Spring 2012

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Great Plains Research 22 (Spring 2012):79–86

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ABSTRACT—We evaluated the reproductive biology of 314 white-tailed jackrabbits (*Lepus townsendii*) in 44 counties throughout South Dakota from June 2004 to September 2005. We classified jackrabbits as juveniles or adults based on the closure of the proximal epiphysis of the humerus using X-ray analysis. We determined annual reproductive activity through fluctuations in measured weights of reproductive organs for both sexes. The 2005 breeding season started in late February and proceeded until mid-July, approximately 142 days, allowing for females to potentially produce 3.3 litters. We found four distinct breeding periods by the overlap of estimated conception and parturition dates. Mean litter size was 4.6 per female (range 1–8). Prenatal mortality from preimplantation and postimplantation loss was highest (32%) in the first littering period in 2005.

Key Words: fecundity, population characteristics, reproduction, South Dakota, white-tailed jackrabbit

INTRODUCTION

Many researchers have suggested that *Lepus* spp. have cyclic populations (Rowman and Keith 1956; Donoho 1972; Gross et al. 1974; Nowak and Paradiso 1983; Anderson and Shumar 1986). Recently, however, Shaible and Dieter (2011) have discovered a general downward trend in jackrabbit populations in the northern Great Plains. There have been many suggestions for the cause of fluctuations in lagomorph populations, but most of the research has been done on snowshoe hares (*Lepus americanus*) (Hik 1995; Boonstra et al. 1998; Hodges et al. 1999; Krebs et al. 2001; Sheriff et al. 2009). Little data exist to evaluate the current status of white-tailed jackrabbits (*Lepus townsendii*). We wanted to examine the reproductive potential of white-tailed jackrabbits to determine if reproductive output may influence fluctuations in jackrabbit populations.

Manuscript received for review, October 2011; accepted for publication, January 2012.

As with most leporids, white-tailed jackrabbits are capable of producing multiple litters per season, and reproductive output may vary geographically (Flux 1971; Conaway et al. 1974; Keith 1981; Dunn et al. 1982; Rogowitz 1992). Jackrabbits have a tendency for postpartum breeding, which may lead to synchronous breeding (Lechleitner 1959; Kline 1963; James and Seabloom 1969; Dunn et al. 1982; Rogowitz 1992).

White-tailed jackrabbits typically reach reproductive maturity after one year of age. The breeding season begins in late February and extends through mid-July (Dunn et al. 1982). In Iowa and North Dakota, the breeding season lasted 148 days (Kline 1963; James and Seabloom 1969) while a 146-day breeding season was noted in southwestern Wyoming (Rogowitz 1992). White-tailed jackrabbits produce three to four litters per year in both North Dakota (James and Seabloom 1969) and Iowa (Kline 1963). The gestation period for white-tailed jackrabbits is typically 42–43 days (Kline 1963).

Since jackrabbits serve an important niche in grassland ecosystems, it is important to understand population demographic composition and fecundity. This information may allow managers to evaluate population fluctuations and understand predator-prey relationships. White-tailed jackrabbits have received little attention with respect to demographic composition within their distribution, and no attention has been given to reproductive parameters in South Dakota (Schaible and Dieter 2011). The objective of this research was to determine population characteristics and reproductive potential of white-tailed jackrabbits in South Dakota.

STUDY AREA

We collected white-tailed jackrabbits throughout South Dakota from June 2004 to September 2005. The eastern portion of the state lies within the Prairie Plains, which was created through glaciation and is characterized by low hills, marshes, and lakes (Visher 1918). Most of the western portion of the state lies within the Great Plains, which includes a more rugged landscape of rolling hills. Tallgrass prairie dominates much of the area in eastern South Dakota and makes a transition to northern mixed-grass prairie to the west (Johnson and Nichols 1982). The northeast quarter of South Dakota tends to be the coldest and the southwestern portions the warmest (Visher 1918). The growing season generally averages 130 days, and annual precipitation averages approximately 50.8 cm for the state (Visher 1918).

Land use is typically for agricultural purposes, especially in eastern South Dakota (Hogan and Fouberg 1998). The most commonly cultivated crops include corn (*Zea* spp.), soybeans (*Glycine max*), alfalfa (*Medicago sativa*), and several small grains including oats (*Avena sativa*), wheat (*Triticum aestivum*), and barley (*Hordeum vulgare*). Livestock production is also prevalent throughout South Dakota. Portions of western South Dakota still contain large areas of grassland.

METHODS

We collected 15–20 jackrabbits each month using a .22 caliber rifle. We also received jackrabbits from personnel of the South Dakota Department of Game, Fish and Parks and Ellsworth Air Force Base. We fit each jackrabbit with an individual identification tag, and the animals were either frozen or necropsied immediately.

We estimated the age of jackrabbits using X-ray analysis (0.15 s exposure time) of the proximal epiphysis of the left humerus (Hale 1949; Lechleitner 1959; James and Seabloom 1969). We classified jackrabbits as juveniles (2–12 months) where the epiphyseal area had a definite groove or as adults (over one year old) where there was no evidence of an epiphyseal line (Lechleitner 1959).

Postmortem examinations involved assessing the reproductive condition of both sexes using methods described by James and Seabloom (1969) and Gross et al. (1974). We determined sexual activity by measuring the mass of paired testes after the epididymides were removed for males, and by measuring the mass of paired ovaries for females. We determined reproductive potential by examination of fetuses that were removed and counted from gravid females. Litter size was defined as the total number of viable fetuses per female (Rogowitz 1992). Following methods similar to James and Seabloom (1969), we approximated fetal age by comparing developmental and morphological characteristics to those of the snowshoe hare (Bookhout 1964) since there were no similar references for white-tailed jackrabbits. We approximated the date of conception by backdating the estimated fetal age from the date of collection. Parturition dates were determined by adding the gestation period of 43 days to conception dates (James and Seabloom 1969; Rogowitz 1992). The breeding season was defined as the length of time between the first conception date and the last conception date. We calculated the annual potential number of litters by dividing the length of the breeding season by the 43-day gestation period. Proc GLM Least Square Means (SAS Institute, Gary, IN) was used to determine seasonal differences in ovarian and testicular weights.

We preserved ovaries removed from gravid female jackrabbits in a 10% formalin solution and then sectioned them to macroscopically count corpora lutea, which represented the number of ova shed per ovary for individual litters (James and Seabloom 1969). We estimated prenatal mortality from the amount of litter loss experienced from preimplantation and postimplantation loss (Lechleitner 1959). Preimplantation loss was defined as failure of ova to implant within the uterine wall, and we estimated the loss by subtracting the number of corpora lutea from the number of implantation sites. We measured postimplantation loss as resorption of implanted embryos, and we calculated it by subtracting the number of implantation sites from the number of viable fetuses (Lechleitner 1959). Resorbing fetuses were identified as swellings that appeared distinctly smaller than viable fetuses (Bookhout 1964). Both causes of prenatal mortality were then incorporated as

$$(\text{Prenatal loss per litter}) / (\text{Number of ova shed}) \times 100$$

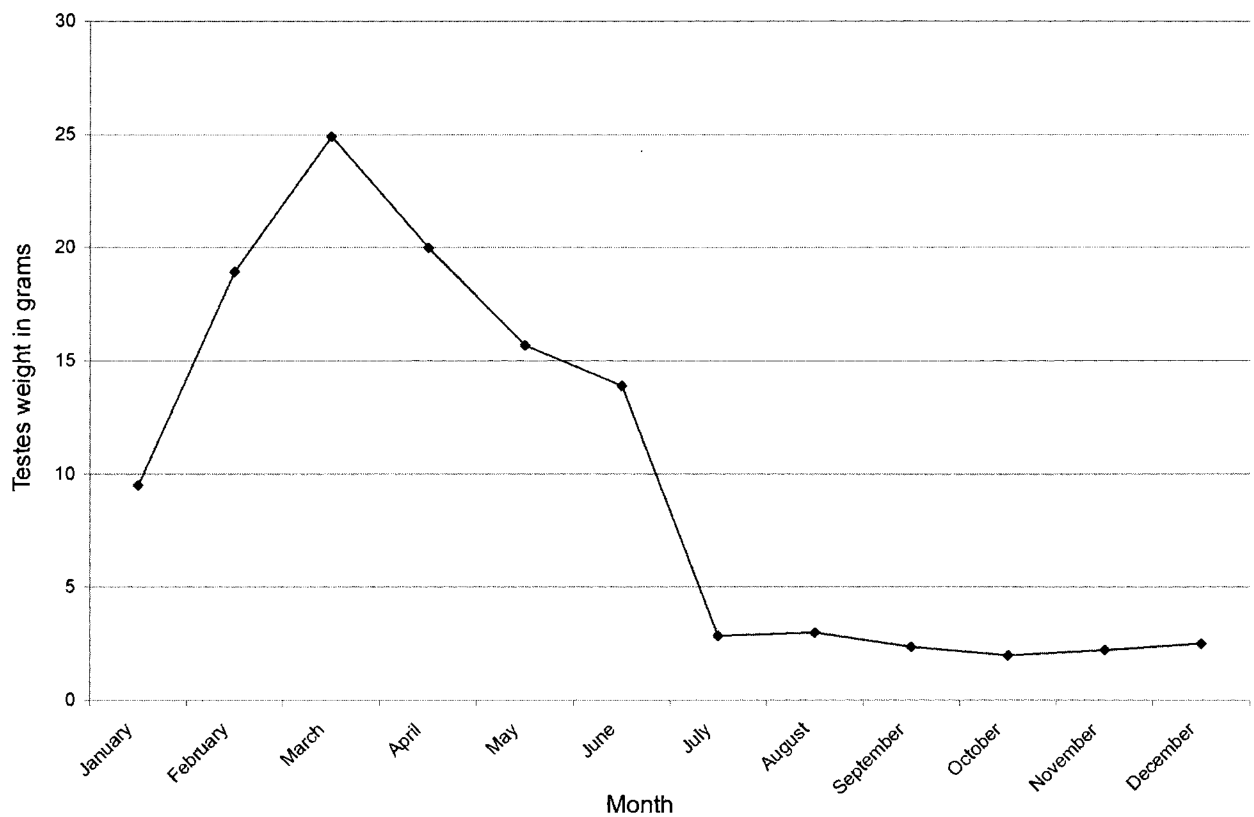

Figure 1. Monthly fluctuation in testes weights of male white-tailed jackrabbits in South Dakota, 2004 and 2005.

to calculate a percentage prenatal mortality for each littering period (Lechleitner 1959).

RESULTS

We collected 314 white-tailed jackrabbits in 44 counties throughout South Dakota. The number of jackrabbits collected monthly ranged from six to 44 ($\bar{x}$ = 19). There were 161 males and 153 females, which was not different than an expected 1:1 sex ratio ($\chi^2 = 0.204$).

We were able to estimate the age of 264 white-tailed jackrabbits. The remaining 50 animals were not included due to damage of the humerus in the collection process. There were 171 adults, which were present in all months of collection. The remaining 93 jackrabbits were classified as juveniles and were collected from June to December 2004 and from May to September 2005.

An annual pattern of reproductive activity was demonstrated by testicular weight fluctuations in male white-tailed jackrabbits (Fig. 1). There was a monthly difference in testicular weights ($F_{11} = 56.38$, $P < 0.001$). The highest testicular weight occurred in March (24.92 g; SE = 1.16) followed by April (19.98 g; SE = 0.74) and February (18.93 g; SE = 1.06). These data indicate that male white-tailed jackrabbits were most sexually active during early spring. Testicular weights were lowest in October (1.95 g; SE = 1.84) and November (2.21 g; SE = 1.39).

Annual fluctuations were also apparent in monthly female ovarian weights ($F_{11} = 14.34$, $P < 0.001$) (Fig. 2). Ovarian weights were highest in May (2.98 g; SD = 0.28) followed by March (2.16 g; SE = 0.18). Ovarian weights in April (1.78 g; SE = 0.18) and June (1.90 g, SE = 0.15) were also high, indicating that females were most sexually active from March to June. Ovarian weights were lowest in October (0.27 g; SE = 0.38) and November (0.23 g; SE = 0.28).

Breeding synchrony was evident as indicated by an overlap of estimated conception and parturition dates (Table 1). In June 2004 eight of the 10 adult female jackrabbits were pregnant. From the estimated conception dates, females collected in June likely represented the third littering period. Conception dates for each female were estimated from May 22 to May 27, and subsequent parturition dates were estimated from July 3 to July 8.

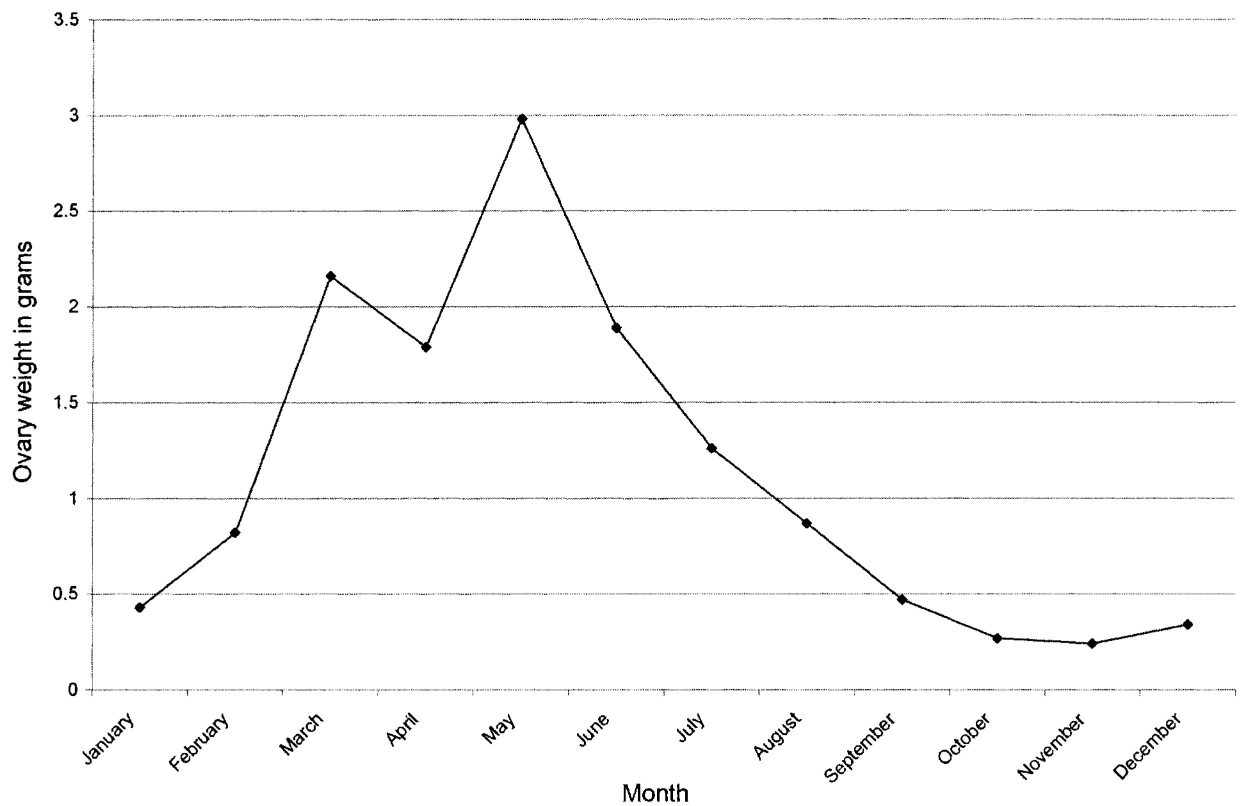

Figure 2. Monthly fluctuations in ovarian weights of female white-tailed jackrabbits in South Dakota, 2004 and 2005.

Litter size ranged from four to eight and averaged 5.5 (SE = 0.50) per female.

In July 2004 two of seven adult females were pregnant and one of 10 adult females was pregnant in August. Estimated conception dates for these females were July 4, July 6, and July 17. Since the estimated conception dates overlap with parturition dates of the third littering period, these three females likely represented the fourth litter in 2004. Litter size ranged from four to seven and averaged 5.0 (SE = 1.0) per female during the fourth littering period. Due to timing of collection, the length of the 2004 breeding season was not determined.

In 2005 the breeding season started in February, based on the first pregnant female's estimated conception date (February 24). Further support for an increase in reproductive activity was demonstrated by the progression of ovarian and testicular weight during this time period. In March, all 13 collected adult female jackrabbits were pregnant, with conception dates estimated from February 24 to March 6. Parturition dates were estimated from April 7 to April 17. Litter size for the first littering period ranged from one to seven and averaged 4.2 (SE = 0.46) per female.

The second littering period in 2005 was determined by an overlap of conception dates demonstrated by three gravid females collected in April and one collected in May. Estimated conception dates for these four females were from March 29 to April 16. There were approximately two weeks of overlap between the first littering period parturition dates and the second littering period conception dates. Parturition dates for the second littering period were from May 10 to May 28. Litter size ranged from five to eight and averaged 6.0 (SE = 0.71) during the second littering period.

The estimated conception dates of six gravid females collected in June 2005 and one in July were from May 27 to June 9. These conception dates were approximately two weeks after parturition of females in the second littering period and likely represented the third littering period. Parturition dates for these females were estimated from July 8 to July 21. Litter size for the third littering period ranged from three to six and averaged 4.7 (SE = 0.42) per female.

In August 2005 two of the 11 adult females collected were gravid, with estimated conception dates of June 30

TABLE 1
REPRODUCTIVE OUTPUT AND ESTIMATED CONCEPTION AND PARTURITION DATES OF FEMALE WHITE-TAILED JACKRABBITS IN SOUTH DAKOTA, 2004 AND 2005

Littering period	No. shot	Gravid females (%)	Mean litter size (SE)	Viable fetuses (SE)	Ova shed*	Prenatal mortality (%)	Conception dates	Parturition dates
2004	3	10	8 (80)	5.5 (0.5)	40, 41	2	22–25 May	3–8 July
	4	17	3 (17)	5.0 (1.0)	15, 15	0	4–17 July	16–29 August
2005	1	13	13 (100)	4.2 (0.46)	54, 79	32	24 February–6 March	7–17 April
	2	5	4 (80)	6.0 (0.71)	24, 25	4	29 March–16 April	10–28 May
	3	10	7 (70)	4.7 (0.42)	33, 35	6	27 May–9 June	8–21 July
	4	11	2 (18)	3.0 (0)	6, 7	14	30 June–15 July	12–26 August

*First number indicates implantation sites and second number represents ova shed.

and July 15. These females likely represented the fourth littering period since conception dates overlap with parturition dates of the third littering period. Parturition dates for the fourth littering period were estimated to be August 12 and 26. Both females were carrying three viable fetuses. The length of the breeding season was estimated from February 24 to July 15, which was 142 days, allowing for 3.3 litters.

In 2004 prenatal mortality occurred in one gravid female white-tailed jackrabbit collected in June (third littering period) that demonstrated resorption of one fetus resulting in 2% prenatal mortality. There were no instances of prenatal mortality during the fourth littering period.

In 2005 prenatal mortality was greatest (32%) in the first littering period. There were 79 ova shed from the 13 collected females with only 54 implantation sites. Two females also showed evidence of resorption at one implantation site during the first littering period. In the second littering period, 25 ova were shed with 24 viable fetuses, since one female exhibited resorption of one fetus (4% prenatal mortality). During the third littering period there were 35 ova shed with only 33 implantation sites. Preimplantation loss of one ova and one instance of resorption resulted in 6% prenatal mortality in the third littering period. Prenatal mortality was 14% in the fourth littering period. Preimplantation loss was the only source of prenatal mortality, with seven ova shed and only six implantation sites. There were 26 gravid females collected in 2005 that shed 146 ova over four littering periods, so the potential annual production was 22.5 per female (Table 1). Overall, higher fecundity was observed during the second littering period as indicated by a large litter size and a low prenatal mortality.

DISCUSSION

Since leporids have a high reproductive rate, demographic stochasticity is expected. There is a paucity of information on sex ratios of white-tailed jackrabbits, but our data indicate that sex ratios are similar to those of black-tailed jackrabbits, which have been reported to be 1:1 throughout much of their range (Lechleitner 1959; Tiemeier 1965; Gross et al. 1974; Dunn et al. 1982; Plettner 1984).

Juvenile jackrabbits are generally not collected until they are about three months old due to their secretive behavior (Lechleitner 1959). Juvenile jackrabbits were present during April in Nebraska (Plettner 1984) and during May in California (Lechleitner 1959). Approximately 35% of the jackrabbits we collected were juveniles and were found from May to December. Adults represented 65% of the total number of white-tailed jackrabbits collected. All jackrabbits collected in March and April were adults. Lechleitner (1959) and Plettner (1984) also found a high percentage of adults during April.

Prolific breeding capabilities in lagomorphs may aid in sudden population increases. White-tailed jackrabbit populations are composed mostly of adults in winter, while juveniles dominate in other seasons (James and Seabloom 1969; Rogowitz and Wolfe 1991). In Wyoming, Rogowitz and Wolfe (1991) reported a rapid rate of population replacement of adults by juveniles, which may have prevented a population decline during times with low survival. Since juveniles reached sexual maturity by March or April in 2005, the entire population may potentially be capable of breeding during the second littering period.

Adult male white-tailed jackrabbits appeared to be reproductively active from January to July during the

2005 breeding season. Female activity was similar to that of males, but there appeared to be a time difference of one month in the onset and cessation of breeding between the sexes. Ovaries of female jackrabbits increased in mass one month after the increase in testes mass and remained at their maximum until one month after male testes began to regress in mass. This breeding strategy assures that males are ready to breed as soon as females ovulate during spring. During the fourth littering period, females may still be able to find some reproductively capable males.

Rogowitz (1992) implied that cues other than ambient temperature stimulate reproductive activity and suggested that snow cover and food accessibility may play a role in the onset of reproduction in white-tailed jackrabbits. The characteristic postpartum heat demonstrated by *Lepus* spp. may increase the instances of breeding synchrony, but synchrony must be present within the first littering period (James and Seabloom 1969). We observed synchronous breeding in the first littering period in 2005, as has been previously reported in North Dakota (James and Seabloom 1969). Since most males are essentially reproductively active when females first become receptive, breeding synchrony of the first littering period is likely to occur. Cues that result in an initial synchronous estrous cycle of females and their tendency for postpartum breeding are likely responsible for synchrony of subsequent litters.

White-tailed jackrabbits may annually produce three to four litters in South Dakota, but only a small percentage of females actually produced four litters per season. In both 2004 and 2005, data indicate that 18% of the adult females that were collected experienced a fourth littering period. James and Seabloom (1969) found that only 29% of female white-tailed jackrabbits in North Dakota produced a fourth litter. Stefan and Krebs (2001) found that snowshoe hares also had the lowest pregnancy rates in the fourth littering period. Lower fecundity rates of the last littering period may be explained by the difference in reproductive cessation for males and females. As male hares cease breeding, testicular weights diminish, causing a loss of libido and potency (Meslow and Keith 1968; James and Seabloom 1969). Since most males become reproductively inactive approximately one month before females, it is likely that only a small percentage of males maintain reproductive potency for a receptive female during the potential fourth littering period. Future research should include counting corpora lutea for nonpregnant parous females throughout the breeding season to determine the percentage of receptive females that are capable of producing a fourth litter.

Prenatal mortality may affect overall reproductive output of female white-tailed jackrabbits. For the last two littering periods during the 2004 breeding season, we found only one mortality from postimplantation loss. There were 56 ova shed among 11 gravid white-tailed jackrabbits, indicating postimplantation loss affected 1.8% of all ova shed and 9.1% of females collected in 2004. Bronson and Tiemeier (1958) reported that resorption was a result of stress such as weather conditions, which if great enough may result in entire litter loss.

Instances of prenatal mortality varied among littering periods throughout the 2005 breeding season. Prenatal mortality was greatest in the first littering period in 2005 (32%), sharply decreased during the second (4%) and third (6%) littering periods, and rose during the fourth littering period (14%). The high incidence of prenatal mortality during the first littering period may have been due to severe weather (Rogowitz 1992). Spring weather was unusually severe, with numerous snowstorms during our study, which likely affected prenatal mortality. During the second and third littering period, conditions were ideal, with warm weather and abundant food supplies. It is unclear why there was high prenatal mortality during the fourth littering period, but variable prenatal mortality in littering periods in lagomorphs is not uncommon (Stefan and Krebs 2001).

Reproductive output of female white-tailed jackrabbits may vary between littering periods. In North Dakota the average number of ova shed by female white-tailed jackrabbits steadily decreased throughout the breeding season (James and Seabloom 1969). The mean number of ova shed by female white-tailed jackrabbits in South Dakota was greatest during the first two littering periods. In Wyoming, Rogowitz (1992) found that reproductive output among white-tailed jackrabbits varied with environmental conditions, and energy expenditure for fetal production was greater when suitable forage became available.

White-tailed jackrabbits in South Dakota are capable of having four litters in each breeding season. However, the incidence of this reproductive output is unclear and may be related to food abundance or predator pressure. We do not believe that the current reproductive characteristics of white-tailed jackrabbits are contributing to their downward population trend. Wildlife managers will need to continue to monitor the population to determine what is causing the apparent continuing population decline of white-tailed jackrabbits.

ACKNOWLEDGMENTS

Funding for this research project was provided by the South Dakota Department of Game, Fish, and Parks (SDGFP), South Dakota State University, and the Federal Aid to Wildlife Fund (Project W-75-R, No. 75) administered by SDGFP. This study was approved as #04-A020 by the South Dakota State Institutional Animal Care and Use Committee. We would like to express our gratitude to Alyssa Kiesow and all the people involved in donating and collecting animals for this research, as well as SDGFP for providing a special permit allowing the collection of jackrabbits throughout the year.

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