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AGGRESSIVE DEFENSIVE BEHAVIOR BY FREE-RANGING WHITE-TAILED DEER

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Maternal investment plays a critical role in neonate survival, and adults can improve survival of offspring by defending them against predators. However, limited information exists documenting ungulate aggression toward humans in defense of neonates. During captures of neonates in spring 2007 and 2008 in north-central South Dakota, we documented 24 aggressive encounters by adult female and yearling male and female white-tailed deer (*Odocoileus virginianus*) defending neonates. Eleven (45.8%) aggressive encounters included yearlings accompanying adult females. Mean ages and weights of neonates that were aggressively defended were greater ($P < 0.0001$) than ages and weights of those that were not; adults began protecting neonates at approximately 4 days of age. Male fawns were more likely ($P = 0.013$) to be defended than female fawns. Examination of our data suggests that sex- and age-biased maternal defensive behavior exists in white-tailed deer, and that deer biased maternal investment toward older, male neonates.

Key words: defensive behavior, maternal investment, neonate, *Odocoileus virginianus*, white-tailed deer

Maternal investment plays a crucial role in juvenile survival, and benefits may continue even after offspring have become relatively independent (Byers 1997; Caro 1994; White et al. 2001). In species with parental care, adults can improve survival of offspring by aggressive defense against predators (Smith 1987). Nonetheless, defensive behavior may incur considerable energetic expense, risk, and loss of time from other activities (Smith 1987). Generally, the amount of parental defense should be determined by the degree of risk to future reproductive potential, the value of present offspring compared with the future reproductive contribution of the parent, increase in offspring welfare (Pressley 1981; Smith 1987), and age of offspring (Smith 1987).

Detailed accounts of maternal defense have been documented for numerous North American ungulates (Lent 1974; Lingle et al. 2005; Smith 1987), including mule deer (*Odocoileus hemionus*—Hamlin and Schweitzer 1979), North American elk (*Cervus elaphus*—Altman 1963), moose (*Alces americanus*—Altman 1963; Murie 1961, 1981), pronghorn (*Antilocapra americana*—Marion and Sexton 1979), and

white-tailed deer (*O. virginianus*—Garner and Morrison 1980; Richardson et al. 1983). Defensive behavior of ungulates normally is directed toward wild predators such as coyotes (*Canis latrans*—Garner and Morrison 1980; Hamlin and Schweitzer 1979; Marion and Sexton 1979), wolves (*C. lupus*—Côté et al. 1997), bobcats (*Lynx rufus*—Garner and Morrison 1980), black bears (*Ursus americanus*—Murie 1981), and grizzly bears (*U. arctos horribilis*—Murie 1961, 1981). Additionally, females have exhibited aggression toward other deer at parturition, defending offspring from domination and competition from conspecifics (McCullough 1979; Ozoga et al. 1982).

Garner and Morrison (1980) documented defensive behavior of white-tailed deer on 10 occasions while capturing neonates. When neonates initiated bleating, females charged the capture crews with ears forward, similar to their response to coyotes, but subsequently fled (Garner and Morrison 1980). Richardson et al. (1983) observed alarm behavior (foot stomps and nervous pacing) by female white-tailed deer in response to distress calls of their young, with 1 female charging and flailing her front legs. Hubbard and Nielsen (2009) documented 13 occurrences of female white-tailed deer attacking humans on the campus of Southern Illinois University Carbondale during multiple fawning seasons; attacks were spatially and temporally clustered and multiple attacks were

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attributed to a single female. Additionally, we observed several occurrences of aggression by females during captures of neonates in western Minnesota while working on 2 research studies.

To our knowledge, factors predicting aggressive maternal defense in white-tailed deer have not been addressed. We evaluated the effects of sex, weight, and age of neonates; length of capture chase; capture habitat; and deer density in the capture area on maternal aggressive behavior. We hypothesized that captures of male neonates were more likely to trigger aggressive defensive behavior because reproductive potential of white-tailed deer can be greater for high-quality males than for females (Clutton-Brock et al. 1981; Trivers and Willard 1973). The benefit from enhancing survival of male neonates to reproductive age also could include increased long-term fitness because the sex ratio of our study population was strongly female-biased. Additionally, maternal defense should increase in intensity as neonates become older and the probability of reaching reproductive age increases (Smith 1987); therefore, we hypothesized that captures of older neonates also were more likely to trigger defensive behavior.

MATERIALS AND METHODS

Study area.—We captured neonatal white-tailed deer in Edmunds County (45°45'N, 99°4'W), located in north-central South Dakota, for a study on survival of neonates and resource selection during summer. Native mixed-grass vegetation was dominated by western wheatgrass (*Elymus smithii*), big bluestem (*Andropogon gerardii*), porcupine grass (*Stipa spartea*), and little bluestem (*Schizachyrium scoparium*). Dominant tree species were green ash (*Fraxinus pennsylvanica*), American elm (*Ulmus americana*), boxelder (*Acer negundo*), hackberry (*Celtis*), and eastern cottonwood (*Populus deltoides*—Johnson and Larson 1999; Petersen 1984). Common wetland vegetation included prairie cordgrass (*Spartina pectinata*), reed canarygrass (*Phalaris arundinacea*), common reed (*Phragmites australis*), cattails (*Typha*), rushes (*Juncus*), and sedges (*Carex*—Johnson and Larson 1999). The region was dominated by row crop agriculture, and cultivated land and pasture–grassland constituted 42.6% and 45.1%, respectively, of total land use (Smith et al. 2002). Cultivated crops included corn (*Zea mays*), soybeans (*Glycine max*), wheat (*Triticum aestivum*), and alfalfa (*Medicago sativa*—South Dakota Agriculture Statistics Service 2008).

Neonate captures.—We captured neonatal white-tailed deer using nocturnal searches with vehicles and daytime ground searches using postpartum behavior of reproductive females as an indicator of parturition and presence of neonates (Downing and McGinnes 1969; Huegel et al. 1985; White et al. 1972). Once a neonate was sighted, we used a quick and loud approach to initiate a “drop” response (Nelson and Woolf 1987). Neonates that attempted to flee were pursued on foot and captured with a net. We documented length of chase (time) for all fleeing neonates captured. We manually restrained neonates and determined sex. We determined age

using hoof growth measurement (age = $-5.728 + 3.141(\text{hoof growth})$) and umbilicus condition (Brinkman et al. 2004). We weighed young using a 4.8-mm-mesh bag suspended from a digital scale (model FS 50; Berkley, Spirit Lake, Iowa) to the nearest 1 g and recorded habitat type in which neonates were captured. For analyses, we combined habitat types where captures occurred into cover (i.e., trees, tall grass—Conservation Reserve Program [CRP], or wetlands) and noncover (i.e., row crops, small grains, pasture, development, or alfalfa). All methods used in this research were approved by the Institutional Animal Care and Use Committee at South Dakota State University (approval number 04-A009) and followed guidelines for the care and use of animals approved by the American Society of Mammalogists (Gannon et al. 2007).

Data analyses.—We estimated diurnal deer density by observing deer 2–3 days/week for 2–4 h by driving a 72.4-km fixed transect in the neonate capture area (Bowyer et al. 1996; Monteith et al. 2007). We then assigned observed deer to 96-ha quadrats (500 m on either side of a 0.96-km segment of transect); we assumed transect width was the maximum distance we could observe and identify deer from the road (Bowyer et al. 1996).

We defined an aggressive encounter as an adult female, yearling female, or yearling male white-tailed deer initiating defensive behavior of a captured neonate. Sex and age class of aggressive animals were identified by size, body conformation, and antler characteristics (Bowyer et al. 1996). Aggressive behavior included antagonistic charging toward field personnel, bluff charges in proximity to personnel (< 5 m), flailing with forefeet, and physical contact with personnel. We used a multivariate analysis of variance to test for relationships of defensive behavior to age, weight, and sex of neonates; sex; length of capture chase; and deer density at capture sites. We used chi-square analyses to test for differences in defensive behavior by capture habitat, and *t*-tests to compare weight and age between sexes. Statistical tests were conducted using SAS version 9.1 (SAS Institute Inc. 2000) with an experiment-wide error rate of 0.05.

RESULTS

We captured 49 neonates during May–June 2007 and 2008 and documented 24 (49.0%) aggressive encounters with adult white-tailed deer defending neonates. Of the 24 aggressive encounters, 11 (45.8%) included aggression by at least 1 yearling animal in addition to the adult female. Three of these multiple-animal encounters included interactions with a yearling male. We captured 30 (61.2%) neonates in tall grass—Conservation Reserve Program (CRP) lands, 5 (10.2%) in forested habitat, 4 (8.2%) in wheat, 3 (6.1%) in corn, 2 (4.1%) in pasture, 2 (4.1%) in wetland habitats, 2 (4.1%) in alfalfa, and 1 (2.0%) in soybeans. We documented no significant difference in habitat type where aggressive encounters occurred ($\chi^2 = 2.00$, *df.* = 1, *P* = 0.157) compared with nonaggressive encounters. Mean weight of male and female neonates was $4.4 \text{ kg} \pm 0.26 \text{ SE}$ (*n* = 18) and

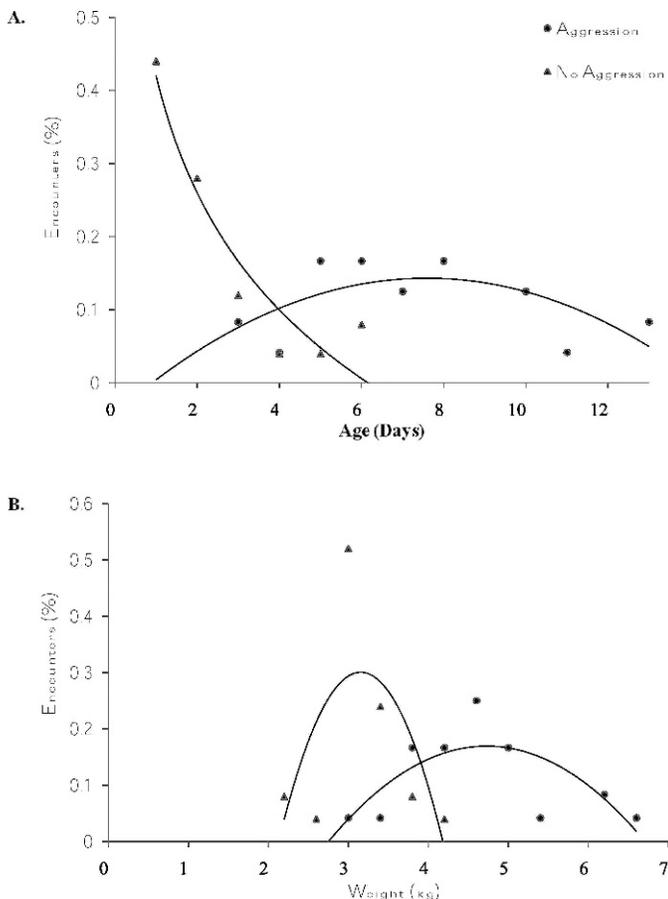


FIG. 1.—Estimated A) age and B) weight of neonatal white-tailed deer (*Odocoileus virginianus*) with aggressive and nonaggressive encounters (%) during captures, May–June 2007 and 2008 in north-central South Dakota. A) Age regression for aggressive ($y = -0.0032x^2 + 0.0468x - 0.0463$; $R^2 = 0.39$) and nonaggressive ($y = -0.231\ln(x) + 0.4201$; $R^2 = 0.91$) encounters indicate an age threshold of approximately 4.0 days. B) Weight regression for aggressive ($y = -0.0332x^2 + 0.3006x - 0.5431$; $R^2 = 0.53$) and nonaggressive ($y = -0.2857x^2 + 1.8209x - 2.5434$; $R^2 = 0.45$) encounters indicate a weight threshold of approximately 3.9 kg.

3.3 ± 0.12 kg ($n = 31$), respectively, and was significantly greater for males ($t = 4.50$, $d.f. = 47$, $P < 0.0001$). Mean age of male and female neonates was 4.8 days ± 0.91 SE ($n = 18$) and 3.8 ± 0.55 days ($n = 31$), respectively, and was similar between sexes ($t = 1.02$, $d.f. = 47$, $P = 0.313$).

Results of a multivariate test of differences relative to age and weight of neonates, sex, length of capture chase, and deer density at capture sites between aggressive and nonaggressive encounters were significant ($F = 9.00$, $d.f. = 5, 36$, $P < 0.0001$). Mean age of neonates at the time of aggressive and nonaggressive encounters was 6.7 days ± 0.57 SE ($n = 24$) and 1.7 ± 0.31 days ($n = 25$), respectively, and was greater for neonates with aggressive encounters, with an inflection point at approximately 4.0 days ($F = 41.74$, $d.f. = 1, 40$, $P < 0.0001$; Fig. 1). Weight was positively correlated with age of neonates ($r = 0.94$, $n = 49$). Mean weight of neonates with aggressive and nonaggressive encounters was 4.4 kg ± 0.18 SE ($n = 24$) and 2.9 ± 0.08 kg ($n = 25$), respectively. Weight of neonates with

aggressive encounters was greater than weight of neonates captured without aggressive encounters; the inflection point for the relationship was approximately 3.9 kg ($F = 43.85$, $d.f. = 1, 40$, $P < 0.0001$; Fig. 1). Additionally, length of chase was greater for neonates with aggressive encounters ($\bar{X} = 23.8$ s ± 6.8 SE, $n = 24$; $F = 8.61$, $d.f. = 1, 40$, $P = 0.06$) compared to nonaggressive encounters ($\bar{X} = 3.6 \pm 2.0$ s, $n = 25$); 15 neonates evaded capture. However, length of chase was positively correlated with weight of neonates ($r = 0.61$, $n = 49$). We documented a significant difference between captures of male and female neonates ($F = 12.87$, $d.f. = 1, 40$, $P = 0.013$); aggressive defensive behavior was associated more with male than female neonates.

Weekly white-tailed deer density in the neonate capture area (72.4-km transect) ranged from 2.3 to 3.3 deer/km² from 15 May to 15 June. Mean white-tailed deer density at neonate capture locations (4.6 deer/km² ± 0.36 SE, $n = 41$) was greater than density for the entire transect. However, no difference ($F = 1.02$, $d.f. = 1, 40$, $P = 0.611$) occurred between deer density in areas where aggressive and nonaggressive encounters occurred.

DISCUSSION

Our study documented that maternal defensive behavior was more likely to occur for male neonatal white-tailed deer, as well as for older neonates. As age of offspring (and reproductive value) increases, parental investment should increase as long as the parent's ability to influence offspring survival does not decrease (Pressley 1981; Smith 1987). Females vary the type and intensity of maternal defensive behavior according to benefit and relative energetic costs (Smith 1987). When females are in good physical condition, natural selection should favor an increase in the frequency of aggressive parental defense (Smith 1987). Females possibly go through a recovery period following parturition and are more physically capable of aggressive behavior several days postparturition. Therefore, maternal defense should increase in intensity as fawns become older and the probability of reaching reproductive age increases (Smith 1987). During our study, older neonates were more likely to be the recipient of aggressive maternal defense. The parabolic shape of the age and weight curves relative to aggressive encounters may be explained by increased ability of young to flee. Neonates older than 10 days rarely are captured (Cook et al. 1971; Downing and McGinnes 1969; Huegel et al. 1985; Robinette and Gashwiler 1950) and young can lead pursuers on lengthy chases (White et al. 1972); older neonates are no longer helpless and have a high probability of escaping predators if encountered (Huegel et al. 1985; White et al. 1972). Additional factors contributing to the shape of the weight and age curves as they relate to aggressive behavior possibly include previous interaction with predators as well as the age of the adult female. A female's neonate-rearing ability increases with experience; older females are more successful in rearing neonates (Ozoga and Verme 1986). Furthermore,

heavier neonates potentially represent a biased sample of the available neonates; abandoned younger and lighter fawns are often not captured.

In ungulates, postnatal growth rate is likely to affect survival rates and age at maturity (Andersen and Linnell 1997; Clutton-Brock et al. 1982; Sæther et al. 1992). In several species, reproductive success among males is related to size (Clutton-Brock et al. 1979; Geist 1971; Le Boeuf 1972, 1974), and body size correlates with early growth rates (Skogland 1986). Reproductive success of males is heavily influenced by maternal investment before weaning (Clutton-Brock et al. 1982; Skogland 1986). Thus, condition of male young likely influences female behavior, thereby inducing a higher investment in heavier fawns (Braza and San José 1988; Braza et al. 2000).

Trivers and Willard (1973) proposed that natural selection favored deviation from 50:50 parental investment in the sexes. Sex allocation theory predicts that females should invest preferentially in the sex of offspring that maximizes their long-term fitness for a particular environment (Frank 1990; Hewison et al. 2005). In species with a long period of parental investment postbirth, parents in better physical condition could be expected to show a bias toward male offspring (Trivers and Willard 1973). Additionally, the sex ratio of the population as well as survival rates of male neonates can influence potential reproductive contribution of male neonates. Reproductive success is affected by maternal investment during the growth period and this relationship is particularly critical for males, where growth during the 1st year of life is related to adult body size and fighting ability (Clutton-Brock et al. 1981, 1982). If reproductive success varies more widely for males than females and variation in success among adults is influenced by maternal investment, parents should maximize their reproductive success by allocating a higher proportion of their resources to male than to female offspring (Clutton-Brock et al. 1981; Trivers and Willard 1973). However, empirical tests of this hypothesis with ungulates are conflicting, and consistent only when appropriate measures are used (Sheldon and West 2004).

Studies of maternal investment suggest that ungulate mothers do discriminate against daughters in the most highly polygynous, dimorphic species (Cameron 2004; Hewison and Gaillard 1999; Hewison et al. 2005; Sheldon and West 2004). Clutton-Brock et al. (1981) concluded that total maternal investment is greater for male progeny in polygynous mammals. Conversely, daughters often adopt territories or home ranges overlapping or adjacent to their mother (Clutton-Brock et al. 1981; Mathews 1989; Mathews and Porter 1993), whereas male offspring disperse. Consequently, investment in daughters by weakly polygynous species and in males by highly polygynous species can improve lifetime fitness via effects on subsequent generations of offspring.

During summer, white-tailed deer live mainly in small, matriarchal groups consisting of an adult doe, her young, and possibly yearlings (Bowyer et al. 2001; Lingle 2003; Schwede et al. 1993). Unlike mule deer, which demonstrate a willingness

of females to defend unrelated neonates, we could find only a single report where >1 female white-tailed deer demonstrated maternal defense of an unrelated fawn (Lingle et al. 2005). Neonatal mule deer were defended at times when their mothers were not in the area and benefited from the willingness of females to defend unrelated offspring (Lingle et al. 2005). Social and aggressive defensive behavior similar to that reported for mule deer tends to be seen in animals inhabiting open habitats (Jarman 1974; Lima 1993; Lingle et al. 2005). The northern Great Plains is relatively open habitat, containing only 1.9% forested habitat with 87.7% pasture, grassland, or row crops (Smith et al. 2002). With limited cover available in this area, white-tailed deer may have adapted their defensive behavior to one more commonly seen in open habitats.

We documented that maternal defensive behavior was more likely to occur for male neonatal white-tailed deer and for older neonates. To what extent this behavior was a result of environmental conditions, physical condition of females, or age of females was unknown. Older females should be more aggressive in defensive behavior because the probability of reproducing in subsequent years decreases with age (Gavin 1979; Smith 1981, 1987). Additionally, females in good physical condition as well as dominant females should demonstrate an increased frequency of aggressive parental defensive behavior regardless of sex of neonate. Smith (1987) determined that deer could vary the type and intensity of defensive behavior as a behavioral adaptation. Further research should investigate additional factors affecting maternal defense in this region.

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