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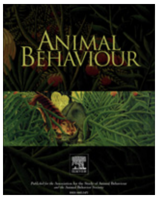

Predator evasion by white-tailed deer fawns

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Despite their importance for understanding predator–prey interactions, factors that affect predator evasion behaviours of offspring of large ungulates are poorly understood. Our objective was to characterize the influence of selection and availability of escape cover and maternal presence on predator evasion by white-tailed deer, *Odocoileus virginianus*, fawns in the northern Great Plains, U.S.A. We observed 45 coyote, *Canis latrans*, chases of fawns, and we participated in 83 human chases of fawns during 2007–2009, of which, 19 and 42 chases, respectively, ended with capture of the fawn. Evasive techniques used by fawns were similar for human and coyote chases. Likelihood of a white-tailed deer fawn escaping capture, however, was influenced by deer group size and a number of antipredator behaviours, including aggressive defence by females, initial habitat and selection of escape cover, all of which were modified by the presence of parturient females. At the initiation of a chase, fawns in grasslands were more likely to escape, whereas fawns in forested cover, cultivated land or wheat were more likely to be captured by a coyote or human. Fawns fleeing to wetlands and grasslands also were less likely to be captured compared with those choosing forested cover, wheat and cultivated land. Increased probability of capture was associated with greater distance to wetland and grassland habitats and decreased distance to wheat. Use of wetland habitat as a successful antipredator strategy highlights the need for a greater understanding of the importance of habitat complexity in predator avoidance.

Animals can behaviourally influence their risk of being preyed upon as well as how they escape predators (Lima & Dill 1990). Prey respond to predation at the landscape level using temporal and spatial changes in activity and selection of safer habitats (Lima 1998; Thaker et al. 2011); reactions of prey species to predators vary from flight to overt aggression (Berger 1979; Bowyer 1987; Bleich 1999). Landscape attributes can influence susceptibility of prey to predation by affecting the probability of encounter and the likelihood of escape (Hebblewhite et al. 2005). For instance, elk, *Cervus elaphus*, in grassland habitat are 4.1 times less likely to encounter wolves, *Canis lupus*, and 1.4 times less likely to be preyed upon by wolves than are elk in other habitats (Hebblewhite et al. 2005). Additionally, moose, *Alces americanus*, are more likely to be preyed upon farther from forested cover (Kunkel & Pletscher 2000), whereas turkey, *Meleagris gallapavo*, and elk have increased survival closer to roads and human disturbance (Thogmartin & Schaeffer 2000; Hebblewhite & Merrill 2007).

In response to high predation risk and substantial loss in lifetime productivity if young perish (Bergerud 1971; Garrott et al. 1985; Smith 1986), many ungulates have evolved an array of maternal–neonate cooperative behaviours to avoid predation, which is reflected by the 'hiding-to-following' spectrum (Rudge 1970; Geist 1971; Lent 1974). While exceptions to this general spectrum of behaviour exist (Bowyer et al. 1998), white-tailed deer, *Odocoileus virginianus*, in the northern Great Plains adhere to a progression of hiding to following with increased age (Grovenburg et al. 2010). 'Following' behaviour is a predator avoidance strategy typical of migratory species that inhabit open habitats (Ralls et al. 1986). Among species that inhabit dense habitat, mothers of less social ungulates, such as white-tailed deer, often select sites with topographical features and dense cover to hide their young (Lent 1974; Estes & Estes 1979; Monteith et al. 2007).

Ungulate species using the 'hider' strategy rely on bed sites to provide protective cover from predators and thermoregulatory protection from the elements (Bowyer et al. 1998; Linnell et al. 1999; Van Moorter et al. 2009; Grovenburg et al. 2010). Bed site selection is determined by the fawn but is limited to the maternal home range. Survival of roe deer, *Capreolus capreolus*, fawns is influenced by the availability of good bed sites within the maternal range (Van Moorter et al. 2009). Therefore, maternal home ranges may represent a compromise or trade-off between habitat that provides secure cover for offspring and habitat that offers adequate forage (Bowyer et al. 1998). Although the influence of habitat

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characteristics on neonatal survival has been documented in several studies (Linnell et al. 1999; Vreeland et al. 2004; Rohm et al. 2007; Grovenburg et al. 2011), information regarding the influence of habitat on survival of young ungulates relative to evasion of predators is limited.

Maternal behaviour also can influence juvenile survival (Byers 1997; White et al. 2001; Grovenburg et al. 2009). For example, Lingle et al. (2005) reported that differences in aggressive defence by females resulted in differential vulnerability of mule deer, *Odocoileus hemionus*, and white-tailed deer fawns. Antipredatory behaviour by maternal females in defence of their offspring is well documented in the ecological literature (Smith 1987; Lingle et al. 2005) and is normally directed towards natural predators, such as coyotes, *Canis latrans* (Hamlin & Schweitzer 1979; Marion & Sexton 1979). However, aggression by parturient females also has been directed towards humans (Richardson et al. 1983; Grovenburg et al. 2009; Hubbard & Nielsen 2009).

Our objectives were to document antipredator behaviour and the factors that influence patterns of predator evasion for white-tailed deer fawns relative to habitat and presence of parturient females. Availability of escape cover most likely plays a persistent role in the ability of neonatal ungulates to avoid predation. Therefore, we predicted that availability of escape cover would influence antipredator behaviour of fawns and that fawns would select for the nearest available escape cover (e.g. grasslands, wetlands, forested cover (mainly tree plantings and shelterbelts) or wheat fields) when pursued. Young also can use the behaviour of adults to guide development of their behavioural responses. Therefore, we expected the presence of parturient females to influence fawns' selection of cover and predator evasion strategies, resulting in a positive influence on the probability of escape from predators.

METHODS

Study Area

We monitored strategies of predator evasion by white-tailed deer fawns in a 5558 km^2 area within the Northwestern Glaciated Plains and the Northern Glaciated Plains level III ecoregions in Edmunds and Faulk counties in north-central South Dakota, U.S.A. (Bryce et al. 1998). Terrain was flat to gently rolling and intermixed with numerous pothole wetlands and mounds of glacial till (Bryce et al. 1998). Agriculture was the predominant land use in the region; cultivated land and pasture represented 40.4 and 43.0% of total land use, respectively, whereas forests, mainly woodland plantings and shelterbelts, represented 2.3% (Smith et al. 2002). The two-county study area had 14 975 ha (2.7% total land cover) converted to perennial grasslands as part of the Conservation Reserve Program (CRP), a voluntary programme that pays annual rent to landowners who convert their agricultural lands to permanent cover (Gray & Teels 2006; Fargione et al. 2009). Although marshes and sloughs occupy a relatively small portion of the northern Great Plains (11.1% of land use in the two-county area; Smith et al. 2002), they serve as cover and foraging areas for white-tailed deer throughout the region (Petersen 1984). In our study area, vegetation cover types of wetlands were primarily those of cover type 1 (dense stands of emergent cover and open water covering <5% of the wetland) or cover type 2 (open water covering 5–95% of the wetland, with scattered dense patches of emergent cover; Stewart & Kantrud 1971). Vegetation height (excluding tree height) among habitats in the study area was highest in wetlands (2.4–3.0 m; Johnson & Larson 1999), followed by grasslands (~76 cm), forested cover (~75 cm) and pasture (~35 cm; Grovenburg et al. 2010). Densities of white-tailed deer during summer within the study area were 2.3–3.3 deer/km^2 (Grovenburg et al. 2009).

Data Collection

We identified 14 distinct coyote dens in the study area that contained two to five adults within each group and were adjacent to areas known to have white-tailed deer fawns. One to three times per week, from 15 May to 31 August 2008–2009, we positioned two observers 500–1000 m from dens to view coyote hunts but avoid interference with their natural behaviours (Lingle et al. 2005). We used Leopold® Wind River Mesa binoculars (10 × 50; Leopold®, Beaverton, OR, U.S.A.), Leopold® Golden Ring binoculars (17 × 50; Leopold®) and a high-resolution spotting scope (Nikon ProStaff Spotting Scope, 16–48 × 65, Nikon Inc., Melville, NY, U.S.A.) to observe coyotes and fawns. We conducted observations from 30 min before sunrise to 1100 hours and from 1700 hours until dark (Lingle 2000) during an approximately equal number of early ($N = 37$) and late ($N = 34$) periods, and we never observed the same den site on consecutive days.

We recorded only coyote–fawn encounters where the fawn was detected and pursued by the coyote, resulting in flight by the fawn. Because of cover and viewing distance, we were unable to determine presence of a hidden fawn during coyote searches unless that fawn left its hiding spot and fled or was radiocollared. We recorded global positioning system (GPS) coordinates of encounters (Universal Transverse Mercator, UTM; Zone 14 NAD 83 coordinates) from observational positions using a Magellan Triton 1500 global positioning system (Magellan Navigation, Inc., Santa Clara, CA, U.S.A.), and we used a rangefinder (Leica Rangemaster CRF 1200, Leica Camera Inc., Allendale, NJ, U.S.A.) to determine distance from observation sight to beginning and end of pursuit locations. We then used a compass (Ranger CL 515 Compass; Silva®, Stockholm, Sweden) to estimate bearings from observation positions to beginning and end of pursuit locations. Lastly, we plotted the locations where the pursuit commenced and ended on United States Geological Survey 3 m Digital Orthophoto Quadrangle maps. We recorded the initial location of the fawn as the starting position and the location where the fawn either escaped (i.e. coyote gave up pursuit) or was captured as the final location. We included only locations where we successfully observed both the beginning and end of the pursuit.

We hand captured fawns during 15 May–15 June 2007–2009 with daytime ground searches using postpartum behaviour of females as an indicator of parturition and presence of fawns (Downing & McGinnes 1969; Huegel et al. 1985). For these fawns, we recorded the location of initial sighting and the location of either capture or escape at the end of pursuit (Grovenburg et al. 2010). We included only those observations where a fawn fled upon encounter because we were interested in predator evasion patterns during a chase, rather than detection probability of bedded fawns. Animal handling methods used during capture of fawns followed guidelines recommended by the American Society of Mammalogists (Sikes et al. 2011) and were approved by the Institutional Animal Care and Use Committee at South Dakota State University (Approval number 04–A009).

For each fawn pursuit, we recorded the number of coyotes involved in the hunt or the number of field personnel involved in the chase. We estimated the age of each fawn that was captured or retrieved using umbilicus condition (Haugen & Speake 1958; Brinkman et al. 2004) and by measuring the distance between the hair line and growth ring on the outer edge of the front hooves using a dial caliper accurate to 0.02 mm (Starrett 120A 6″ (15.24 cm) dial caliper, L. S. Starrett Company, Athol, MA, U.S.A.; Haugen & Speake 1958). For fawns more than 1 day of age, we calculated age based on hoof-growth equations developed for deer in the midwestern United States (Brinkman et al. 2004). We estimated age of all other fawns that escaped field personnel or coyotes