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.

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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 anti-predator 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 peren-nial 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 grass-lands (~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 deter-mine 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 Insti-tutional 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 esti-mated age of all other fawns that escaped field personnel or coyotes

based on the date of chase and the mean date of parturition for the study area; the birth pulse for this region was highly synchronous (SD = 5.0 days; Grovenburg et al. 2012). We recorded whether the parturient female (i.e. based on observations of interactions between the female and fawn, such as attentiveness of female, nursing, grooming, vocalizing) was present (<50 m of fawn), number of additional adult or yearling animals present within 50 m of fawns (deer group size) when the pursuit first began, and whether adults showed aggressive defence of the fawn. We identified a parturient female as the dam of the fawn if we observed her interacting with the fawn, if the female ran with the fawn during the chase, or if the female showed aggression towards the predator or the chase crew during the chase. We recorded general habitat type where chases began and ended and estimated the length of each chase (in metres and seconds).
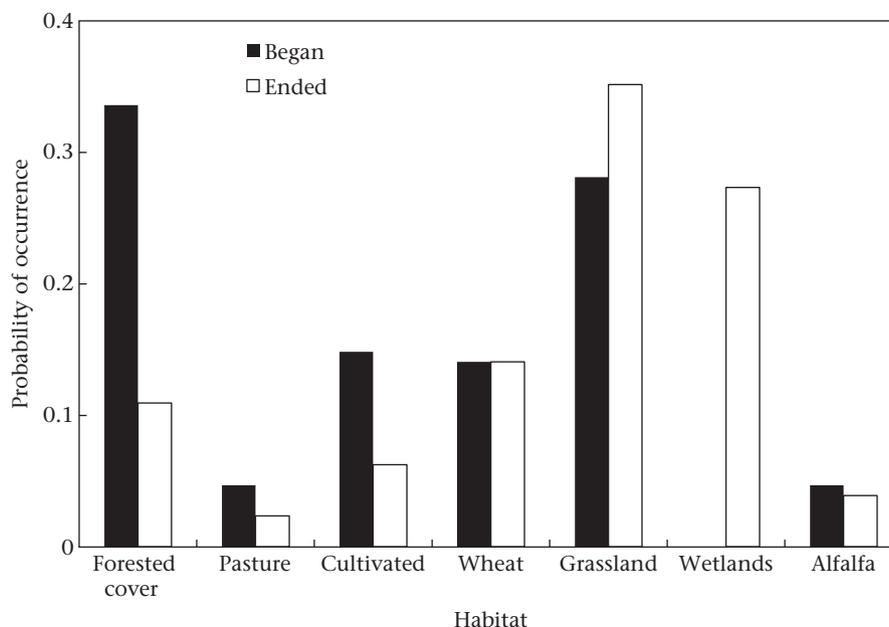
Analysis

We used ArcGIS 9.2 (ESRI, Inc., Redlands, CA, U.S.A.) and 2001 National Land Cover Data (Homer et al. 2007) to analyse available land cover. We field verified individual habitats and annual land use changes (i.e. grasslands placed into production, crop rotations, wetland condition) using GPS and created a unique digitized map for each summer. We classified forested, grassland, wetland and wheat as cover habitats, and pasture, cultivated (corn and soybeans) land, alfalfa and development (including roads) as noncover habitats. We calculated distance from the beginning of a chase or hunt to the nearest habitat patch of each habitat type, and determined the size (ha) of each habitat patch. To test for potentially confounding relationships, we evaluated collinearity between predictor variables using Pearson's correlation coefficient. When two variables were correlated ($r > |0.50|$), we retained the variable most relevant to white-tailed deer fawn survival based upon the literature (Vreeland et al. 2004; Rohm et al. 2007; Grovenburg et al. 2011, in press). Habitat variables included distance to and size (ha) of nearest patch of grassland and forested cover, wetland and wheat field. Additional variables included age of fawn, presence (or absence) of adult female and distance of chase. We included a categorical variable to determine whether pursuer (coyote or

human) influenced the outcome of a chase. We used MANOVA to test for relationships between fawn age, presence or absence of adult female, pursuer (human or coyote) and aggressive defence and predictor variables (habitat variables and distance of chase). We used chi-square analyses to test for differences in habitat type where the chase began and the final habitat type chosen by fawns relative to presence or absence of the parturient female, pursuer, and whether the fawn escaped or was captured. We used t tests to test for differences in group size when the mother was present, and distance of chase and predator group size (range 1–5 coyotes/humans) between fawns that escaped or were captured.

To determine the percentage of fawns that would have crossed into another habitat if they had fled in a random direction, we buffered fawn locations where chases began using the mean distance of flight for all fawns (276 m). We overlaid buffered chase starting points onto our digitized habitat map and generated a random direction of flight using ArcGIS. We then extended each random flight to the edge of the buffered area to determine whether the flight path crossed into a different habitat from the initial habitat where the chase began. For each fawn, we replicated random flights 100 times and calculated the average probability of crossing into another habitat for each fawn. We calculated the overall mean probability of crossing into another habitat based on random flight direction for all fawns and used a chi-square analysis to compare observed and expected flight probabilities.

We used logistic regression to determine effects of predictor variables on the outcome of a chase (fawn killed by a coyote, captured by field crew, or evaded capture). We posited 20 models of how the outcome of a chase might be influenced by predictor variables and used all measured variables in our models. We used Akaike's Information Criterion (AIC) to select the most parsimonious model and considered models differing by ≤2 ΔAIC units from the selected model as potential alternatives (Burnham & Anderson 2002). We used Akaike weights (w_i) as an indication of support for each model. Models ≤2 ΔAIC units from the best model were examined to determine whether they contained at least one parameter more than the best model but had essentially the same maximized log likelihood. In these instances, models with additional parameters were unsupported and noncompetitive (Burnham &

Figure 1. Probability that predator chases ($N = 128$) of white-tailed deer fawns began and ended in various habitats in north-central South Dakota, U.S.A., 2007–2009.

Anderson 2002); thus, we eliminated those models from consideration in our analyses. We used the Hosmer–Lemeshow goodness-of-fit test to determine model fit ($P > 0.05$; Hosmer & Lemeshow 2000). We used post hoc pairwise t tests to assess differences of habitat variables between capture and escape of fawns among top-ranked models, and conducted statistical tests using SAS version 9.2 (SAS Institute, Cary, NC, U.S.A.) while maintaining an experiment-wide error rate of 0.05.

RESULTS

We observed 45 coyote–fawn chases (19 in 2008, 26 in 2009) and conducted 83 human–fawn chases (49 in 2007, 22 in 2008 and 12 in 2009). Nineteen (42.2%) coyote–fawn and 42 (50.6%) human–fawn chases ended with capture of a fawn. Only 25.8% of 128 fawns used the closest escape cover and 78.8% (26 of 33) of those fawns were captured by predators. Conversely, 63.2% (60 of 95) of fawns that did not choose the first available escape cover eluded capture. Of 33 fawns using the closest escape cover, 23 (69.7%) were not accompanied by a parturient female. Most chases began in forested (33.6%) or grassland (28.2%) habitat and ended in grassland (35.2%) or wetland (27.3%) habitat (Fig. 1). During chases, approximately 70% (90 of 128) of fawns left their initial habitat and crossed into at least one other habitat, travelling in directions that differed significantly (chi-square test: $\chi_1^2 = 18.39$, $P < 0.001$) from random ($\overline{X} \pm SE$; $43.1 \pm 3.9\%$, range $0.00–87.1\%$, $N = 128$). Mean deer group size (when doe was present) was greater (t test: $t_{64} = 4.15$, $P < 0.001$) for fawns that escaped (6.0 ± 0.5 deer, $N = 37$) than for fawns that were captured (2.9 ± 0.5 deer, $N = 29$). Fawns also were more likely to escape (chi-square test: $\chi_1^2 = 5.39$, $P = 0.020$) when adults demonstrated aggressive defensive behaviour; 24 of 35 chases where the parturient female displayed aggression resulted in escape of the fawn. Distance of chase differed significantly (t test: $t_{126} = 2.54$, $P = 0.006$) between fawns that escaped (323.7 ± 30.3 m) and fawns that were captured (224.1 ± 24.2 m). Predator group size was similar ($t_{126} = -1.03$, $P = 0.305$) between fawns that escaped (2.2 ± 0.1 predators, $N = 67$) and fawns that were captured (2.4 ± 0.1 predators, $N = 61$).

Initial habitat where a chase began was similar for pursuer (coyote or human; chi-square test: $\chi_5^2 = 6.38$, $P = 0.271$); 68.9% (31 of 45) of coyote–fawn chases and 61.4% (51 of 83) of human–fawn chases began in forested cover or grasslands. Additionally, initial habitat where a chase began was similar relative to the presence or absence of does ($\chi_5^2 = 9.01$, $P = 0.109$); 73.1% (49 of 67) of chases with doe present and 57.4% (35 of 61) of chases with doe absent began in forested cover or grasslands. Initial habitat, however, differed for fawns that escaped and fawns that were captured ($\chi_5^2 = 27.92$, $P < 0.001$); 77.8% (28 of 36) of fawns that escaped were initially located in grasslands, whereas 62.8% (27 of 43), 66.7% (12 of 18) and 57.9% (11 of 19) of fawns that were captured were initially located in forested cover, wheat and cultivated land, respectively.

Final habitat where the chase ended was similar for pursuer (chi-square test: $\chi_2^2 = 1.22$, $P = 0.543$), but differed significantly relative to the presence and absence of a doe ($\chi_2^2 = 16.89$, $P < 0.001$) and whether fawns escaped or were captured ($\chi_6^2 = 54.30$, $P < 0.001$). Grasslands accounted for 44.4% (20 of 45) and 30.1% (25 of 83) of final habitats selected by fawns during coyote and human chases, respectively, whereas 33.3% (15 of 45) and 24.1% (20 of 83) of coyote and human chases, respectively, ended in wetlands. Fawns accompanied by does were more likely to flee to wetland (41.8%, 28 of 67) habitat, whereas fawns without does selected wetland habitat in 11.5% (7 of 61) of pursuits. Fawns selected nearest cover when fleeing 25.8% (33 of 128) of the time and were more likely (chi-square test: $\chi_1^2 = 15.63$, $P < 0.001$) to be captured when selecting the closest forested cover, grasslands or

wheat field than when selecting more distant cover habitat. Additionally, fawns fleeing to wetlands (94.3%, 33 of 35) and grasslands (60.0%, 27 of 45) were less likely to be captured, whereas those choosing forested cover (71.4%, 10 of 14), wheat (88.9%, 16 of 18) and cultivated land (100%, 8 of 8) were more likely to be captured.

Results of multivariate tests of differences in predictor variables relative to age of fawn were significant (Wilk's λ: $F_{615,1083} = 1.22$, $P = 0.002$). Distance to wetlands (MANOVA: $F_{41,86} = 2.15$, $P = 0.001$) decreased with fawn age, whereas distance to grasslands (MANOVA: $F_{41,86} = 4.57$, $P < 0.001$) increased with fawn age. Mean distance to wetlands for fawns 0–30, 31–60 and >60 days of age was 563.5 ± 62.7 m ($N = 87$), 397.9 ± 78.7 m ($N = 19$) and 317.9 ± 53.7 m ($N = 22$), respectively. Mean distance to grasslands for fawns 0–30, 31–60 and >60 days of age was 419.7 ± 58.0 m ($N = 87$), 498.94 ± 84.6 m ($N = 19$) and 634.8 ± 79.4 m ($N = 22$), respectively. Habitat characteristics and distance of chase also differed with presence or absence of adult females (Wilk's λ: $F_{15,112} = 3.87$, $P < 0.001$). Distance to forested cover (MANOVA: $F_{1,126} = 6.82$, $P = 0.010$), patch size of alfalfa ($F_{1,126} = 6.18$, $P = 0.014$) and distance of chase ($F_{1,126} = 22.76$, $P < 0.001$) increased with presence of parturient female (Fig. 2a, b). Habitat characteristics and distance of chase were not affected by whether fawns were pursued by humans or coyotes (Wilk's λ: $F_{14,113} = 0.65$, $P = 0.814$). Habitat characteristics and distance of chase, however, differed with aggression of adult deer (Wilk's λ: $F_{14,51} = 2.70$, $P = 0.005$). Aggression by adult deer towards both humans and coyotes was more likely with greater distance to grasslands (MANOVA: $F_{1,64} = 9.27$, $P = 0.003$), forested cover ($F_{1,64} = 5.21$, $P < 0.026$) and
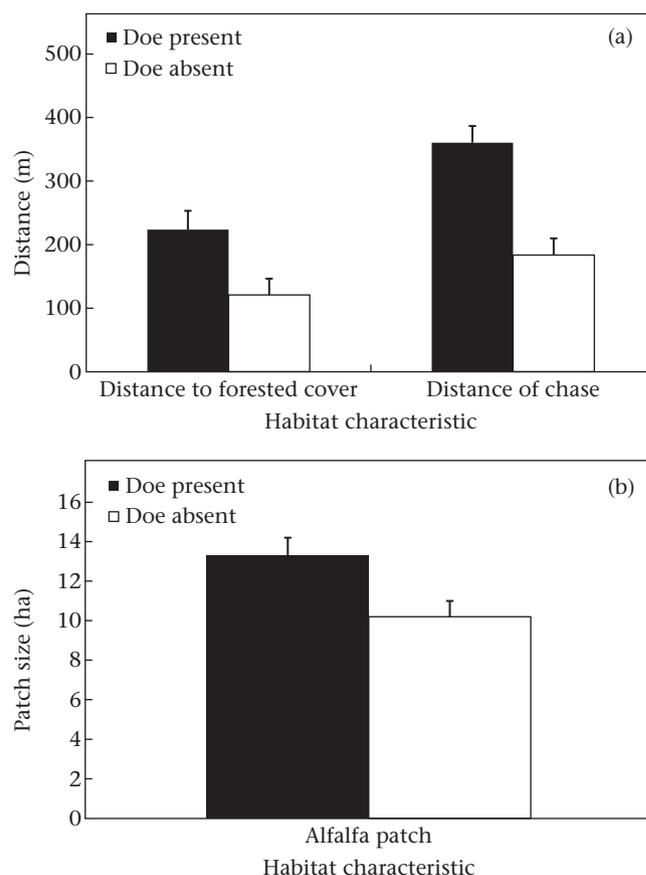
Figure 2. Mean + SE significant habitat characteristics (distance (a); patch size (b)) during fawn–predator chases for presence ($N = 66$) and absence ($N = 62$) of parturient female white-tailed deer in north-central South Dakota, U.S.A., 2007–2009.

wetlands ($F_{1,64} = 7.64$, $P = 0.008$) and with decreasing distance to wheat ($F_{1,64} = 14.53$, $P < 0.001$; Fig. 3a). Additionally, aggression was associated with larger patches of forested cover (MANOVA: $F_{1,64} = 7.51$, $P = 0.008$) and with smaller patches of cultivated land ($F_{1,64} = 7.17$, $P = 0.009$; Fig. 3b).

We initially considered two models, $D_{wet} + D_{grass} + D_{wheat}$ and $D_{wet} + D_{grass} + D_{wheat} + Doe$, as supported by the data for estimating the influence of predictor variables (habitat characteristics and distance of chase) on probability of capture of fawns (Table 1). Model $D_{wet} + D_{grass} + D_{wheat}$ had supporting weight of evidence 2.46 times greater than the second best model (Table 1). Model $D_{wet} + D_{grass} + D_{wheat} + Doe$ differed by only a single variable from the top model and had approximately (difference of 1.06%) the same maximized log likelihood; therefore, we eliminated this model from consideration. Logistic odds ratios from the top-ranked model indicated that the odds of being captured were 1.023 (95% CI = 1.009−1.037) times greater for each 1 m increase in distance to wetlands and 1.005 (95% CI = 1.001−1.009) times greater for each 1 m increase in distance to grasslands (Fig. 4). Additionally, odds ratios indicated that the odds of being captured were 0.991 (95% CI = 0.983−0.999) times less for each 1 m increase in distance to wheat. Indeed, mean distance to wetlands (t test: $t_{126} = -8.72$, $P < 0.001$) and distance to grasslands ($t_{126} = -8.44$, $P < 0.001$) were greater for fawns that were captured, while mean distance to wheat was less ($t_{126} = 9.64$, $P < 0.001$) for captured fawns (Fig. 5).
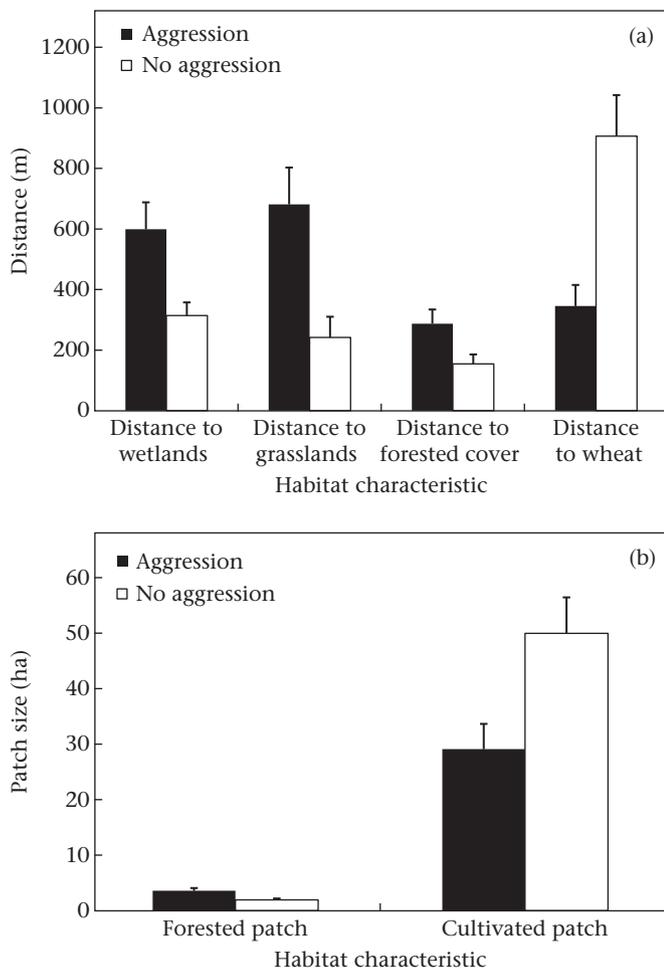
Table 1
Top-ranked a priori logistic regression models to determine the influence of predictor variables on capture of white-tailed deer fawns during predator chases in north-central South Dakota, U.S.A., 2007–2009

Model covariates	K*	Log likelihood	AIC†	ΔAIC‡	w§
$D_{wet} + D_{grass} + D_{wheat}$	4	16.09	24.09	0.00	0.59
$D_{wet} + D_{grass} + D_{wheat} + Doe$	5	15.92	25.92	1.83	0.24
$D_{wet} + D_{grass} + D_{wheat} + Doe + Age$	6	14.71	26.71	2.62	0.16
$D_{wet} + D_{grass} + D_{wheat} + D_{chase}$	5	21.94	31.94	7.84	0.01
$D_{wet} + D_{grass} + D_{wheat} + D_{fc}$	5	32.53	42.53	18.44	0.00

Distance to wetlands (D_{wet}), grasslands (D_{grass}), wheat (D_{wheat}) and forested cover (D_{fc}); distance of chase (D_{chase}); doe present (Doe); fawn age (Age).
 * Number of parameters.
 † Akaike's Information Criterion (Burnham & Anderson 2002).
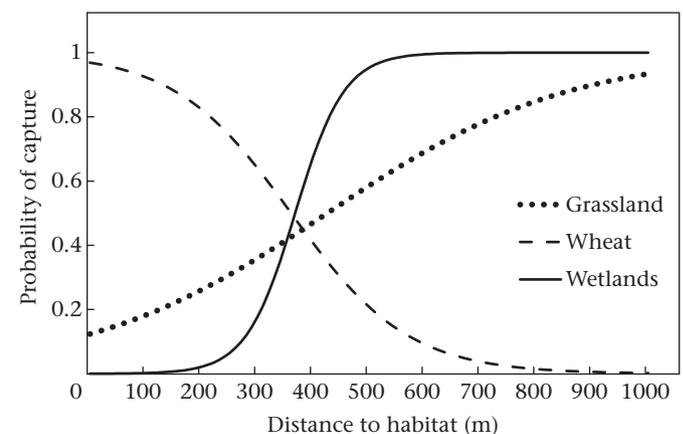 ‡ Difference in AIC relative to minimum AIC.
 § Akaike weight (Burnham & Anderson 2002).

Predictive capability of the final model was acceptable (Hosmer−Lemeshow goodness-of-fit test: $\chi_7^2 = 1.08$, $P = 0.993$).

DISCUSSION

The likelihood of a white-tailed deer fawn escaping predation was influenced by a number of antipredator behaviours and characteristics, including deer group size, aggressive defence by females and initial habitat and distance to escape cover, which was modified by presence of parturient females. Therefore, fawn selection of the closest escape cover may have been influenced by the presence of the parturient female. Vertical height and density of understory vegetation differed between cover types in the study area (Grovenburg et al. 2010), offering varying degrees of concealment. As a result, the type of cover selected by fawns when fleeing from predators was more important to their successful escape than was selecting for the closest cover.

Our hypothesis that presence of the parturient female would influence selection of escape cover and subsequent capture of fawns was supported by our analyses; presence of parturient females resulted in longer chases, selection of wetland habitat for escape cover and greater probability of escape. Lingle & Pellis (2002) documented that older white-tailed deer fawns (5−9 months of age) always flee when pursued or attacked by coyotes and those that survive do so by outrunning coyotes. Contrary to our findings, Patterson & Messier (2000) documented that mean distance of chases of deer during winter did not differ between successful chases (279 m) and unsuccessful chases (314 m);

Figure 3. Mean + SE significant habitat characteristics (distance (a); patch size (b)) during fawn−predator chases for aggressive ($N = 35$) and nonaggressive ($N = 31$) defensive behaviour by parturient female white-tailed deer in north-central South Dakota, U.S.A., 2007−2009.

Figure 4. Capture probability of white-tailed deer fawns during predator chases ($N = 128$) as a function of distance to wetlands, grasslands and wheat fields in north-central South Dakota, U.S.A., 2007−2009.
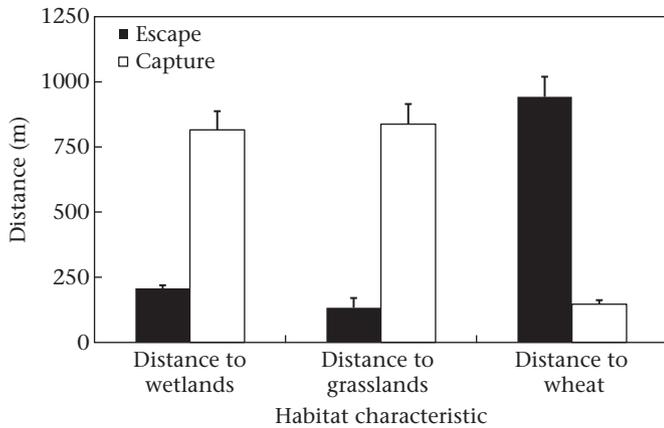
Figure 5. Mean + SE significant habitat characteristics (from logistic modelling) during predator chases between escape ($N = 67$) and capture ($N = 61$) of white-tailed deer fawns in north-central South Dakota, U.S.A., 2007–2009.

however, fawns in Patterson & Messier's study most likely approached the size of adult deer at that time of year. When fawns were accompanied by a parturient female, longer chases directed towards wetland habitats probably allowed the fawns to reach quality cover and reduced the coyotes' ability to catch them.

Defence of fawns by females increases the fawns' probability of survival (Lingle et al. 2005), and mule deer and white-tailed deer have been documented cooperating with conspecifics to defend fawns (Lingle & Pellis 2002; Grovenburg et al. 2009). Social and aggressive defensive behaviour tends to occur in animals inhabiting open habitats (Jarman 1974; Lingle et al. 2005). Indeed, Grovenburg et al. (2009) hypothesized that white-tailed deer inhabiting the relatively open habitat in the northern Great Plains may have modified their behaviour to that of the closely related mule deer, which is adapted to these more open habitats (Lingle et al. 2005).

The relationship between fawn survival and their proximity to wetlands and grasslands may be explained, in part, by antipredator behaviour of the species. Availability of quality bed sites is important for younger fawns (Huegel et al. 1986; Grovenburg et al. 2010), whereas proximity to escape cover is important for older fawns exhibiting greater activity (Rohm et al. 2007). In general, white-tailed deer fawns transition from 'hider' to 'follower' behaviour with increasing age (Nelson & Woolf 1987; Schwede et al. 1994), which corresponded to a decrease in distance to wetlands and an increase in distance to grasslands with fawn age during our study. However, increased distance to grasslands during late summer indicates that grasslands are not as important to fawns with increased mobility; fawns show a strong preference for grasslands until mid-July, and summer survival is positively influenced by greater numbers of grassland patches, in addition to more wetland patches, available within fawn home ranges (Grovenburg et al. 2012, in press).

Interestingly, we documented an increased probability of capture for fawns fleeing to forested cover. Rohm et al. (2007) documented increased fawn survival associated with large patches of forested cover (>5.0 ha). In our study area, however, forested patches were small (0.36 ha), highly fragmented, linear in shape and mainly composed of tree plantings and shelterbelts (Smith et al. 2002). In this region, forested patches provide minimal cover and are associated with higher fawn mortality (Grovenburg et al., in press). Similarly, when pursued, closer proximity to fields of wheat reduced the probability of escape by fawns. Vertical height of understory vegetation in wheat was approximately 20% less than in grasslands, providing less cover and concealment (Grovenburg et al. 2010). Additionally, during chases in wheat, we observed

the formation of trails following the passage of the fawn. Coyotes pursuing fawns into wheat used these newly created trails, enhancing the ease of pursuit and capture of fawns.

Coevolution of predators and prey has produced an impressive array of morphological and behavioural characteristics that enhance survival and reproductive success (Bertram 1978; Harvey & Greenwood 1978). Juvenile ungulates are generally the age class most vulnerable to predation, show high year-to-year variation in survival rates, and are often the critical component in herbivore population dynamics (Gaillard et al. 2000). Because of fragility, cognitive factors and naiveté, death from predation remains the primary cause of mortality for young ungulates (Barber-Meyer & Mech 2008). Our results demonstrate that survival of fawns also is affected by predator evasion strategies once a fawn is detected and pursued by a predator; the success of which is modified by available habitat and presence of the parturient female. Escape behaviour of fawns was positively influenced by the presence of a parturient female, the parturient female's aggressive defence and the choice of wetland habitat as escape cover. Predator evasion strategies that are beneficial are most likely constrained as wetland and grassland habitats are being rapidly converted to other land uses across the Midwestern United States (Grovenburg et al. 2010). How the loss of this important habitat may modify selective pressures on predator evasion strategies remains to be determined.

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