Columbian ground squirrels (*Spermophilus columbianus*) usually copulate underground in a burrow. Underground copulations might be associated with two nonexclusive benefits: reducing probability of predation during copulation and reducing interference by conspecific males. We tested whether either of these benefits was involved in determining if the copulation site was underground or aboveground. In 2006 and 2007, we obtained detailed information on the copulatory behavior and social interactions of free-ranging individuals in southwestern Alberta, Canada. During the 3-week annual breeding period, we also recorded the activity of predators of Columbian ground squirrels such as ravens, foxes, and hawks. Squirrels that lived on the periphery of the population were more susceptible to predation than squirrels in the center. Despite this risk, aboveground copulations usually occurred on peripheral territories. In addition, aboveground copulations were not further removed in time from predator attacks or sightings than underground copulations. Copulations that occurred aboveground were sometimes disrupted by previous mates of the estrous female. Probability that copulation would occur aboveground increased when the density of reproductive males around an estrous female was low. Our results suggest that although underground copulations protect individuals from predation, male–male competition for females and interference with copulations have been more important than predation in determining copulatory sites for Columbian ground squirrels in our study population.

Key words: Columbian ground squirrel, copulation, *Corvus corax*, local density, mating, prairie dog, predation, raven, red-tailed hawk, *Spermophilus columbianus*
mutually exclusive and testing them requires detailed information on both mating behavior and predator risk as breeding occurs.

Foraging aboveground from dawn until dusk, Columbian ground squirrels (Spermophilus columbianus) are burrowing, colonial rodents (e.g., Betts 1976; Murie 1995). Columbian ground squirrels usually copulate underground in a burrow, but occasionally copulate aboveground (Manno et al. 2007; Murie 1995). During a 3-week mating period, females live in philopatric kin clusters that are overlapped by a territorial reproductive male (usually ≥4 years old—King and Murie 1985; Manno 2008). Younger, subordinate males (2–3 years old) usually do not maintain a territory, but are physically able to reproduce and sometimes obtain copulations. Females mate with multiple males during their single annual day of estrus, which occurs 2–12 days after emergence from hibernation in April (Betts 1976; Murie 1995); estrous females may solicit copulations with their territorial male, adjacent territory holders, and subordinate nonterritorial males (Manno et al. 2007). The 1st male to mate with a female (usually the nearest territorial male) has sperm precedence (Hare et al. 2004; Murie 1995) and may mate guard via postcopulatory vocalizations, fighting with approaching males, and hostile behavior toward the female as she attempts to flee the copulatory site (Manno et al. 2007).

Columbian ground squirrels are prey for myriad terrestrial and aerial predators during April–May, including mustelids (Mustela), northern goshawks (Accipiter gentilis), red-tailed hawks (Buteo jamaicensis), and ravens (Corvus corax—reviewed by Elliott and Flinders 1991; see also Murie 1992). Thus, predation pressure may potentially influence mating location. Individuals on the periphery of a population are expected to be especially vulnerable to predation because this is where predators 1st appear, because fewer squirrels are available on the periphery to detect predators, and because alarm call warnings increase as a predator moves toward the center of the population (Brown and Brown 1987; Hamilton 1971; Hoogland 1981; Hoogland et al. 2006; Manno 2007). If risk of predation is the primary factor determining the site of copulation, then the likelihood that copulation will occur aboveground should decrease when a mating pair is on the periphery of the population rather than the center, particularly during periods of heightened predator activity.

In contrast, if male–male competition for females and interference with copulations are the primary factors influencing mating site, then the likelihood that copulation will occur aboveground should decrease in areas where presence of conspecifics and competition for mates are heightened. Increased competition should occur when the mating pair is in the center of the population rather than on the periphery, because more reproductive males should be present near the estrous females in central areas. At the periphery of the site, however, the density of individuals is usually decreased, potentially leading to decreased competition and reduced pressure to mate underground. Thus, the hypotheses considered here lead to distinct predictions that can be used to assess the relative impacts of predation and intraspecific competition on the locations of copulations by S. columbianus.

Materials and Methods

Study population.—From April to July in 2006 and 2007, we observed free-ranging Columbian ground squirrels of known age and matrilineal genealogy at a hill called DOT in Sheep River Provincial Park, Alberta, Canada (50°38′N, 114°38′W, elevation 1,500 m above sea level). All squirrels were trapped 1–2 days after they emerged from hibernation, ushered into a cloth bag, weighed, and fitted with numbered metal fingernail ear tags (National Band and Tag Co., Newport, Kentucky) for long-term identification. For visual identification from a distance, we painted each animal with a unique symbol using black hair dye (Lady Claird Hydrence; Proctor and Gamble, Stamford, Connecticut). During 2006–2007, the 2.5-ha site was inhabited by 14–17 adult males (≥2 years old), 41–48 adult females (≥2 years old), and 20–40 yearlings of both sexes, for a density of 32.8–39.2 individuals/ha and 23.2–24.8 adults/ha.

We considered males to be reproductive if they exhibited a pigmented scrotum and large, descended testes at the time of capture. We trapped females several additional times during the 3-week breeding period and examined their vulvar condition (i.e., fully opened) to determine whether they would be in estrus (Michener 1984; Schwagmeyer and Brown 1983). Our methods followed guidelines approved by the American Society of Mammalogists for animal care and use (Gannon et al. 2007), and field methods were approved by the Institutional Animal Care and Use Committees at Auburn University and the University of Calgary.

Behavioral observations.—Breeding extended from the 3rd week of April to the 1st week of May but, as for other ground-dwelling sciurids (e.g., Davis 1982; Hoogland 1995; Lacey et al. 1997; Manno 2007; Schwagmeyer 1990; Sherman 1976, 1989), each female was sexually receptive for only a few hours on a single day. When a social interaction occurred (e.g., chasing, fighting, sniffing, allogrooming, playing, or females “leading” males), we used all-occurrence sampling (Altmann 1974) to record the identities of the animals involved. We then scored individuals that chased conspecifics or remained at the location of a fight as victorious in the interaction (Hoogland 1995; Lacey and Wieczorek 2001), and recorded the time and location of the interaction (ascertained from a 10 × 10-m grid placed with flags on the ground—Manno 2008).

Copulations occasionally occurred aboveground and were therefore observed directly (Murie 1995). We used established methods to infer underground copulations from the following aboveground diagnostic behaviors: female movements to elicit social interaction with males and to “lead” them into prospective copulatory burrows; immurgence of a male and female in the same burrow on the night before the female exhibited a fully opened vulva; other immersions of both partners into the same burrow, where they remained for at least several minutes; self-grooming of genitals by both partners upon later emergence, which was sometimes accompanied by dust-bathing; a postcopulatory “mating call” by the male; and other behaviors indicating that males were mate guarding, such as chasing the female into a burrow, sitting on or “herding” the
female into that burrow as she attempted to flee the area, and fighting with other males (Hoogland 1995; Lacey and Wieczorek 2001; Lacey et al. 1997; Manno et al. 2007; Murie 1995). Aboveground copulations also featured all or most of these behaviors.

Detecting predators.—Using 10 × 42 binoculars and 4-m-high towers, we followed the methods of Hoogland (1995) and Sherman (1976) to observe marked individuals from dawn until dusk every day. Thus, we documented the frequency of sightings for predators of Columbian ground squirrels and the number of predator attacks at the study site. An attack occurred when a predator moved to capture a particular individual, via either a “swoop” close to the ground (including landing on the ground) for aerial predators or a “pounce” toward a squirrel by terrestrial predators. Predation events occurred when the predator was successful in killing a squirrel during an attack. When a predator of ground squirrels was seen at the site but no attack occurred, we recorded our sighting of the predator. We also checked the colony daily for signs of subterranean predation events by animals such as badgers (Taxidea taxus) and weasels (Mustela; e.g., fresh diggings or enlargement of burrows, predators emerging from burrows, or suddenly absent individuals—Hoogland 1995; Hoogland et al. 2006; Murie 1992; Sherman 1976). We recorded the location, time of day, and an anecdotal description for all predator sightings and attacks (Altman 1974; Hoogland et al. 2006; Sherman 1976). Thus, we were able to measure predation in terms of number of predation events, attacks, or sightings per day, as well as the time elapsed since each of these types of events last occurred (Sherman 1976). Unfortunately, we usually could not determine whether predator sightings resulted from the observations of different individuals or the same individual at different times (Hoogland et al. 2006). We therefore considered all predator sightings to be independent incidents.

Estimating reproductive competition.—Operational sex ratio is the number of breeding males per estrous female. During the breeding period, 1–6 females per day were estrus. Using this variation, we calculated a daily operational sex ratio for our study population that served as a measure of intraspecific variation, we calculated a daily operational sex ratio for our study population that served as a measure of intraspecific variation, we calculated a daily operational sex ratio for our breeding period, 1–6 females per day were estrus. Using this daily sex ratio, we determined whether a female was in estrus the day of copulation, and position of the copulation (peripheral or central territory). We also included the following independent variables related to mate competition: order of copulation in males, weight and age of the consort male and estrous female, operational sex ratio, and number of males that were neighboring to or familiar with the estrous female. Weight and age of males were included because young or small males may be unable to monopolize heavy females with breeding experience (Hoogland 1998), leading to an increased chance of interference by male competitors or the inability to bring a female underground where she will be easier to guard after copulation. Copulation order was included because, given the pattern of 1st male sperm precedence in this species (Hare et al. 2004; Murie 1995), males that copulate early in a female’s series of matings may be more likely to pursue unmolested copulations underground (but see Tryjankowski et al. 2007).

Because our study yielded multiple observations of the same individuals in the same or different years, we used a mixed-model regression that treated the identity of individuals as a random variable, along with the date and year of the copulation. We examined our data for significant interactions (i.e., colinearity) among independent variables and tested for such influences via interaction terms. We then generated all possible models and determined the best-fit model by minimizing Akaike’s information criterion corrected for small sample sizes (AICc—Burnham and Anderson 1998), removing any interactions or variables that negatively impacted the fit of the data to the model. Thus, our multivariate approach augments our univariate analyses by allowing us to determine the relative influence of independent variables on the dependent variable.

For seemingly similar analyses, sample sizes sometimes varied because we did not have complete data on every individual in the sample required for a particular comparison. The number of individuals in the sample is indicated by n. Values are presented as means ± 1 SE. All P-values result from 2-tailed tests (α = 0.05).
RESULTS

We observed the complete series of matings for 56 females (28 in each year). These females copulated with an average of 2.8 ± 0.2 males (n = 151 copulations). About 6% (9/151) of the copulations took place aboveground, with the rest occurring underground in a burrow. No female copulated aboveground more than once.

We routinely observed predator attacks and male interference with copulations during the 3-week breeding period, with these events sometimes occurring in rapid succession. For example, on 1 May 2007 at 0900 h (Mountain Standard Time), a reproductive male on a peripheral territory copulated aboveground with an estrous female, the male having been attacked and nearly killed by a raven only 19 min before the copulation. A minute or so into the copulation, a male that had mated with the estrous female an hour earlier attacked the consort male and interrupted the mating pair. The female left the area during the ensuing agonistic interactions and, hence, the copulation with the focal male was not completed.

During the breeding periods of 2006–2007, we observed predators on 120 occasions (Table 1). Across years, ravens were both the most commonly observed (64 [53%] of 120 sightings) and most successful predators (6 [30%] of 20 attacks yielded prey). Red-tailed hawks were the only predator to attack ground squirrels during breeding in 2007 (8 [53%] of 15 sightings involved attacks), although none of these attacks were successful. The 2006 breeding season featured significantly more predator sightings (G = 34.9, n = 120, d.f. = 1, P < 0.001), attacks (G = 19.1, n = 43, d.f. = 1, P < 0.005), and successful predation events (G = 13.8, n = 8, d.f. = 1, P < 0.01) than the 2007 breeding season. We never found evidence of underground predation.

Individuals living on peripheral territories were more vulnerable to predation than individuals living in central territories (Fig. 1). Specifically, all 6 individuals captured by ravens as well as the single individuals captured by a lynx (Lynx canadensis) and red fox (Vulpes vulpes) lived on peripheral territories (G = 13.8, n = 8, d.f. = 1, P < 0.01). The red fox victim was a 2-year-old scrotal male; the lynx victim was a nonreproductive yearling female. Other victims were killed before we were able to capture them and hence they were of unknown age and sex. However, we suspect that these individuals may have been breeding males that had recently immigrated to the population because they did not appear from our observations to have ear tags.

More than two-thirds of the aboveground copulations (7 [77.8%] of 9 copulations) occurred on peripheral territories. Indeed, the likelihood that copulation would occur aboveground was significantly higher on the periphery than in the center of the population (G = 16.6, n = 151, d.f. = 1, P < 0.01; Fig. 2). The percentage of copulations that occurred aboveground also was significantly related to the local density of males around an estrous female (the number of reproductive males that neighbored the estrous female). Overall, 14.0% ± 8.6% of copulations occurred aboveground when females had ≤3 neighboring males versus 0.0% ± 0.0% of copulations

<table>
<thead>
<tr>
<th>Predator</th>
<th>2006</th>
<th></th>
<th></th>
<th>2007</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No. sightings</td>
<td>No. attacks</td>
<td>No. predations</td>
<td>No. sightings</td>
<td>No. attacks</td>
<td>No. predations</td>
</tr>
<tr>
<td>Black bear</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Coyote</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Golden eagle</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lynx</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Northern goshawk</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Northern harrier</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Prairie falcon</td>
<td>16</td>
<td>9</td>
<td>0</td>
<td>9</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Raven</td>
<td>55</td>
<td>20</td>
<td>6</td>
<td>9</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Red fox</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Red-tailed hawk</td>
<td>7</td>
<td>0</td>
<td>0</td>
<td>15</td>
<td>8</td>
<td>0</td>
</tr>
<tr>
<td>Unidentified hawk</td>
<td>4</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>91</td>
<td>35</td>
<td>8</td>
<td>29</td>
<td>8</td>
<td>0</td>
</tr>
</tbody>
</table>

**TABLE 1.**—Predator sightings, number of predator attacks, and number of successful predation events during the 3-week breeding season (April–May) for Columbian ground squirrels (Spermophilus columbianus) in southwestern Alberta, Canada. Data are from observations of predators completed during 2006 and 2007.

![Observed versus expected frequencies of predation events on Columbian ground squirrels (Spermophilus columbianus) living in peripheral (left) and central (right) territories. Data are from 8 predation events observed during the breeding seasons of 2006 and 2007; expected numbers are based on the assumption that predation was equally likely for individuals on central and peripheral territories. Peripheral territories were located at the edge of the study colony and were not surrounded by other territories.](https://academic.oup.com/jmammal/article-abstract/89/4/882/870929/1)

**FIG. 1.**—Observed versus expected frequencies of predation events on Columbian ground squirrels (Spermophilus columbianus) living in peripheral (left) and central (right) territories. Data are from 8 predation events observed during the breeding seasons of 2006 and 2007; expected numbers are based on the assumption that predation was equally likely for individuals on central and peripheral territories. Peripheral territories were located at the edge of the study colony and were not surrounded by other territories.
with >3 neighboring males \((G = 33.1, \, n = 151, \, d.f. = 1, \, P < 0.001; \text{Fig. 3})\). Thus, females that copulated aboveground had fewer neighboring males than females that never copulated aboveground \((U = 791, \, d.f. = 54, \, P < 0.05)\).

With regard to predation, aboveground copulations were not significantly further removed in time than underground copulations from the most recent predator sighting \((451.3 \pm 153.8 \text{ min when aboveground versus } 481.9 \pm 26.4 \text{ min; } U = 697, \, d.f. = 149, \, P = 0.66)\) or attack \((1,102.8 \pm 330.6 \text{ min when aboveground versus } 1,029.7 \pm 99.3 \text{ min; } U = 737, \, d.f. = 149, \, P = 0.45)\). Number of predator sightings or predator attacks did not differ significantly between days when an aboveground copulation occurred and days when no aboveground copulations occurred \((U = 682, \, d.f. = 149, \, P = 0.86 \text{ and } U = 749, \, d.f. = 149, \, P = 0.40, \text{ respectively})\). Although the 2006 breeding period featured 3 times as many predator sightings and 4 times as many predator attacks as the 2007 breeding period \(\text{(Table 1)}\), two-thirds of the aboveground copulations \(\text{we witnessed} (6 \, [67\%] \text{ of } 9 \text{ copulations}) \text{ occurred in } 2006\). None of the individuals that copulated aboveground were attacked by predators while mating \((0 \, [0\%] \text{ of } 9 \text{ individuals})\).

With regard to interference by conspecifics, we never observed a nonconsort male enter the burrow where a pair was believed to be copulating \((0 \, [0\%] \text{ of } 142 \text{ copulations})\). In contrast, one-third of aboveground copulations \(3 \, [33\%] \text{ of } 9 \text{ copulations}) \text{ were disrupted by males that mated previously with the estrous female; this difference was significant} \((G = 36.0, \, n = 151, \, d.f. = 1, \, P < 0.001)\). In all instances of male interference, the previous sexual partner of the estrous female harassed the consort male by instigating a hostile interaction as the consort male mounted the female. The mating pair then split as the males fought, after which the female left the area.

Multivariate logistic regression also revealed that position in the population \(\text{(central versus peripheral)}\) and number of neighboring reproductive males \(\text{were significantly related to where copulation occurred} \text{(Table 2a)}\). AIC\(_C\) analyses yielded similar results; the best-fit model included position in the population and number of neighboring males, both of which had a significant relationship with the dependent variable \(\text{(Table 2b)}\). The next 2 best-fit models that were within 5 points of the AIC\(_C\) for the best-fit model included only position in the population or number of neighboring males. None of the interaction effects \((n = 5)\) had a significant relationship with the dependent variable \(\text{(all } P > 0.05)\).

**DISCUSSION**

Our results indicated that individuals living on peripheral territories were more likely to be preyed upon than individuals living on central territories; aboveground copulations were more likely to occur at the periphery of the population; aboveground copulations were sometimes disrupted by previous mates of the estrous female, and the probability that a mating would occur underground increased when the local density of reproductive males was high. Examination of these data suggests that predation and interference by conspecifics were potentially important influences on the location of copulations by members of the study population.

If risk of predation is the primary factor determining the site of copulation, then the likelihood that copulation will occur aboveground should decrease when predation risk is heightened. Our results did not support this prediction. Under the predation hypothesis, aboveground copulations should have occurred on central territories, where predation is less frequent. However, aboveground copulations were more common on the
periphery of the population. Further, if predation is important, squirrels should have avoided underground copulations during periods of high predator presence, including just after a predator attack or sighting. However, underground copulations appeared to be no further removed temporally from such events than underground copulations. Underground and aboveground copulations also were equally common in both years of our study, even though 2006 featured a much higher rate of predator activity. We acknowledge that predation may be a factor in determining the overall prevalence of underground copulations and that predation-related variation in the frequency of underground copulations may be evident among populations. Nevertheless, our results do not support the hypothesis that immediate risk of predation is the primary determinant of mating location.

In contrast, if male–male competition for females and interference with copulations are the primary factors determining the site of copulation for Columbian ground squirrels, then the likelihood that copulation will occur aboveground should decrease when risk for either is heightened. Our results supported this prediction. Although no mating pairs that copulated aboveground were attacked by predators, each such pair had their copulations disrupted by a previous mate of the estrous female. Indeed, aboveground copulations were significantly more likely to be disrupted than underground copulations. Estrous females never copulated aboveground when few neighboring males were present. Peripheral territories where aboveground copulations typically occurred featured decreased conspecific presence and, presumably, decreased competition for mates because they were not surrounded by other territories. Thus, the local density of males around an estrous female was related negatively to the likelihood that copulation would occur aboveground.

We emphasize that efforts to test these hypotheses in additional populations of Columbian ground squirrels and other species with varied frequencies of predation and copulation interference are important. In addition to assessing the generality of the relationships identified here, such comparative studies can exploit naturally occurring variation in population structure to explore determinants of mating location in greater detail. Therefore, our results may be applicable to other animals, particularly other mammals (Davis 1982; Möller and Birkhead 1989; Schwagmeyer 1990), but future research will be necessary to increase our understanding of why animals vary the locations of their copulations.

**Acknowledgments**

K. S. Wright provided excellent help in the field. F. S. Dobson provided insightful comments on the manuscript and partial funding for the data collection (United States National Science Foundation research grant DEB-0089473). This study was also funded by an Auburn University Graduate School research award to TGM. J. L. Hoogland trained 2 of us (TGM and LMD) in the field methods used for the study. Trapping and handling of animals was conducted under permits from Alberta Community Development and Alberta Sustainable Resource Development (Fish and Wildlife Division). Methods were approved by the Institutional Animal Care and Use Committees at Auburn University and the University of Calgary. Housing during the field research was provided by the University of Calgary’s R. B. Miller Field Station, and we particularly thank the Station Manager, J. Buchanan-Mappin, and the Station Director, E. Johnson.

**Literature Cited**


