period 1 $\bar{x}$	Period 1 SE	Period 2 $\bar{x}$	Period 2 SE
Males	306, 286	Coastal Plain	1.88	0.12	1.84	0.11
	24, 204	Piedmont	1.96	0.42	2.17	0.14
	0, 34	Mountains			2.35	0.39
	330, 524	All	1.89	0.12	2.00	0.09
Females	274, 160	Coastal Plain	1.71	0.13	1.73	0.15
	0, 118	Piedmont			1.68	0.18
	0, 20	Mountains			1.61	0.33
	274, 298	All	1.71	0.13	1.71	0.11
All	580, 446	Coastal Plain	1.80	0.09	1.80	0.09
	24, 322	Piedmont	1.96	0.42	1.99	0.11
	0, 54	Mountains			2.10	0.28
	604, 822	All	1.81	0.09	1.90	0.07

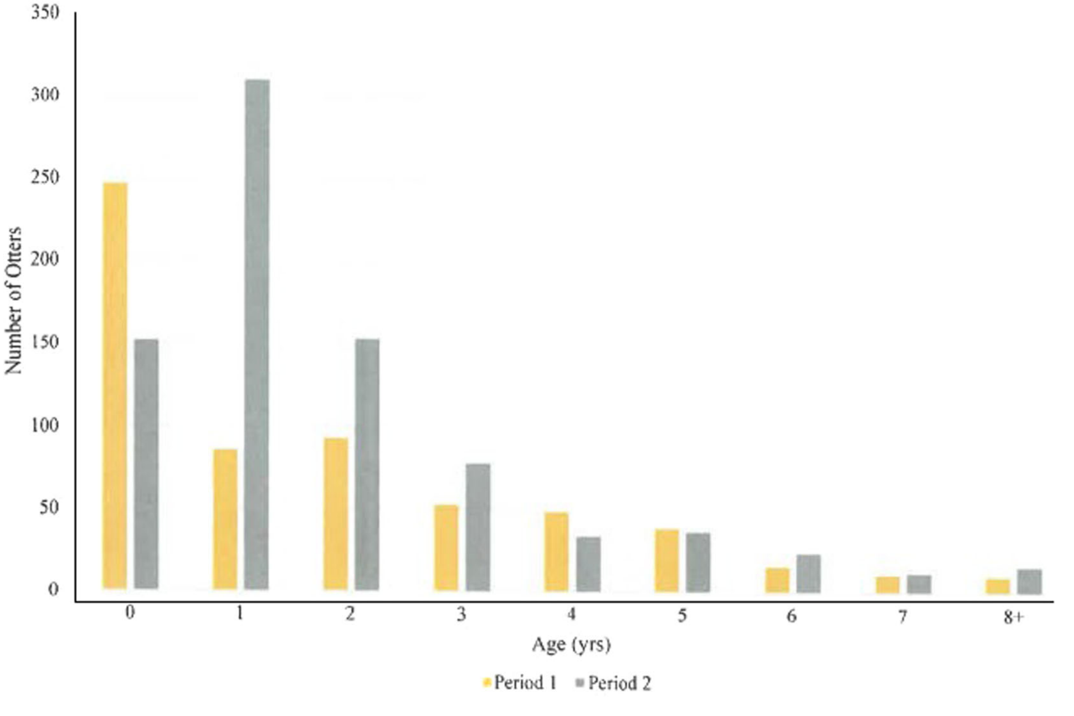

FIGURE 3 Age distribution of harvested river otters during period 1 (1978–1980) and period 2 (2009–2016) in North Carolina, USA.

was evidence that male and female age distributions differed within the Piedmont FMU (F_{318} = 4.34, P = 0.038), but there was not evidence for differences in the Mountain FMU (F_{50} = 1.59, P = 0.214) or Coastal Plain FMU (F_{440} = 0.35, P = 0.553; Table 1).

Corpora lutea counts

During period 1, the number of corpora lutea for juveniles ($\bar{x}$ = 0.02), yearlings ($\bar{x}$ = 0.00), and adults ($\bar{x}$ = 2.49) differed (F_{271} = 250.86, P < 0.001; Table 2), with adults being more likely to have active corpora lutea than yearlings or juveniles (Q_{271} = 3.33, α = 0.05). During period 2, the number of corpora lutea for juveniles ($\bar{x}$ = 1.11), yearlings ($\bar{x}$ = 1.42), and adults ($\bar{x}$ = 2.05) differed (F_{145} = 13.73, P < 0.001; Table 2); adults were more likely to have corpora lutea than yearlings or juveniles (Q_{145} = 3.35, α = 0.05). Within the Coastal Plain FMU, corpora lutea counts differed between period 1 ($\bar{x}$ = 1.05) and period 2 ($\bar{x}$ = 1.62; t_{405} = 4.76, P < 0.001). Adults during period 1 produced higher corpora lutea counts than during period 2 (t_{170} = −2.52, P = 0.013), while yearlings (t_{47} = 11.96, P < 0.001) and juveniles (t_{35} = 6.92, P < 0.001) produced higher counts of corpora lutea during period 2.

During period 2, corpora lutea counts differed by FMU (F_{275} = 8.44, P < 0.001); counts in the Mountains ($\bar{x}$ = 2.56) were higher (Q_{275} = 3.33, α = 0.05) than in the Piedmont ($\bar{x}$ = 1.91) and Coastal Plain ($\bar{x}$ = 1.62; Table 2). Mountain FMU corpora lutea counts differed by age class (F_{15} = 5.59, P = 0.015) where counts for adults ($\bar{x}$ = 2.89) were higher than those of juveniles ($\bar{x}$ = 1.75) but not yearlings ($\bar{x}$ = 2.60, Q_{15} = 3.67, α = 0.05; Table 2). Also, Piedmont FMU corpora lutea counts differed by age class (F_{109} = 7.79, P < 0.001), where counts for juveniles ($\bar{x}$ = 1.35) were lower than those for adults ($\bar{x}$ = 2.24) and yearlings ($\bar{x}$ = 2.00, Q_{109} = 3.36, α = 0.05). The top model for corpora lutea included FMU as a classification variable and age as a numeric variable with all effects fixed. This model held 99% of the model weight, the next closest model was >13 ΔAIC, and all covariates were significant via model averaging (Tables 3 and 4).

Fetus counts

During period 1, adults in the Coastal Plain averaged 2.00 fetuses and adult fetus counts were higher (F_{271} = 175.58, P < 0.001) than those of juveniles ($\bar{x}$ = 0.00) and yearlings ($\bar{x}$ = 0.00; Q_{271} = 3.33, α = 0.05; Table 2). During period 2, fetus counts in the Coastal Plain differed across age classes (F_{144} = 13.90, P < 0.001); counts for adults ($\bar{x}$ = 1.03) were greater than for yearlings ($\bar{x}$ = 0.21) and juveniles ($\bar{x}$ = 0.00; Q_{144} = 3.35, α = 0.05). Fetus counts for all females from the Coastal Plain FMU differed between period 1 ($\bar{x}$ = 0.84) and period 2 ($\bar{x}$ = 0.52; t_{419} = −2.51, P = 0.013). Adults during period 1 produced higher fetus counts ($\bar{x}$ = 2.00) than during period 2 ($\bar{x}$ = 1.03; t_{177} = −4.50, P < 0.001), while we did not find strong evidence for a difference between periods for yearlings (t_{47} = 1.75, P = 0.086).

During period 2, fetus counts for all females differed by FMU (F_{274} = 3.61, P = 0.028); counts in the Mountains ($\bar{x}$ = 1.22) were higher (Q_{274} = 3.33, α = 0.05) than those in the Piedmont ($\bar{x}$ = 0.47) and Coastal Plain ($\bar{x}$ = 0.52; Table 2). Mountain FMU fetus counts differed by age class (F_{15} = 7.34, P = 0.006) where counts for adults ($\bar{x}$ = 2.22) were higher than those for juveniles ($\bar{x}$ = 0.00) and yearlings ($\bar{x}$ = 0.40, Q_{15} = 3.67, α = 0.05; Table 2). Also, Piedmont FMU fetus counts differed by age class (F_{109} = 15.02, P < 0.001), where counts for juveniles ($\bar{x}$ = 0.06) were lower than those for adults ($\bar{x}$ = 1.07) and yearlings ($\bar{x}$ = 0.15, Q_{109} = 3.36, α = 0.05). The top model for fetus counts incorporated FMU as a classification variable and age as a numeric variable with all effects fixed. This model held 54% of the model weight. The next closest model (age only) received support (ΔAIC = 0.46) and carried 46% of the model weight. The covariates were significant via model averaging except for the Coastal Plain FMU variable (Tables 3 and 4).

TABLE 2 Corpora lutea and fetus counts in river otters in 1978–1980 (period 1) and 2009–2016 (period 2) in North Carolina, USA, by Furbearer Management Unit (FMU) and age class. Otters <1 year old were juveniles, 1-year-old otters were yearlings, and all otters ≥2 years old were adults.

				Period 1		Period 2	
Age class	n_1, n_2	**FMU**	**Variable**	$\bar{x}$	**SE**	$\bar{x}$	**SE**
Juveniles (0–1)	116, 35	Coastal Plain	Corpora lutea	0.02	0.02	1.11	0.16
			Fetuses	0.00	0.00	0.00	0.00
	0, 31	Piedmont	Corpora lutea			1.35	0.16
			Fetuses			0.06	0.06
	0, 4	Mountains	Corpora lutea			1.75	0.25
			Fetuses			0.00	0.00
	116, 70	All	Corpora lutea	0.02	0.02	1.26	0.02
			Fetuses	0.00	0.00	0.03	0.03
Yearlings (1–2)	43, 48	Coastal Plain	Corpora lutea	0.00	0.00	1.42	0.12
			Fetuses	0.00	0.00	0.21	0.12
	0, 39	Piedmont	Corpora lutea			2.00	0.14
			Fetuses			0.15	0.09
	0, 5	Mountains	Corpora lutea			2.60	0.24
			Fetuses			0.40	0.40
	43, 92	All	Corpora lutea	0.00	0.00	1.73	0.09
			Fetuses	0.00	0.00	0.20	0.08
Adults (≥2)	115, 65	Coastal Plain	Corpora lutea	2.49	0.13	2.05	0.12
			Fetuses	2.00	0.13	1.03	0.18
	0, 42	Piedmont	Corpora lutea			2.24	0.17
			Fetuses			1.07	0.20
	0, 9	Mountains	Corpora lutea			2.89	0.20
			Fetuses			2.22	0.46
	115, 116	All	Corpora lutea	2.49	0.13	2.18	0.09
			Fetuses	2.00	0.13	1.14	0.13
All	274, 148	Coastal Plain	Corpora lutea	1.05	0.09	1.62	0.08
			Fetuses	0.84	0.08	0.52	0.09
	0, 112	Piedmont	Corpora lutea			1.91	0.10
			Fetuses			0.47	0.09
	0, 18	Mountains	Corpora lutea			2.56	0.17
			Fetuses			1.22	0.35
	274, 278	All	Corpora lutea	1.05	0.09	1.80	0.06
			Fetuses	0.84	0.08	0.55	0.07

TABLE 3 Model selection results using Akaike's Information Criterion (AIC) for the effect of age and Furbearer Management Unit (FMU) on corpora lutea and fetus counts for river otters in North Carolina, USA, during November–February 2009–2016. We present the model weight (wi), the number of parameters (K), and log likelihood (log like).

	Corpora lutea					Fetuses				
Model	AIC	ΔAIC	w_i	K	Log like	AIC	ΔAIC	w_i	K	Log like
Age + FMU	743.95	0.0	0.999	5	−366.97	776.83	0.0	0.544	5	−383.41
Age	757.50	13.5	0.001	2	−375.75	777.18	0.4	0.456	2	−385.59
FMU	785.04	41.1	0.000	4	−388.52	850.64	73.8	0.000	4	−421.32
Null	797.61	53.7	0.000	1	−396.80	853.84	77.0	0.000	1	−424.92

TABLE 4 Model-averaged coefficients for the effects of age (per year) and Furbearer Management Unit (FMU) on the corpora lutea and fetus counts of river otters in North Carolina, USA, 2009–2016.

	Corpora lutea			Fetuses		
Variable	Estimate	Unconditional variance SE	Unconditional 95% CI	Estimate	Unconditional variance SE	Unconditional 95% CI
Age	0.180	0.030	0.121, 0.240	0.256	0.037	0.183, 0.329
FMU (Coastal Plain)	−0.318	0.116	−0.545, −0.090	0.007	0.124	−0.236, 0.250
FMU (Mountain)	0.596	0.247	0.112, 1.079	0.536	0.263	0.020, 1.052

Litter sizes

We examined litter sizes by eliminating all samples without visually verified fetuses or blastocysts (blastocysts were only collected during period 1). Hence, we had 87 and 57 specimens from periods 1 and 2, respectively. Corpora lutea counts for this subset ($\bar{x} = 3.01$, $\bar{x} = 2.63$) differed from fetus counts during period 1 ($\bar{x} = 2.64$, $t_{86} = 4.90$, $P < 0.001$) but not period 2 ($\bar{x} = 2.65$, $t_{56} = -0.11$, $P = 0.910$). During period 1, all specimens with visible fetuses were adults, but during period 2 we identified visible fetuses in 49 adults, 7 yearlings, and 1 juvenile. The 1 juvenile was aged by a broken tooth and was given a 1-year error, making it a possible yearling. Between adults and yearlings, period 2 corpora lutea counts ($\bar{x} = 2.73$, $\bar{x} = 2.14$) and fetus counts ($\bar{x} = 2.67$, $\bar{x} = 2.57$) were similar ($F_{54} = 0.44$, $P = 0.649$), suggesting that fetus counts supported the corpora lutea counts as accurate estimators of litter size, and the difference between the 2 metrics during period 1 could be from the difficulty of isolating and identifying blastocysts.

DISCUSSION

Across North Carolina, the age distribution of harvested otters was stable across the 2 collection periods that spanned 40 years. During period 2, the NCWRC estimated approximately 2,400 otters were harvested annually, and based on the age distributions, the population appears to be healthy (Sanders et al. 2020*a*) with high reproduction and recruitment. The long-term stable age distribution of harvested otters indicates that habitat and water quality are good (Sanders et al. 2020*b*) and that reproduction is stable or increasing (Sulkava et al. 2007, Barrett and Leslie 2012, Graser et al. 2012, Marvá and San Segundo 2018, Nadal et al. 2018). Further, an abundance of young otters in the harvest is indicative of high recruitment and population stability (Rolley 1985, Koons et al. 2006, Flynn and Schumacher 2009, Rughetti 2016).

Within the Coastal Plain FMU, fecundity for all females increased by 45% from period 1 to period 2 based on corpora lutea counts. Although adult reproduction dropped 16% from period 1 to period 2, juvenile and yearling reproduction occurred at a higher rate during period 2. Early reproduction has been recorded previously (Liers 1958, Crimmins et al. 2011, Barding and Lacki 2014) but not to the extent that we detected. Our results indicate the reproductive load has shifted to include juvenile and yearling otters. In general, water quality has improved over the years (White 1996, Sanders et al. 2020*b*), and the expansion and recolonization of beavers (*Castor canadensis*) has provided more aquatic habitat across the landscape (Naiman et al. 1988, Snodgrass and Meffe 1998, Hood and Larson 2015), which may have contributed to the stability and recovery of the otter population and reproduction by younger age classes across North Carolina.

During the 1990s, the otter reintroduction focused on moving otters from the Coastal Plain FMU, where they were abundant, to the Mountain FMU where they had been extirpated (Spelman 1998). Crimmins et al. (2011) determined that 59% of yearling females in Missouri, USA, produced active corpora lutea, while a similar collection effort in Virginia, USA, showed active corpora lutea in 47% of yearling females (M. Fies, Virginia Department of Wildlife Resources, personal communication). During period 2, we detected higher reproductive rates in the Mountain FMU compared to the Piedmont or Coastal Plain FMUs. While the sample size in the Mountain FMU was low, the reproductive rate is consistent with other reintroduced populations (Docktor et al. 1987, Crimmins et al. 2011, Barding and Lacki 2014). The Mountain FMU had been extirpated and reintroduced, the Piedmont FMU had been extirpated and recovered naturally, and the Coastal Plain FMU has been stable over time.

Reproduction in the Mountain FMU was significantly higher than the Piedmont FMU and the Coastal Plain FMU largely because of juvenile reproduction. All juveniles from a particular area (Mountain FMU) were verified as reproductively active. Adult otters typically average 2–3 pups/litter, especially in reintroduced and recovering populations (Tabor and Wight 1977, Hill and Lauhachinda 1980, Docktor et al. 1987, Melquist and Dronkert 1987, Johnson et al. 2007). Hence, the high reproductive rate detected in the Mountain FMU may be indicative of high population growth rates, which would explain the rapid and high degree of success of otter restorations in the Mountain FMU and other states (Crimmins et al. 2011, Barding and Lacki 2014, Brandt et al. 2014, Rutter et al. 2018).

The number of juveniles and yearlings that we detected as reproductively active is encouraging because it suggests that potential reproductive output is not a limiting factor (Crimmins et al. 2011). Increased fecundity in the presence of abundant resources is an established principle in wildlife management (King et al. 2003, Gamelon et al. 2017), and can explain increased litter size along with yearling and juvenile breeding activity. For example, hard and soft mast fluctuations influence the reproduction of bears (*Ursus* spp.), small mammals, and predators (Jensen et al. 2012, Bogdziewicz et al. 2016, Hertel et al. 2018), and food-caching birds respond to food abundance (Ruffino et al. 2014). Normally, otters become reproductively active at age 2, with delayed implantation causing them to produce their first litter slightly before or around their third birthday (Liers 1958, Hamilton and Eadie 1964, Melquist and Dronkert 1987). Although Liers (1958) documented captive yearling otters successfully mating, it has been considered a rare event in wild populations (Liers 1951, Hamilton and Eadie 1964, Docktor et al. 1987). In the last several years, studies of otters in reintroduced populations documented that reproductive activity in younger individuals has become more common than once thought (Crimmins et al. 2011, Barding and Lacki 2014).

Juvenile and yearling breeding in a species known to not sexually mature until age 2 may be attributed to environmental pressures (Hamilton and Eadie 1964). A variety of external and internal pressures affect mammal reproduction including endocrine-disrupting chemicals (Bergman et al. 2013, Pow et al. 2017), heavy metals (Rzymski et al. 2015), polychlorinated biphenyls (Henson and Chedrese 2004, Sonne et al. 2006, Murphy et al. 2015, Folland et al. 2016), hormones (Petrulis 2013), diet (Ruiz-Olmo et al. 2002, 2011; Ruiz-Olmo and Jiménez 2008), habitat quality (Ruiz-Olmo et al. 2011), and chemical signals (Bieber et al. 2012, Grassel et al. 2016, Coombes et al. 2018). Specifically, endocrine-disrupting chemicals affect wildlife (Bergman et al. 2013, Pow et al. 2017), and while North Carolina has areas of high concentrations of endocrine-disrupting chemicals (Sackett et al. 2015), a recent landscape-level evaluation of river otters determined that concentrations of 14 heavy metals from 14 river basins across North Carolina were all below toxic levels (Sanders et al. 2020*b*).

While the reproduction levels we observed may be driven by environmental contaminants, numerous researchers have documented breeding in river otters at earlier ages in reintroduced populations (Docktor et al. 1987, Crimmins et al. 2011, Barding and Lacki 2014). Also, we detected breeding in juvenile and yearling otters, in a naturally recovered population (Piedmont FMU), and in a population that has been stable for decades (Coastal Plain FMU). Abundant resources contribute to reproduction and fish abundance, in general, has improved throughout our study (Rulifson and Batsavage 2014, Lynch et al. 2016), but it does not fully explain why we failed to detect juvenile and yearling reproduction during the 1970s.

Although the early reproduction we observed in the Mountain FMU may be attributed to the reintroduction, reintroduced populations did not always show the same effects (Chilelli et al. 1996) and we observed early reproduction in naturally regenerated (Piedmont FMU) and stable populations (Coastal Plain FMU), although at lower levels. Hence, we speculate that a combination of complex factors that include contaminants, resources, population density, and other unknown pressures may be contributing to earlier reproduction in otters. We suggest researchers focus on the effect each covariate has on reproduction, which will enable us to better understand the environmental influence on otter populations.

MANAGEMENT IMPLICATIONS

Based on age distributions and fecundity estimates, the otter population in North Carolina appears to be stable and healthy with high reproduction and recruitment. Otter populations across the range may experience different age structure and fecundity levels depending on various stressors. Harvest should be closely monitored and regulated, and future studies should be conducted to further assess the effects of environmental stressors (e.g., contaminants, water quality) on otters and other semi-aquatic mammals.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

ETHICS STATEMENT

All methods involving the handling and capture of live animals in this study were approved by the North Carolina State University Institutional Animal Care and Use Committee (protocol number 15-171-O). Methods involving deceased animals were overseen by North Carolina State University and NCWRC personnel.

DATA AVAILABILITY STATEMENT

Data are not publicly available. Potential collaborators are encouraged to contact the authors.

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