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Estimating reproductive rates of Fisher (*Pekania pennanti*) and Northern River Otter (*Lontra canadensis*) in North Dakota from post-mortem carcasses

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Abstract

Information about reproduction is a critical component of wildlife species population monitoring, particularly game species. Evidence of reproductive activity from animal carcasses is often used in lieu of direct observations for secretive mesocarnivores. Fisher (*Pekania pennanti*) and Northern River Otter (*Lontra canadensis*) have expanded their populations in North Dakota over the past two decades, which has resulted in regulated trapping seasons for the two species. This has given us the ability to collect post-mortem information about their breeding phenology, pregnancy rates, and litter sizes. We examined reproductive tracts from 252 female Fishers and 116 river otters collected between 2011 and 2023. We found that *corpora lutea* were the most reliable sign of pregnancy for Fishers, regardless of the time of year, whereas placental scars were more consistent for otters. Fishers ≥2 years old had an average pregnancy rate of 0.82 and litter size of 2.4 across all years. River otters ≥3 years old had an average pregnancy rate of 0.68 and litter size of 2.6. We documented a pattern of age-structured fecundity for both species, where reproductively mature Fishers contribute substantially more to population growth than yearlings, with older individuals still breeding, although at lower rates. A similar trend was observed for otters, but the effect was less pronounced. As such, age-structured fecundity should be accounted for in population models used to guide management decisions.

Key words: Delayed implantation; diapause; Fisher; litter size; *Lontra canadensis*; Northern River Otter; *Pekania pennanti*; pregnancy rate; reproduction

Introduction

Integrated population models (IPMs) are increasingly used in furbearer management to estimate population size, survival, recruitment, and other demographic rates (Fieberg *et al.* 2010; Skalski *et al.* 2011; Linden *et al.* 2017). These models often rely on age-at-harvest data paired with age-specific demographic data, such as pregnancy rates and litter sizes, to estimate annual abundance or reconstruct populations sequentially over time. While IPMs generally produce more reliable estimates when they closely reflect real-world conditions, this level of detail is not always possible, either because of data limitations or computational constraints. In such cases, if there is evidence that certain assumptions can be relaxed (such as variation in pregnancy rates across age classes or time), models can be simplified without significantly reducing their accuracy (Clawson *et al.* 2017). Therefore, examining patterns in pregnancy rates across age classes and over time can help identify the most appropriate sources to inform model development.

Furbearer managers use examination of post-mortem reproductive tissue from Fisher (*Pekania pennanti*) and Northern River Otter (*Lontra canadensis;* hereafter, otters) taken during harvest seasons or after incidental mortality (e.g., incidental trapping or roadkill) to provide information on pregnancy (Gilbert 1987). Specific examination of anatomical reproductive indicators such as *corpora lutea* in the ovaries as well as blastocysts, gestating embryos, and placental scars in the uterine horns are well-established methods to estimate breeding phenology, age-specific pregnancy rates, and litter sizes (Hamilton and Cook 1955; Eadie and Hamilton 1958; Hamilton and Eadie 1964; Wright and Coulter 1967; Leonard 1986; Douglas and Strickland 1987).

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Pregnancy rates and litter sizes for Fishers and otters have been well studied in regions where populations are stable, but little is known about these rates in North Dakota. The history of Fishers and otters in North Dakota mirrors that for the two species elsewhere in the United States (US). Both were widely distributed across Canada and the northern US, but their abundance declined significantly because of habitat loss and unregulated trapping in the late 19th and early 20th centuries (Adams 1961). Their disappearance from North Dakota eventually led to protection as furbearers with closed seasons (Adams 1961).

It was not until 1976 that the first verified report of a Fisher was documented in eastern North Dakota, and reports of occurrence began increasing in the late 1990s (Seabloom 2020). Since then, Fisher populations in North Dakota continued to expand and eventually recolonized the species' former range in the state (Serfass *et al.* 2010; Tucker 2024a). In 2011, a regulated trapping season opened in late November and has continued annually. A recent survey showed that, although Fishers are normally considered inhabitants of dense forests, they have established a population in riparian woodlands along the Red River and its tributaries in eastern North Dakota (Triska *et al.* 2020). Their reproductive performance in this non-traditional habitat has not been estimated previously.

Similarly, occasional reports of otters were documented during the 1960s and have increased since 2002 (Seabloom 2020). Otters eventually re-colonized most of the species' historical range in the state (Serfass *et al.* 2010; Tucker 2024b). In 2017, a regulated trapping season was opened in late November, governed by a small harvest limit (Tucker 2024b). A limited trapping season has continued annually. The sparsely wooded riparian corridors typical of North Dakota are thought to be suboptimal habitat for otters (Melquist and Dronkert 1987), and as a result, the species has not been historically abundant, nor is it today, compared to other areas within its range (Bailey *et al.* 1914; Adams 1961). Therefore, reproductive rates reported for otters elsewhere may not be applicable to populations in North Dakota.

Little is known about Fisher and otter pregnancy rates in North Dakota, particularly in the non-traditional habitats where the species now occur. Additional challenges exist as a result of each species' reproductive biology (Douglas and Strickland 1987; Gilbert 1987; Melquist and Dronkert 1987). Both species undergo a prolonged period of reproductive diapause caused by delayed implantation after breeding. Moreover, reproductive rates reported in the literature vary widely by region and age, making it difficult to generalize findings across populations. To address these information gaps, we used post-mortem tissue to estimate breeding phenology, age-specific pregnancy rates, and litter sizes of Fishers and otters in North Dakota. Our specific objectives were to describe pregnancy rates and litter sizes for each species across time and age classes.

Methods

Study area

Animal carcasses were collected from across North Dakota, with most from the eastern part of the state (Figure 1). This area includes the Red River Valley and the Drift Prairie region, roughly demarcated by the James River in the west and the Red River in the north and east (Seabloom 2020). This is a relatively flat plain with elevation between 228 and 457 m (750 to 1500 feet) above sea level. Average precipitation ranges from 35 cm in the northwest to 48 cm in the southeastern extent of the study region. The average temperature in the eastern part of the state is ~4°C with January being the coldest month (average of −13°C over most of the range) and July being the warmest (average of about 20°C). More than 90% of North Dakota is privately owned farms and ranches. The vegetation in the Red River Valley historically was considered tall-grass prairie that transitioned to mid-grass prairie in the Drift Prairie region. Most of the animals in this study were collected in riparian habitats around the river systems, dominated by White Elm (*Ulmus americana* L.) and Red Ash (*Fraxinus pennsylvanica* Marshall) trees (Haugen *et al.* 2009; Seabloom 2020). Several other animals were collected from the deciduous forest of the Pembina escarpment, in the northeast corner of the state. This forested region is particularly rich in Bur Oak (*Quercus macrocarpa* Michaux), Trembling Aspen (*Populus tremuloides* Michaux), Paper Birch (*Betula papyrifera* Marshall), and Manitoba Maple (*Acer negundo* L.; Haugen *et al.* 2009; Seabloom 2020).

Carcass collection and examination

Trappers are required to submit the carcasses of Fishers and otters to the North Dakota Game and Fish Department after the pelt was removed so that data could be collected to monitor population trends. However, given there has been limited trapping seasons on these species, we also collected carcasses of Fishers and otters that were incidentally killed (e.g., roadkill) throughout the rest of the year. This provided opportunities for evaluation of reproductive indices across seasons and ultimately increased samples sizes. We froze carcasses until necropsy. We thawed carcasses completely before necropsy. During necropsy, we confirmed sex and removed female reproductive tracts, including uteri and ovaries, which we then rinsed and refroze in a small amount of water. We also removed a tooth and sent it to Matson's Laboratory

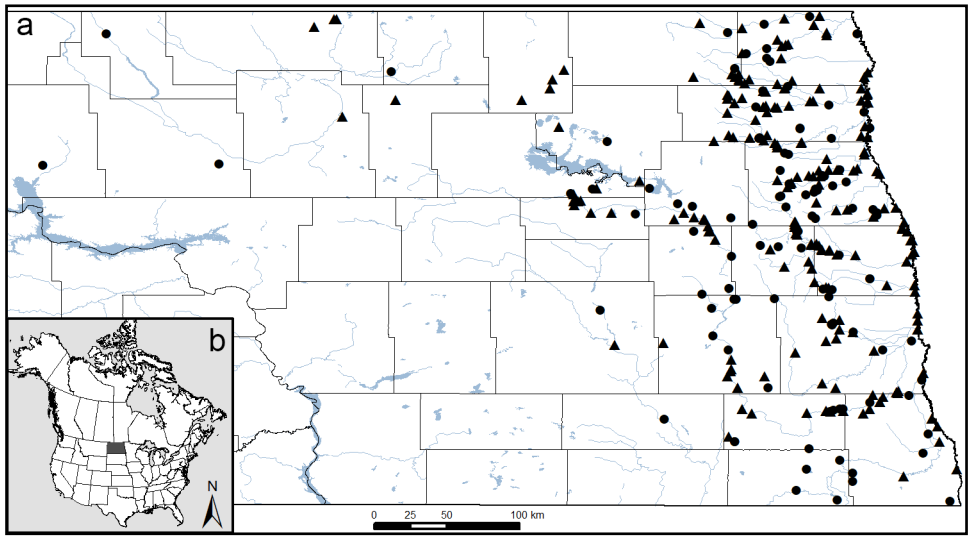


FIGURE 1. a. Locations of female Fisher (*Pekania pennanti*; triangles) and Northern River Otter (*Lontra canadensis*; circles) carcasses in North Dakota, 2011–2023 and b. location of North Dakota in North America.

(Manhattan, Montana, USA) for age determination via cementum analysis (Stephenson 1977; Arthur *et al.* 1992). We classified animals as <1 year old, yearlings, two year olds, three year olds, etc.

After thawing the reproductive tracts, we inspected the uterine body and horns for obvious bulges indicating the presence of post-implantation gestating embryos (Figure 2a; Gilbert 1987). We then made horizontal cuts bilaterally to separate the uterine horns from the uterine body and feathered open the uterine horns by making a sagittal incision basally up the entire length to the ovary. We used a dissecting scope (Leica S9i, Leica Microsystem Ltd., Heerbrugg, St. Gallen, Switzerland) to examine the inside of the uterine horns and ovaries for signs of current (embryos and blastocysts) or previous (placental scars) pregnancy (Figures 2, 3; Gilbert 1987). Placental scars were recognized as dark discolourations of the uterine wall (Figure 3b; Gilbert 1987). After inspecting the uterine horns, we removed the ovaries by horizontal excision and then removed the connective tissue completely exposing the ovarian surface. We inspected the ovaries by making ~1 mm incisions along the long axis and examining both sides of the sections under the dissecting scope to determine presence and number of *corpora lutea* (Gilbert 1987). *Corpora lutea* were distinguished as lightly coloured cell clusters of differing sizes (Figures 2, 3).

Data analysis

We assessed pregnancy status based on reproductive tract evidence from female Fishers and otters. This included counts of embryos, blastocysts, *corpora lutea*, and placental scars from the most recent breeding season. We assessed litter size by calculating summary statistics based on observed counts and evaluated relationships with litter size using count-based regression. To assess pregnancy rates, we converted counts of reproductive indicators into binary variables to calculate summary statistics and model relationships with pregnancy rates. Moreover, we used the reproductive indicator that provided the most complete assessment of pregnancy status, which was *corpora lutea* for Fisher and placental scars for otter (described in greater detail below).

We fit models in two phases. First, we used a generalized linear model (GLM) to evaluate relationships between binary pregnancy responses and the year of the breeding season to identify any temporal trends in pregnancy rates. Data were collected sporadically over a 12-year period (2011–2023). Similarly, a GLM was used to evaluate relationships between litter sizes and year of the breeding season. A significant relationship with year would suggest the need to account for it as a random effect in subsequent models assessing pregnancy across age groups. The results of this analysis indicated there was no relationship between pregnancy rates and year of breeding season, or litter sizes and year of breeding season (which we present more formally in the Results), so we excluded year as a random effect in the second modelling phase.

In the second phase, we used a generalized additive mixed model (GAMM) to evaluate the relationship between pregnancy and age, and litter size and age. We hypothesized that fecundity for Fisher and

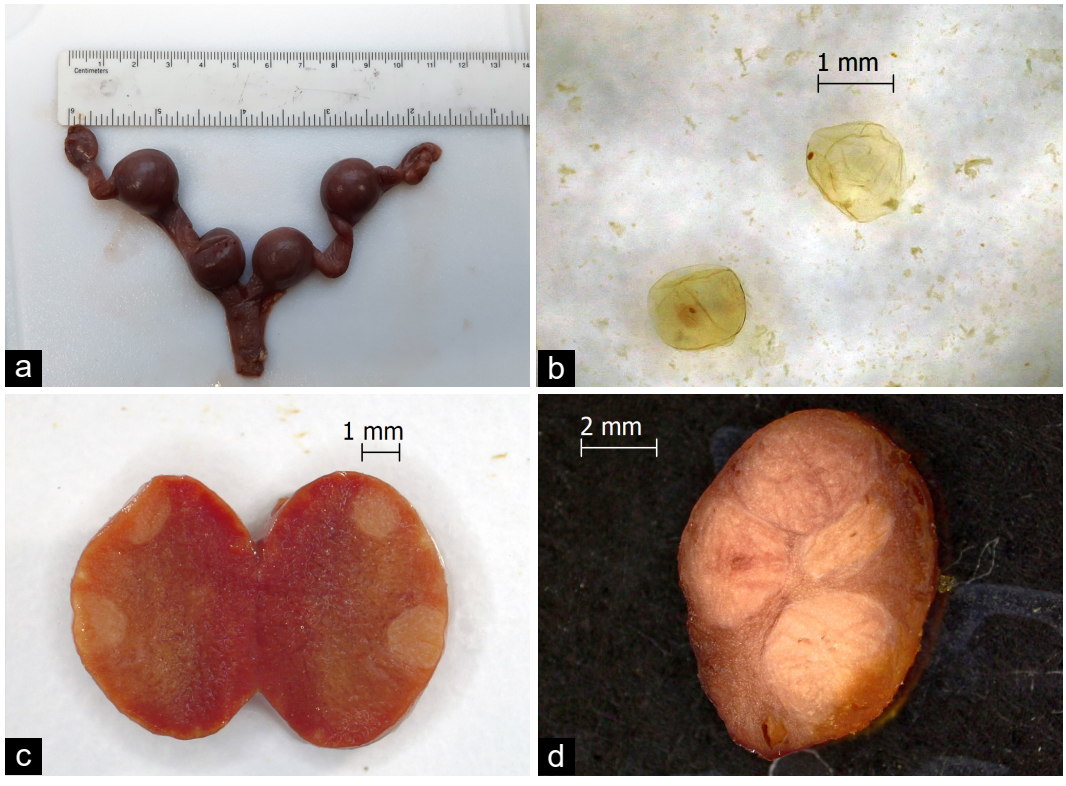


FIGURE 2. Examples of signs of pregnancy in Fisher (*Pekania pennanti*) carcasses collected in North Dakota, 2011–2023. a. Reproductive tract showing bulges from four gestating embryos. b. Two blastocysts in diapause found in the reproductive tract. c. An ovary that was sliced open longitudinally along the long axis revealing two small *corpora lutea* during diapause on the inside of the ovary. d. The inside of one half of an ovary with gestating embryos showing four large *corpora lutea* illustrating their size during active gestation. Photos: North Dakota Game and Fish Department.

otter follow a non-linear pattern across their lifespan (i.e., increasing with age to some intermediate age and then stabilizing or decreasing). Based on this, we chose GAMMs over traditional linear models that attempt to approximate non-linear relationships (e.g., GLMs fit with quadratic terms, piecewise regression), as our primary goal was to describe the relationship between pregnancy and age, rather than to generate predictions from less interpretable models. The underlying model to assess pregnancy rates was based on a logistic regression with a logit link to transform the binary pregnancy variable into log-odds, which were modelled as a smoother function for age. The model to assess litter sizes was based on a Poisson regression with a log link function to model the natural log of expected counts as a smoother function for age. When presenting coefficient estimates or plots from these modelled relationships, we back-transformed predicted values back to their original scales taking the inverse of the logit function (to convert log-odds to probabilities around a reference of 0.5) and exponentiating for Poisson regression (to convert log-transformed expected counts).

We included season of capture as a random effect to account for variation across seasons in both pregnancy rate and litter size models. While pregnancy typically occurs during spring, diapause may delay implantation for both Fisher and otter. Because the timing of carcass collection may influence pregnancy detectability, we specified a random intercept according to the season an animal was captured. The seasons were defined as spring (February–April), summer (May–July), fall (August–October), and winter (November–January).

All analyses were conducted using R version 4.4.3 (R Development Core Team 2025). We used the "gamm4" package to fit GAMMs, which estimates random effects using the Laplace approximation. This method provides more reliable estimates for binary response variables compared to the partial quasi-likelihood approach used in some other packages (Bolker 2008).

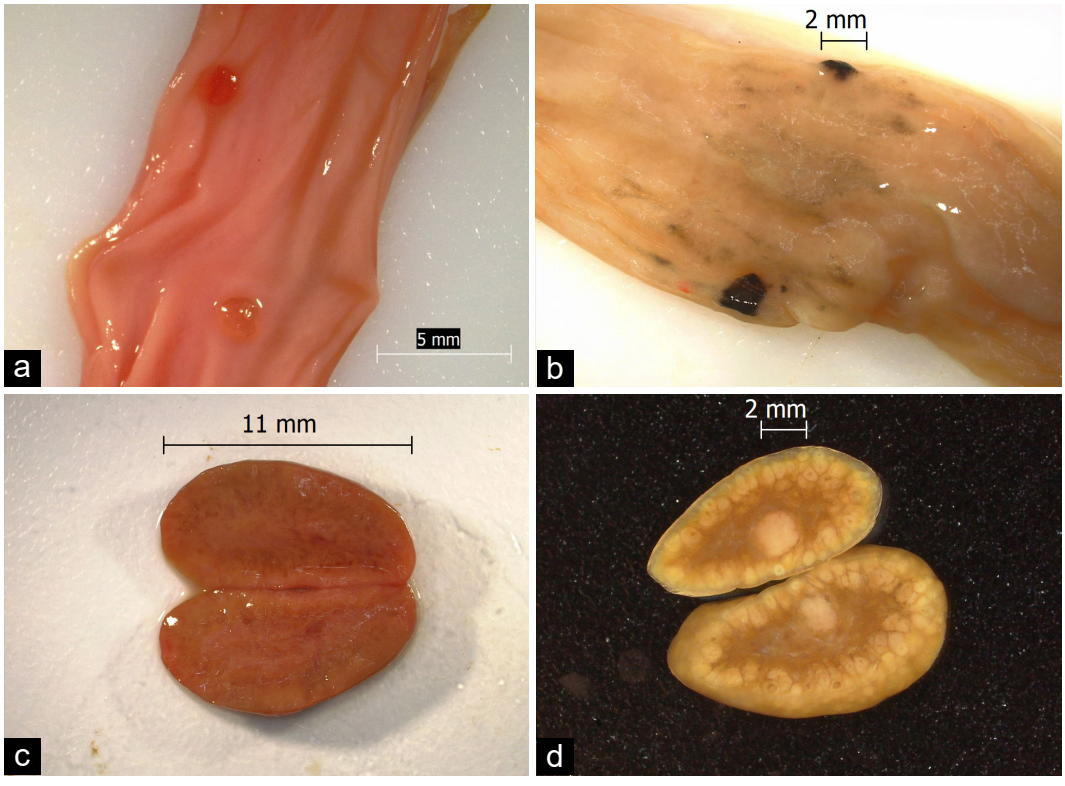


FIGURE 3. Examples of signs of pregnancy in Northern River Otter (*Lontra canadensis*) carcasses collected in North Dakota, 2011–2023. a. Inside of a uterine horn with two blastocysts laying freely and unattached. b. Inside of a uterine horn showing the obvious dark pigmentation of a placental scar, which was cut in half during dissection. c. An ovary that was sliced open longitudinally along the long axis but had no *corpora lutea* present, indicating a lack of pregnancy. d. The inside an ovary revealing one *corpora lutea* during diapause and many follicles. Photos: North Dakota Game and Fish Department.

Results

Fishers

We examined uteri and ovaries from 252 Fishers collected between 2011 and 2023. Most (83%, n = 210) were collected during winter, which aligns with the trapping season in North Dakota. The remainder were collected in spring (n = 27), fall (n = 11), and summer (n = 4; Table 1). Evidence of pregnancy was observed in 47% (n = 122) of Fishers with signs detected in all seasons. *Corpora lutea* were of the most common pregnancy indicator across all seasons, followed by blastocysts (Table 1). Embryos were only found during spring captures. Placental scars were less prevalent (n = 24) and absent from individuals captured during spring. Because of their prevalence and reliability, we only used *corpora lutea* for comparisons between breeding years and age classes.

We detected embryos in four Fishers, confirming active gestation between 15 February and 4 March. We detected blastocysts or diapaused *corpora lutea* in Fishers as early in the breeding season as 28 March through late-winter on 4 February, indicating pregnancy in diapause occurs year round. *Corpora lutea* during diapause were easily distinguished from *corpora lutea* during active gestation based on their smaller size (Figure 2). Of the four Fishers with embryos, the number of *corpora lutea* found in their ovaries matched the number of embryos exactly in three of them. One Fisher with three embryos had four *corpora lutea* present, possibly indicating intrauterine loss (i.e., prenatal mortality).

Fishers ranged in age from zero to nine years, with a mean age of 1.4 ± 1.6 (SD) years (Table 2). One-third (33%, n = 84) were <1 year-old and only one showed any sign of pregnancy (a single blastocyst). Among yearlings (n = 91), 58% showed signs of pregnancy, including two with placental scars, indicating pregnancy in the previous year. Among Fishers ≥1 year-old (n = 168), which is the typical age of first breeding for fishers (Douglas and Strickland 1987), 72% (n = 121) had signs of pregnancy. The oldest Fishers examined (two, eight year olds and

TABLE 1. Number of reproductive tracts from known-age female Fisher (*Pekania pennanti*) where we detected signs of current (embryos, *corpora lutea*, blastocysts) or previous (placental scars) pregnancy by season in North Dakota, 2011–2023. The regulated trapping season in North Dakota is typically held in late November, thus the bias in Fishers collected in winter.

Season		Embryos		*Corpora lutea*		Blastocysts		Placental scars	
	n	No.	Rate	No.	Rate	No.	Rate	No.	Rate
Spring (Feb–Apr)	27	4	0.15	6	0.22	2	0.07	0	0.00
Summer (May–Jul)	4	0	0.00	2	0.50	2	0.50	1	0.25
Fall (Aug–Oct)	11	0	0.00	3	0.27	1	0.09	1	0.09
Winter (Nov–Jan)	210	0	0.00	106	0.50	67	0.32	22	0.10
Total	252	4	0.02	117	0.46	72	0.29	24	0.10

TABLE 2. Number of female Fisher (*Pekania pennanti*) in each age class with evidence of current (embryos, *corpora lutea*, or blastocysts) or previous (placental scars) pregnancy and their associated pregnancy rates and litter sizes in North Dakota, 2011–2023. Ages were determined by cementum analysis (Matson's Laboratory, Manhattan, Montana, USA).

Age class	*n*	Embryos			*Corpora lutea* (CL)			Blastocysts (blasto)			Placental scars (PS)		
		No. with embryos	Preg. rate	Litter size	No. with CL	Preg. rate	Litter size	No. with blasto	Preg. rate	Litter size	No. with PS	Preg. rate	litter size
<1	84	0	0.00		0	0.00		1	0.01	1.0	0	0.00	
1–2	91	2	0.02	3.5	52	0.57	2.3	34	0.37	2.0	2	0.02	3.0
2–3	34	0	0.00		24	0.71	2.0	15	0.44	1.7	10	0.29	1.3
3–4	15	1	0.07	3.0	14	0.88	2.8	8	0.50	2.1	4	0.25	2.0
4–5	14	1	0.07	3.0	14	1.00	2.4	6	0.43	1.8	3	0.21	2.0
5–6	6	0	0.00		6	1.00	2.3	4	0.67	2.3	2	0.33	3.5
≥6	8	0	0.00		6	0.75	2.8	3	0.38	1.7	2	0.25	1.5
Total	252	4	0.02	3.3	116	0.82	2.3	71	0.28	1.9	23	0.09	1.9

one, nine year old) all showed *corpora lutea* or blastocysts, indicating they were reproductively active at the time of their death.

Among pregnant Fishers ≥2 years old (n = 68), 29% (n = 20) had both placental scars and either *corpora lutea* or blastocysts, suggesting reproduction in consecutive years. However, this is likely an underestimate because of the infrequent detection of placental scars in Fishers.

Otters

We examined uteri and ovaries from 116 otters collected from 2011 to 2023. Most were collected during winter (43%, n = 50), with additional carcasses from spring (n = 17), summer (n = 27), and fall (n = 22; Table 3). Overall, 49% (n = 57) of otters showed signs of pregnancy. As with Fishers, pregnancy was detected in all seasons and gestating embryos were only found in otters that died during spring. In contrast to Fishers, placental scars were the most common pregnancy sign in otters across all seasons, followed by *corpora lutea* (Table 3). Therefore, we used placental scars to compare breeding years and age classes.

We detected embryos in two otters, confirming active gestation between 11 March and 9 April. *Corpora lutea* associated with active gestation in otters were easily distinguished from those in diapause by their larger size. However, *corpora lutea* in diapause were more difficult to discern in otters compared to Fisher (Figure 3). Of the two otters with embryos, the number of *corpora lutea* found in their ovaries matched the number of embryos exactly in both. Blastocysts or diapaused *corpora lutea* were present in all months except March, indicating pregnancy in diapause occurs nearly year round.

Otters ranged in age from zero to nine years, with the mean age being 2.2 ± 2.1 (SD) years (Table 4). None of the 18 otters <1 year-old showed signs of pregnancy. Among the 42 yearlings, 40% (n = 17) showed signs of pregnancy, including eight with placental scars, indicating that pregnancy could have occurred in their first year (Table 4). The oldest otters included an eight year old and three, nine year olds, three of which had placental scars, but no *corpora lutea* or blastocysts.

Among 40 otters ≥2 years old that showed signs of pregnancy, 48% (n = 19) had both placental scars and either blastocysts or *corpora lutea*, suggesting

TABLE 3. Number of reproductive tracts from known-age female Northern River Otter (*Lontra canadensis*) where we detected signs of current (embryos, *corpora lutea*, blastocysts) or previous (placental scars) pregnancy by season in North Dakota, 2011–2023. The regulated trapping season in North Dakota is typically held in late November, thus the bias in river otters collected in winter.

Season	*n*	Embryos		*Corpora lutea*		Blastocysts		Placental scars	
		No.	Rate	No.	Rate	No.	Rate	No.	Rate
Spring (Feb–Apr)	17	2	0.12	6	0.35	2	0.12	5	0.29
Summer (May–Jul)	27	0	0.00	7	0.26	2	0.07	9	0.33
Fall (Aug–Oct)	22	0	0.00	6	0.27	1	0.50	10	0.45
Winter (Nov–Jan)	50	0	0.00	14	0.28	13	0.26	17	0.34
Total	116	2	0.02	33	0.28	18	0.16	41	0.35

TABLE 4. Number of female Northern River Otter (*Lontra canadensis*) in each age class with evidence of current (embryos, *corpora lutea*, or blastocysts) or previous (placental scars) pregnancy and their associated pregnancy rates and litter sizes in North Dakota, 2011–2023. Ages were determined by cementum analysis (Matson's Laboratory, Manhattan, Montana, USA).

Age class	*n*	Embryos			*Corpora lutea* (CL)			Blastocysts (blasto)			Placental scars (PS)		
		No. with embryos	Preg. rate	Litter size	No. with CL	Preg. rate	Litter size	No. with blasto	Preg. rate	Litter size	No. with PS	Preg. rate	Litter size
<1	18	0	0.00		0	0.00		0	0.00		0	0.00	
1–2	42	1	0.02	2.0	8	0.19	1.5	7	0.17	1.7	8	0.19	2.3
2–3	18	0	0.00		7	0.39	2.1	5	0.28	1.4	7	0.39	2.4
3–4	13	0	0.00		7	0.54	2.1	4	0.31	2.3	11	0.85	2.6
4–5	11	1	0.09	2.0	4	0.36	2.0	0	0.00		7	0.64	2.6
5–6	3	0	0.00		2	0.67	2.0	1	0.33	2.0	1	0.33	4.0
≥ 6	11	0	0.00		5	0.45	2.4	1	0.09	2.0	7	0.64	2.6
Total	116	2	0.02	2.0	33	0.28	2.0	18	0.16	1.8	41	0.35	2.5

nearly half of adult otters were pregnant in consecutive years.

Generalized additive mixed models

We found no statistically significant trends in pregnancy rates or litter sizes over time for either Fishers or otters (Tables 5, 6). Pregnancy rates were constant across breeding seasons for both Fishers (β = 0.50, 95% CI 0.48–0.52, P = 0.759) and otters (β = 0.49, 95% CI 0.46–0.52, P = 0.590) between 2011 and 2023. Litter sizes for Fishers increased 4% per year, but the relationship was weak (β = 1.04, 95% CI 0.99–1.07, P = 0.051), and litter sizes for otters was constant throughout the duration of the study (β = 1.00, 95% CI 0.94–1.06, P = 0.931).

We observed significant non-linear relationships between age and both pregnancy rates and litter sizes in Fishers and otters (Table 7). In general, Fishers had greater reproductive output than otters based on higher pregnancy rates and larger litter sizes. However, otters appeared to be more reproductively active at older ages, despite having lower overall reproductive output (Figure 4). Pregnancy rates in Fishers stabilized by age two, peaked at 0.72 (95% CI 0.69–0.74) at age four, and began to decline around age five. In otters, pregnancy rates stabilized around age three and remained relatively constant, peaking at 0.67 (95% CI 0.63–0.70) at age four. Litter sizes for Fishers showed a pronounced peak, increasing sharply until ages 3–4, where they reached 2.9 (95% CI 2.39–3.42), followed by a sharp decline. In contrast, litter sizes for otters increased more gradually, peaking at 1.4 (95% CI 0.84–1.96) at age five, then declined more gradually.

Overall pregnancy rates for Fisher, including all seasons and years, were 0.57 ± 0.50 (SD) for yearlings and 0.82 ± 0.39 for adults (≥2 years; Table 5). Litter sizes for Fisher averaged 2.3 ± 1.07 for yearlings and 2.4 ± 1.10 for adults (Table 5). Overall pregnancy rates for otters were 0.39 ± 0.50 for two year olds and 0.68 ± 0.46 for otters aged ≥3 years (Table 6). Litter sizes for otters averaged 2.5 ± 1.51 for two year olds and 2.6 ± 1.13 for older otters (≥3 years; Table 6).

Discussion

We used post-mortem tissue to provide information about the reproductive ecology of Fishers and

TABLE 5. Estimates of pregnancy rates and litter sizes of yearling (one year old) and adult (≥2 years old) Fisher (*Pekania pennanti*) in North Dakota estimated by presence of *corpora lutea*, 2011–2023.

Breeding year (1 Apr–31 Mar)	*n*		Pregnancy rate		*Litter* size	
	Yearlings	Adults	Yearlings	Adults	Yearlings	Adults
2011–2012	12	4	0.42	0.75	2.4	1.0
2012–2013	11	11	0.50	0.91	2.0	2.4
2013–2014	8	10	0.50	0.60	2.3	2.0
2014–2015	11	8	0.73	0.75	2.0	2.0
2015–2016	11	8	0.55	0.63	2.7	1.4
2016–2017	7	3	0.71	1.00	2.6	2.7
2017–2018	8	12	0.75	0.92	1.7	3.0
2018–2019	8	6	0.63	0.83	2.2	2.0
2019–2020	7	4	0.57	1.00	1.8	2.8
2020–2021	6	5	0.33	1.00	3.0	2.2
2021–2022	4	2	0.25	1.00	2.0	2.0
2022–2023	7	4	0.71	1.00	2.8	4.0
Total	92	78	0.57	0.82	2.3	2.4

TABLE 6. Estimates of pregnancy rates and litter sizes of two year old and older (≥3 years) Northern River Otter (*Lontra canadensis*) in North Dakota estimated by presence of placental scars, 2011–2023.

Breeding year (1 Apr–31 Mar)	*n*		Pregnancy rate		Litter size	
	2 years	≥3 years	2 years	≥3 years	2 years	≥3 years
2011–2012	1	1	0.00	1.00		3.0
2012–2013	2	5	0.50	0.60	1.0	2.0
2013–2014	0	2		1.00		4.5
2014–2015	1	2	1.00	0.50	1.0	2.0
2015–2016	2	0	0.50		1.0	
2016–2017	0	2		0.50		1.0
2017–2018	4	4	0.25	0.75	5.0	3.3
2018–2019	0	4		0.75		2.0
2019–2020	2	6	0.50	0.67	3.0	2.0
2020–2021	1	3	1.00	0.67	3.0	3.0
2021–2022	1	8	0.00	0.63		2.6
2022–2023	4	1	1.00	1.00	3.0	4.0
Total	18	38	0.39	0.68	2.5	2.6

otters in North Dakota. *Corpora lutea* were the most reliable indicator of pregnancy for Fishers, regardless of season, whereas placental scars were more consistent for otters. Blastocysts were likely under-detected in both species because of their fragility, limiting their reliability as an indicator of pregnancy. Although placental scars were not observed commonly in Fishers, they were consistently detected in otters across all seasons. Even when otter placental scars were faded, we were able to identify their presence using a dissecting scope. Accordingly, through the examination of *corpora lutea* and placental scars, we described the timing of key reproductive events for Fishers and otters in North Dakota.

The use of *corpora lutea* for estimating reproductive rates has been questioned by others because it is possible that intrauterine loss could result in an overestimation of litter size (Gilbert 1987). Our examinations of a small sample of Fishers with foetuses showed a high degree of correlation between the number of *corpora lutea* and foetuses, agreeing 75% of the time. The agreement between counts of *corpora lutea* and foetuses has also been documented by others (Wright and Coulter 1967; Douglas and Strickland

TABLE 7. Coefficient estimates for relationships between a smoother function of age, and both pregnancy rates and litter sizes in Fisher (*Pekania pennanti*) and Northern River Otter (*Lontra canadensis*). Generalized additive mixed models were fit to reproductive data for Fishers and otters collected from North Dakota between 2011 and 2023. Logistic regression was used to model relationships with pregnancy rate and Poisson regression was used to model relationships with litter size. A random intercept for season of capture was specified to account for variation among seasons.

Species	Reproductive indicator	EDF*	χ^2	*P*
Fisher	Pregnancy rate	2.65	70.8	< 0.001
	Litter size	2.88	132.0	< 0.001
Otter	Pregnancy rate	2.44	26.3	< 0.001
	Litter size	2.21	16.3	< 0.001

*EDF (Effective Degrees of Freedom) describes the complexity of the smoothing term; an EDF = 1 is a completely linear relationship, while an EDF >1 indicates a non-linear relationship.

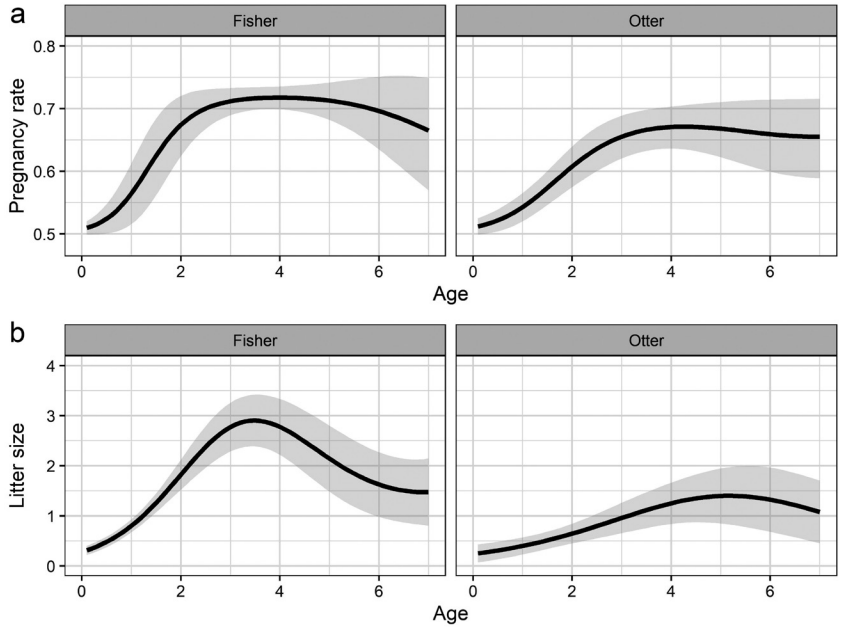


FIGURE 4. Fitted relationships between a smoother function for age and a. pregnancy rate and b. litter sizes for Fisher (*Pekania pennanti*) and Northern River Otter (*Lontra canadensis*) in North Dakota between 2011 and 2023.

1987). Therefore, given the constraints of collecting carcasses during active gestation or documenting litter sizes at or soon after birth in wild populations, *corpora lutea* provided us with a suitable alternative to estimating pregnancy rates and litter sizes.

Likewise, using placental scars may also be problematic because you may be able to see scars from foetuses that did not make it to full term (Gilbert 1987). Several previous researchers indicated that placental scars were not a reliable indicator of pregnancy or litter size, but that may be due to how their tissue was preserved and/or examined (Wright and Coulter 1967; Tabor and Wright 1977). By simply freezing our otter reproductive tracts in water, we reduced the risk of chemicals (e.g., formalin) "washing" away placental scar pigment. Additionally, by examining the tracts under a dissecting scope, we were able to easily recognize even a small number of dark flecks of pigmentation from placental scars that were otherwise hard to discern with the naked eye. Therefore, we are confident that placental scars provided us with suitable estimates given our collection and laboratory constraints.

Fishers and otters in North Dakota give birth in spring, as indicated by the presence of embryos only during March–April. Shortly after giving birth, they breed again, followed by a prolonged period of delayed implantation (diapause) until the following January or February when active gestation resumes. This pattern is supported by the presence of diapaused

corpora lutea and blastocysts during the remainder of the year. Our findings are consistent with the breeding phenology of fishers and otters reported elsewhere (Douglas and Strickland 1987; Melquist and Dronkert 1987; Green *et al.* 2018).

Our study in North Dakota showed slightly higher fecundity relative to other studies, with a pregnancy rate of 0.82 in Fishers >1 year old and an average litter size of 2.4 based on *corpora lutea*. A recent nationwide review of Fisher reproduction studies based on direct observations reported that ~74% of female Fishers >1 year old showed evidence of pregnancy with an average litter size of 2.4 (Green *et al.* 2018).

The percentage of pregnant Fishers increased with age, peaking at four years old, although reproductive activity was still evident in individuals as old as nine years old. We also detected evidence of reproductive activity in a small number of Fishers <1 year old. However, these findings may reflect misidentification of pregnancy or imprecise age estimates because of limitations in cementum aging (Arthur *et al.* 1992). Blastocysts in particular were difficult to identify because they were often damaged during sectioning and can resemble non-specific tissue from poorly preserved uterine horns. Therefore, our results largely agree with previous research indicating that Fishers typically breed at one year old.

Observations of pregnancy in otters are difficult, which results in pregnancy rates and litter sizes varying widely. For example, some studies suggest that litter size ranges from one to six, with a common average of about 2.4 (Melquist and Hornocker 1983; Melquist *et al.* 2003). Several studies have used postmortem tissues to estimate pregnancy rates, which have ranged from 0.66 to 0.92, with predicted litter sizes of 2.1–2.9 depending on the parameter used (Eadie and Hamilton 1964; Tabor and Wright 1977; Docktor *et al.* 1987; Crimmins *et al.* 2011; Barding 2014). Based on placental scars, our study indicated a pregnancy rate of 0.68 with an average litter size of 2.6 for otters >2 years old. This lower pregnancy rate may reflect sampling variation due to small sample sizes because otters in North Dakota occur at lower population densities than elsewhere within their range, resulting in smaller harvests. As a result, fewer specimens are available for evaluation of pregnancy rates.

Finally, we described patterns in pregnancy rates and litter sizes for Fishers and otters, observed across seasons, through time, and across age classes, using a GAMM. We hypothesized a non-linear relationship, reflecting some intermediate age at which reproductive maturity is reached, fecundity peaks, and then declines with age (Green *et al.* 2018; Sanders *et al.* 2023). Season and year of capture had little influence on pregnancy rates or litter sizes, likely because both species readily undergo diapause. This suggests seasonal variation does not substantially affect reproductive parameters. Additionally, we found no evidence of a relationship between pregnancy and year of breeding season, which is consistent with findings observed for American Marten (*Martes americana*) in Michigan (Skalski *et al.* 2011) and river otters in Illinois (Nielsen 2016). Accordingly, we treated year as a random effect in GAMM to account for year-to-year variation in pregnancy differences.

We found clear evidence of age-structured reproduction in Fishers and otters. Our results suggest that reproductively mature Fishers contribute substantially more to population growth than yearlings, with older individuals still breeding, although at lower rates. This may indicate reproductive senescence in older Fishers, which has been documented in other mustelids (Sea Otter [*Enhydra lutris*]; Bodkin *et al.* 1993). A similar trend was observed for otters, but the effect was less pronounced. Older otters appeared to maintain reproductive activity and contribute meaningfully to population growth, which has been documented elsewhere (Docktor *et al.* 1987; Crimmins *et al.* 2011). However, it is important to note that fitting a GAMM involves applying a smoothing function to age class, which interpolates a non-linear relationship based on the observed data. Because we had relatively few observations of older-aged Fishers and otters, interpretations at the extremes of the age range should be made with caution.

It is difficult to contextualize our results to the literature for Fishers and otters because few IPM studies that incorporate age-specific demographic data exist. This is because IPMs require multiple sources of auxiliary data to reconstruct populations, which are often unavailable for elusive furbearer species like Fishers and otters. We are not aware of any IPM studies pertaining to otters, however, several IPMs have been applied to Fishers. For example, Bellier *et al.* (2024) used simulated recruitment and survival data for Fishers to evaluate the robustness of abundance estimates under different age class scenarios and found that parameter accuracy improved as the number of age classes increased. Other studies have applied IPMs to Fishers using age-specific demographic data, but their primary focus was not to evaluate the importance of age structure. Berg *et al.* (2025) used survival data to assess the effects of different season lengths on Fisher harvest rates.

In general, it is well-established that IPMs require multiple age classes to adequately capture contrast in pregnancy rates and ensure model convergence (Gove 2002). Thus, the presence of age-structure in a population becomes important when management relies

on population models such as IPMs. For example, in North Dakota, most of the Fishers we observed were under two years old. If an IPM were to apply a composite or average pregnancy rate across all individuals, it would likely overestimate the reproductive contribution of younger Fishers and underestimate that of reproductively mature individuals, leading to biased population growth estimates. When age structure exists in a real population, it must be explicitly incorporated into models, otherwise estimates of abundance may be inaccurate and meaningful trends can be masked. Accordingly, an important feature of data collection for Fishers and otters is the inclusion of age-specific demographic rates to ensure data remain useful for future analyses.

Management implications

Our study provides a valuable reference point for pregnancy rates in Fishers and otters where baseline reproductive data for each species are lacking in North Dakota. The patterns in pregnancy rates and litter sizes for Fishers and otters we found are consistent with reproductive output observed for Fishers and otters in other regions. Finally, by assessing age through *cementum annuli* and pairing this information with reproductive metrics, we documented the existence and pattern of age-structured fecundity for each species. This is especially useful for furbearer managers in North Dakota and beyond because it underlies the importance of accounting for age structure in population models used to guide management decisions. A limitation of our study was limited representation of older individuals in our sample, particularly for otters. Thus, to improve future evaluations of pregnancy rates, sampling efforts should prioritize collecting data from older-aged individuals to ensure coverage across the full reproductive age range.

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