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Territoriality and male reproductive success in arctic ground squirrels

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Although territorial defense is a common form of reproductive competition among male vertebrates, the exact reproductive consequences of this behavior are often poorly understood. To explore relationships between territoriality and reproductive success in a nongroup-living mammal, we quantified patterns of space use, mating success, and fertilization success for males in a free-living population of arctic ground squirrels (*Spermophilus parryii plesius*). Because litters of this species are sired almost exclusively by a female's first mate, we predicted that territory ownership would be associated with first access to estrous females. During the 2-week period when mating occurred, each male in the study population attempted to defend a distinct portion of the habitat, although the success of this defense varied among individuals. Twenty-six of 28 females monitored mated with the male on whose territory they resided. However, the majority of females observed throughout estrus (65%; *n* = 20) also mated with at least one other male, indicating that territory ownership was not associated with exclusive access to females. In contrast, territory ownership was significantly associated with first access to estrous females; 20 (71.4%) of 28 females mated first with the male on whose territory they resided. In this regard, the behavior of *S. parryii plesius* parallels that of socially monogamous birds in which territorial defense by males functions to deter extrapair copulations by females. Although territorial defense represents an important component of male reproductive success in arctic ground squirrels, other aspects of male behavior (e.g., the ability to dominate agonistic interactions on the day of a female's estrus) are also critical. We suggest that future studies of vertebrate mating systems will benefit by viewing such defense as only one of multiple axes along which conspecific males compete for access to females. *Key words:* extrapair copulation, ground squirrels, reproductive success, *Spermophilus parryii plesius,* territoriality. *[Behav Ecol 12:626–632 (2001)]*

Territorial defense by males is a conspicuous component of many vertebrate mating systems (Clutton-Brock, 1989; Davies, 1991; Ligon, 1999). For species in which each male defends an area occupied by one or more females, such defense is generally assumed to prevent reproductive competitors from gaining access to those females (Clutton-Brock, 1989; Emlen and Oring, 1977), thereby increasing the copulatory success of the territory owner relative to other males. Studies of sperm competition (e.g., Birkhead and Møller, 1992; Ginsberg and Huck, 1989; Møller and Birkhead, 1989), however, suggest that not all copulations are equally likely to result in offspring. As a result, both copulatory and fertilization success must be considered when evaluating the adaptive significance of male behavior, including territorial defense associated with mating.

Relationships between territorial defense and male copulatory and fertilization success have been examined for a number of avian species, frequently in the context of extrapair copulations in socially monogamous birds (e.g., Birkhead and Møller, 1992; Møller, 1990; Rodrigues, 1998). These studies have revealed that, in many species, male defense of a territory does not preclude the female resident on that territory from engaging in genetically effective copulations with other males (Birkhead and Møller, 1992). The well documented occurrence of extrapair fertilization suggests that male reproductive success must be influenced by more than just territory ownership, raising the possibility that factors such as dominance relationships among individual males or the reproductive interests of females are also important determinants of male success.

In comparison, the reproductive consequences of male territorial defense have received relatively little attention in mammals. Because social monogamy is rare among mammalian species (Clutton-Brock, 1989; Kleiman, 1977), a parallel literature on extrapair copulations has not developed. Although a number of studies have examined patterns of male fertilization success in group-living mammals in which adults of both sexes defend a common territory (e.g., black-tailed prairie dogs: Hoogland, 1995; European marmots: Goossens et al., 1998; dwarf mongooses; Keane et al., 1994), fewer data are available for mating systems in which the spatial distributions of opposite-sexed adults overlap but in which males and females do not form explicit social bonds. Because the latter type of system appears to be relatively common among mammals (Clutton-Brock, 1989), understanding patterns of copulatory and fertilization success in this context is critical to understanding the adaptive significance of territorial defense as a form of male reproductive competition.

The mating system of the arctic ground squirrel (*Spermophilus parryii plesius*) provides an ideal opportunity to investigate the effects of territorial defense on both male copulatory and fertilization success. During the approximately 2-week-long period each year when mating occurs, male *S. parryii plesius* defend territories on which multiple females reside (McLean, 1983). Individual females exhibit behavioral estrus on only one afternoon per year, and, while sexually receptive, a female mates with one to four different males (Lacey et al., 1997). Paternity analyses based on allozyme and DNA fingerprinting data indicate that >90% of young are sired by the first male with which a female mates (Lacey et al., 1997). This pronounced bias in fertilization success does not vary with differences in mating behavior (e.g., interval between succes-

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sive copulations); instead, the primary correlate of male fertilization success appears to be mating order (Lacey et al., 1997). As a result, males are expected to compete primarily for access to females that have not yet mated. If territorial defense by male *S. parryii plesius* functions as a form of reproductive competition, then this defense should be associated with access to unmated, estrous females. Specifically, a male should typically be the first to mate with the females resident on his territory.

To test this prediction, we monitored the copulatory success of males in a free-living population of *S. parryii plesius*. We observed individual females throughout behavioral estrus and quantified mating order and territorial status for each of a female's consorts. These data were then compared to the results of paternity analyses (Lacey et al., 1997) to determine if territory ownership is correlated with fertilization success. Here, we characterize the relationship between territorial defense, copulatory success, and paternity in *S. parryii plesius* and relate these data to patterns of male territorial defense in other mammals and in birds.

METHODS

Study population

We studied a population of *S. parryii plesius* located in the Kluane Game Sanctuary, Yukon, Canada (60°47′N, 137°40′W, elevation 650 m). The study site consisted of an open meadow bounded to the east by Bear Creek and on all other sides by dense vegetation that was not occupied by ground squirrels. Detailed descriptions of the site are provided in Lacey (1991) and Lacey et al. (1997). Typically, the 5-ha study site was inhabited by 15–25 adult male and 50–55 adult female ground squirrels, for a density of 13–16 adults per hectare.

We trapped members of the study population using National or Tomahawk live-traps ($16.5 \times 16.5 \times 48.0$ cm) baited with peanut butter. All ground squirrels residing on the study site were permanently marked with two numbered ear tags (Monel #1, National Band and Tag Company). To allow visual recognition of individuals during behavioral observations, each animal was also uniquely marked with black hair dye (Lady Clairol #124 natural blue-black). We conducted behavioral observations from 3-m high observation stands ($n = 9$) positioned around the perimeter of the study site. To facilitate data collection, the study site was gridded into 20-m squares, the corners of which were marked with orange surveyors' flags labeled with a Cartesian coordinate system.

We monitored territorial and reproductive behavior by males during 24 April–3 May 1988, 20 April–11 May 1989, and 23 April–1 May 1990. Animals in the study population began emerging from hibernation in mid-April, with the first males typically emerging 7–10 days before the first females (Lacey, 1991). Because male emergence was not synchronous, we did not begin recording behavioral data until approximately 1 week after emergence began, at which point most males had become active above ground. Females became sexually receptive on their third or fourth day above ground. Although individual females exhibited behavioral estrus on only 1 day of the active season (Lacey et al., 1997), mating activity in the study population continued for a period of about 2 weeks.

Male territorial defense

Definitions of territoriality frequently include both spatial and social criteria for territorial defense (reviewed by Kaufman, 1983; Maher and Lott, 1995). More specifically, definitions of territoriality often stipulate that individuals must (1) occupy at least partially non-overlapping portions of the habitat and (2) display aggressive defense of those areas (e.g., Jarman, 1974; Meier, 1992; Ostfeld, 1985). Because male *S. parryii plesius* have been characterized as territorial during the mating period (McLean, 1983), we used these criteria as a starting point for analyses of reproductive competition among males in our study population. To document the spatial distribution of males during the mating period, we used scan sampling (Altmann, 1974) to delineate the areas occupied by animals resident on the study site during 1988 and 1989. To reduce the distance over which animals were observed, we divided the study site into four non-overlapping sections, the boundaries of which were determined largely by the shape of the open meadow in which the ground squirrels resided. In general, two scan sampling periods per section were completed daily, typically between 1200 and 1900 h (0700–1200 h was used to assess the reproductive status of females; Lacey et al., 1997); a minimum of 2 h was allowed between successive sampling periods in the same section. During each sampling period, the locations of all animals (male and female) visible in that section of the study site were determined at 5-min intervals for a total of 25 min ($n = 6$ samples). Locations were recorded to the nearest meter; trials conducted using objects placed at known locations revealed this procedure to be accurate to within 2.5 m.

We conducted scan sampling on all days during the approximately 2-week-long period in which mating occurred. Because spatial relationships among males in other ground squirrel species are influenced by the presence of estrous females (e.g., Michener and McLean, 1996), the area occupied by each male in the study population was determined using only data collected on days when no females were in estrus. Specifically, for each section of the study site, we divided scan sampling sessions into those conducted on days when no females in that section were in estrus versus days when at least one female in that section was in estrus. Analyses of male spatial relationships on nonestrous days were based on data collected during 9.3 ± 4.9 (range = 4–20) 25-min scan periods distributed over 5.8 ± 2.5 (range = 3–12) days per male ($n = 16$ males).

For each male, we included all positional data recorded on nonestrous days in spatial analyses to maximize the probability of detecting spatial overlap between the sexes (see below). Analyses of positional data for five males resident on the study site in 1988 indicated that using a subset of positional data records (e.g., only first or last records from a 25-min observation period) reduced estimates of the area occupied by a male by a mean of $33.1 \pm 30.5\%$, leading to underestimation of the degree of overlap between opposite-sex individuals. Because no more than six positions per individual were recorded during each scan session and because numerous sampling periods were conducted over multiple days, we assumed that temporal dependence of positional data for an individual was limited. To prevent extreme outliers (e.g., occasional excursions from the home area) from biasing spatial relationships, we excluded the 5% of data points farthest from an animal's center of activity (arithmetic mean x and y coordinates) from our analyses. We analyzed spatial data using the minimum convex polygon option in the Ranges V software package (Kenward and Hodder, 1996); this method of quantifying the area used by an animal is the least sensitive to interdependence of successive data points (Hundertmark, 1997). Estimates of both the number of square meters occupied by a male and the percentage of overlap between areas occupied by different males were also generated using Ranges V.

We did not conduct scan sampling of male locations during the 1990 field season due to a shortage of observers. Instead, we estimated the area occupied by a male using the locations at which males were captured during the period between emergence from hibernation and the end of mating activity (4.7 ± 1.2 locations per male, median = 4, range = 3–6 trap records, $n = 10$ males). To assess the accuracy of this procedure, we compared trapping locations for males resident on the study site during 1988 and 1989 to minimum convex polygons for the same animals generated from scan sampling data. In all cases, trapping locations for an individual fell within the boundaries of that animal's area of activity as determined from scan data. Because trapping data tended to underestimate an individual's area of activity, spatial data from 1990 were used only to assign females to male territories for analyses of male reproductive success (see below); these data were not used to quantify spatial relationships among males on the study site.

We characterized social relationships among males using all-occurrence sampling (Altmann, 1974) of male–male encounters during the mating period. Specifically, we were interested in determining if males actively defended the areas on which they were resident. For all interactions observed, we recorded the identity of each participant and the location of the encounter. In addition, we recorded all occurrences of the following agonistic behaviors (Lacey, 1991; McLean, 1983): chases, fights, parallel runs, and squeal displays. For each interaction, we scored the participants as "dominant," "subordinate," or "undetermined" based on the behaviors observed. For example, individuals that were chased from an encounter site or that fled an encounter after a fight were considered subordinate. Conversely, individuals that chased conspecifics or that remained at the location of a fight were scored as dominant. Not all interactions generated clearly identifiable outcomes; relationships among males participating in these encounters were scored as undetermined.

Male-female associations

To determine if spatial relationships among males were associated with access to unmated females, it was first necessary to identify which females were resident in each male's area of activity. Although individual females visited areas occupied by several different males, each female appeared to be most closely associated with a single male. To quantify this association, we used both scan sampling data and the locations of females' burrows to assign individuals to specific male areas. For data from 1988 and 1989, we calculated the center of activity (arithmetic mean x and y coordinates) for each female from positional data obtained from scan sampling conducted on pre- and postestrous days (6.8 ± 5.5 postestrous days per female, range = 0–15, $n = 30$ females, data from 1988 and 1989 combined); these values were superimposed onto maps of male spatial distributions, and each female was assigned to the male on whose area her center of activity was located. The location of each female's burrow was then superimposed onto male distribution maps, and this position was used to assign individuals to male areas. Comparisons of spatial relationships generated by these procedures revealed no discrepancies between assignments based on scan sampling data and those based on burrow locations ($n = 38$ females). No scan sampling data were obtained in 1990 (see above), and thus only the locations of females' burrows were used to assign individuals ($n = 18$ females) to male territories for that year.

Male copulatory success

A detailed description of the procedures used to document mating behavior is given in Lacey et al. (1997). Briefly, we captured pre-estrous females each morning and examined their external genitalia to determine which individuals were likely to be sexually receptive later that day. We observed sexually receptive females continuously during the afternoon and evening of estrus; observations typically began at 1400 h (about 3 h before a female's first copulation) and continued until all focal females had entered their home burrows for the night (at about 2100 h). Because arctic ground squirrels frequently mate underground, copulations were detected using five behavioral criteria developed during observations of above-ground matings (see also Hoogland, 1995; Hoogland and Foltz, 1982; Sherman, 1989). By monitoring individual females throughout behavioral estrus, we were able to determine the identity of each of a female's mates, as well as the order in which each male copulated with a given female.

Data analysis

Behavioral and spatial data from only a single estrous period per female were included in this study; as a result, each female represented an independent sample of reproductive behavior. In contrast, because some males were observed mating with more than one of the females included in this study, assumptions of statistical independence among estrous periods may not have been strictly met. Previous work by Lacey et al. (1997), however, has revealed no reproductively significant variation in male copulatory behavior, suggesting that analyses of behavioral data were not confounded by the identity of a female's mate(s). Because small sample sizes for most analyses precluded accurate determination of whether data were normally distributed (Wilkinson, 1986), we used nonparametric procedures to examine spatial and social relationships among individuals. Statistical analyses were performed using Statistica 5.1 (StatSoft, Inc.). Throughout the text, means are reported ±1 SD.

RESULTS

Spatial relationships among males

Spatial distributions were determined for 16 males ($n = 5$ in 1998; $n = 11$ in 1989) based on scan sampling data collected on nonestrous days during the mating period. The mean number of visual fixes used to map spatial relationships among these animals was 49.0 ± 23.9 (range = 23–82) in 1988 and 26.5 ± 13.0 (range = 6–41) in 1989. Minimum convex polygons for these individuals indicated that, during the mating period, each male in the study population occupied a discrete portion of the study site, the majority of which was not shared with other males (Figure 1). The mean area occupied by an individual was 1415.3 ± 730.8 m^2 (range = 488.8–2565.2 m^2) in 1988 and 573.3 ± 319.5 m^2 (range = 103.1–1151.2 m^2) in 1989. This difference between years was significant ($F_{4,10} = 10.8$, two-tailed $p = .010$). The mean percent overlap between areas occupied by adjacent males was 14.6 ± 16.7 (range = 0.0–46.6%) in 1988 and 7.7 ± 19.6 (range = 0.0–89.2%) in 1989; this difference was not significant ($F_{1,29} = 0.775$, two-tailed $p = .386$). The data from 1989 included one male whose area of activity was almost completely encompassed by that of an adjacent male (Figure 1b); when this conspicuous outlier was removed, the mean percent overlap between adjacent males was 4.0 ± 8.6 (range = 0.0–28.8%). This difference between years was significant ($F_{1,28} = 5.21$, two-tailed $p = .030$). The decrease in the mean area occupied by a male from 1988 to 1989 was associated with a nearly twofold increase in the density of males and females on the study site. Based on these data, it is unclear whether males reduced the area over which they were active in response to the increased density of reproductive competitors or the increased density of potential mates. Marked variation in the number of females per male area (range = 1–14; see below), however, suggests

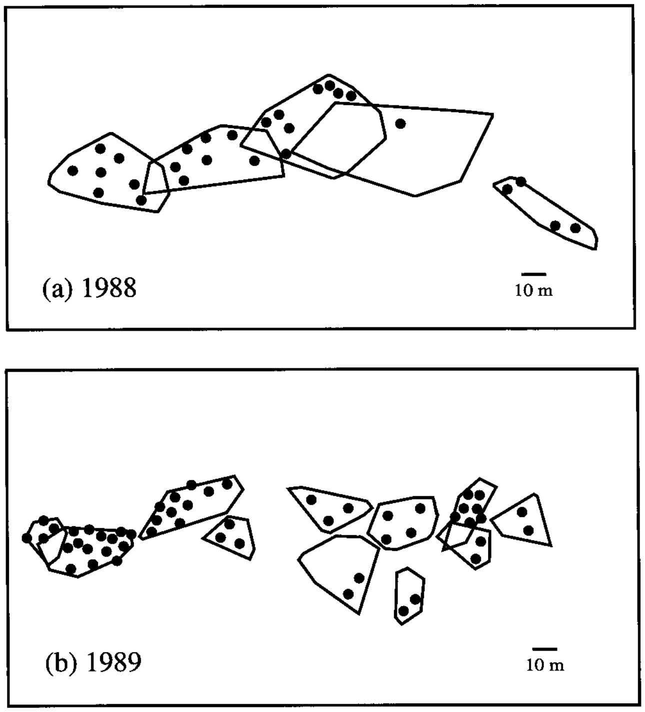

Figure 1
Minimum convex polygons representing the territories of male *S. parryii plesius* resident on the study site during the mating period in (a) 1988 (n = 5) and (b) 1989 (n = 11). In 1988, scan sampling data of male locations were collected during 24 April–3 May. In 1989, scan sampling was conducted during 20 April–11 May. The mean number of days per male on which scans were completed (both years combined) was 5.8 ± 2.5 (range = 3–12). For both years, points denote the locations of burrow systems occupied by females (one burrow system per female) during mating (n = 27 females in 1988 and 53 females in 1989).

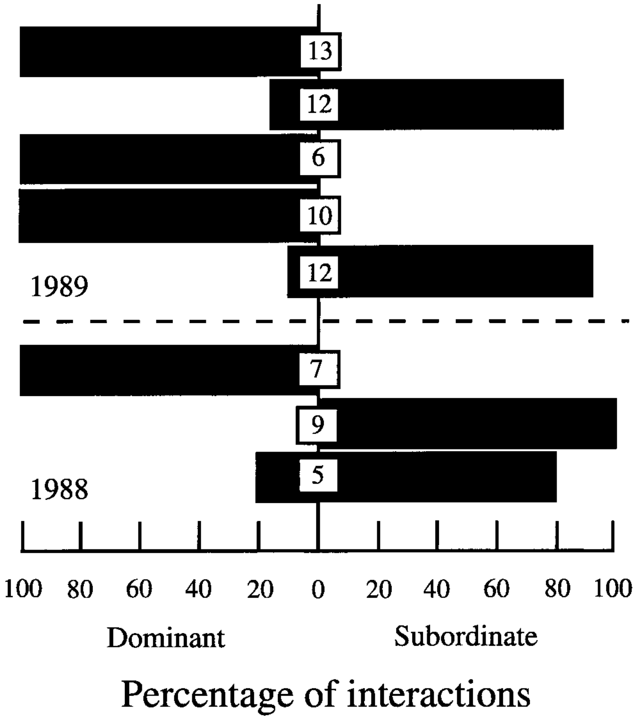

Figure 2
The outcomes of agonistic interactions involving eight males resident on the study site during the mating period in 1988 (n = 3) and 1989 (n = 5). Only males observed engaging in five or more encounters were included in these analyses; for each male, the number of interactions observed is indicated in the box centered on the vertical axis. The percentage of interactions in which a male was scored as dominant is indicated to the left of the vertical axis; the percentage of interactions in which a male was scored as subordinate is indicated to the right of this axis. The behavioral criteria used to determine the dominant and subordinate animals in each encounter are described in the text.

that males did not defend a fixed number of potential mates, implying that increased reproductive competition was responsible for the reduction in mean area occupied.

Social relationships among males

Social interactions among males appeared to be influenced more by the identities of the interacting individuals than by the locations at which encounters occurred. Of those interactions recorded on nonestrous days that had identifiable outcomes (n = 44), the number dominated by the male on whose area of activity the encounter occurred was not significantly different from random (H_0: equal numbers of encounters dominated on and off the home area) in 1989 (n = 20 of 33 interactions; $\chi^2 = 1.48$, df = 1, $p > .10$) or when data from both years were combined (n = 23 of 44 interactions; $\chi^2 = 0.09$, df = 1, $p > .50$); the small number of interactions with identifiable outcomes during 1988 (n = 11) precluded independent analysis of data from that year. Similar results were obtained when analyses were restricted to interactions involving chases, which have been used to characterize male dominance interactions in other ground squirrel species (e.g., Davis and Murie, 1985; Murie and Harris, 1978); the number of these interactions that occurred on the chasing male's area of activity was not significantly different from random (n = 20 of 43 interactions, data from both years combined, $\chi^2 = 0.21$, df = 1, $p > .50$). Collectively, these data suggest that males in the study population did not exhibit site-specific dominance during interactions with reproductive competitors.

In contrast, when the outcomes of agonistic interactions were examined as a function of male identity (n = 8 males with >5 interactions each; data from 1988 and 1989 combined), we found that four animals were consistently scored as dominant, while four others were consistently scored as subordinate (Figure 2). Each of these males interacted with 3.3 ± 1.2 (range = 2–5) different individuals, suggesting that the tendency to win or lose encounters was not due to the dominance relationship between a specific dyad of males. This tendency was even more pronounced among males that were consistently scored as subordinate; these males interacted with 4.0 ± 1.2 (range = 3–5) different individuals. For both dominant and subordinate individuals, the number of interactions that occurred on the focal animal's area of activity was not significantly different from random (H_0: equal numbers of interactions on and off the home area; $\chi^2 \leq 0.44$, df = 1, $p > .50$). All consistently subordinate individuals engaged in fights, parallel runs, or squeal displays (6.3 ± 4.0 agonistic interactions during 13.8 ± 3.4 interactions), indicating that although all males attempted to defend the area on which they were resident, the success of this defense varied among individuals (Figure 2). Thus, although the behavior of males in the study population appeared to be generally consistent with spatial and social criteria for territoriality, an individual's tendency to consistently win or lose agonistic interactions suggested that access to females may have been influenced by more subtle differences in male competitive ability.

Spatial distribution of females

All burrows occupied by females were located on male territories, and, conversely, each male's territory contained the burrow system of at least one female (Figure 1). The mean number of females per male area in 1988 was 5.4 ± 2.6 (range = 1–8, $n = 5$ male areas); in 1989, the mean was 4.8 ± 3.9 females per male area (range = 2–14, $n = 11$ male areas). This difference between years was not significant (Mann-Whitney $U = 22.0$, $n = 5{,}11$, $p = .58$). The number of females per male territory was not correlated with territory size ($r = .398$, $n = 11$, $p = .254$; data for 1989 only), suggesting that occupation of a larger portion of the habitat did not increase the number of a male's potential mates.

Territoriality and male copulatory success

Copulatory records for 28 females (1989, $n = 13$; 1990, $n = 15$) were used to test the hypothesis that territoriality was associated with access to unmated females. Twenty of these females were monitored continuously throughout behavioral estrus; although copulatory records for the remaining eight females were not complete, these animals were observed continuously through the end of their first mating. Because previous research (Lacey et al., 1997) has revealed that the number of mates per female did not differ among years, data for 1989 and 1990 were combined for the following analyses.

Twenty-six (92.9%) of the 28 females monitored mated with the male on whose territory they resided ($n = 12$ males); 20 (76.9%) of these females mated first with the resident male, indicating that territory ownership was significantly associated with access to unmated females ($\chi^2 = 5.2$, df = 1, $p < .025$). Males did not, however, have exclusive access to the females resident on their territories; 13 (65.5%) of the 20 females monitored throughout estrus mated with at least one nonresident male, and 51.1% of all copulations detected ($n = 47$) involved nonresident males.

All first copulations by females occurred on the male territory on which they resided. On the afternoon of estrus, the resident male appeared to actively defend the receptive female(s) on his territory. During this period, the distance between the resident male's center of activity and that of the estrous female was significantly less than on nonestrous days (Wilcoxon signed-rank, $z = 2.56$, $n = 11$, $p = .010$). In contrast, the rate of agonistic interactions between the resident and other males was significantly greater on estrous days (estrous: 1.8 ± 0.7 interactions/h, range = 0.5–3.4, based on 3.8 ± 1.3 h of observation; nonestrous: 0.5 ± 0.4 interactions/h, range = 0.2–0.7, based on 11.8 ± 4.3 h of observation; Wilcoxon signed-rank, $z = 2.7$, $n = 10$, $p = .007$), with such interactions generally occurring within 10 m of the receptive female. Collectively, these observations suggest that males shifted from defense of an area to direct defense of resident females on afternoons when those females were in estrus.

First copulations with nonresident males (1989, $n = 3$; 1990, $n = 5$) occurred when the resident male was actively displaced by a neighboring animal. Several hours before the onset of behavioral estrus, the neighboring male began making incursions onto the resident's territory; the locations visited by the nonresident were outside of that animal's typical area of activity. Agonistic interactions were observed whenever the nonresident and resident male encountered each other; in this context, the number of interactions dominated by nonresidents (22 of 43 interactions) was significantly greater than expected given the percentage of interactions dominated by nonresidents on nonestrous days (33.3%, $n = 63$ interactions, $\chi^2 = 4.1$, df = 1, $p < .05$).

Displacement of the resident male lasted only until the neighboring animal had copulated with the female; after copulation, the neighboring animal returned to the area in which he was usually active. All displacements of resident males occurred before a female's first copulation; this association between displacement of the resident male and mating order was significant (8 of 28 first copulations; 0 of 13 second copulations; Fisher's Exact test $p = .03$). Pairwise comparisons revealed no tendency for the body weights of displacing males to be greater than those of the residents that they displaced (Wilcoxon signed-rank, $z = 0.14$, $n = 8$, $p = .889$); insufficient data prevented similar comparisons of other male traits such as age or dominance status on nonestrous days.

Territoriality and fertilization success

Lacey et al. (1997) presented data on paternity for 16 litters of arctic ground squirrels reared by females that were observed continuously throughout behavioral estrus. Fifteen of these litters were sired exclusively by the female's first mate, with paternity of the 16th litter divided among the female's first and third mates. Eleven of these females had mated first with the male on whose territory they resided. The five remaining females (including the mother whose litter was of mixed paternity) mated first with a neighboring male. The percentage of young sired by a female's first mate did not differ between these groups (Mann-Whitney $U = 0$, $n = 5{,}11$, $p = 1.0$), indicating that first copulations resulted in fertilization success for either resident or nonresident males.

DISCUSSION

The behavior of male *S. parryii plesius* during the mating period was consistent with traditional criteria for territoriality in that each male occupied a discrete portion of the habitat that he attempted to defend against incursions by reproductive competitors. Territory ownership was significantly associated with male reproductive success. Paternity analyses (Lacey et al., 1997) indicated that litters in the study population were sired almost exclusively by a female's first mate; in the present study, more than two-thirds of the females monitored during estrus mated first with the male on whose territory they resided. Territoriality did not, however, provide males with exclusive access to females; nearly half of the copulations detected involved nonresident males, indicating that territory ownership did not prevent reproductive competitors from gaining access to females. Instead, territoriality appeared to increase fertilization success by allowing a male to mate first with the females on his territory, thereby providing the resident male with the copulations that were most likely to result in offspring.

Territorial defense alone was not sufficient to prevent reproductive competitors from gaining access to sexually receptive females. On the afternoon of estrus, the resident male actively attempted to deter competitors from gaining access to the estrous female(s) on his territory. These efforts were not always successful, and about 28% of first copulations involved nonresident males that had succeeded in displacing the resident male, thereby gaining access to the receptive female. Observations of male-male interactions on nonestrous days revealed that individuals either consistently won or consistently lost agonistic encounters (Figure 2). Although our data did not allow us to assess the relative reproductive success of winners versus losers, we suspect that males that consistently lost agonistic encounters on nonestrous days were more likely to be displaced by neighboring animals on days when females were receptive. Thus, defense of a portion of the habitat may represent only one aspect of reproductive competition among males; layered on top of this defense may be more subtle differences in competitive ability that significantly affect reproductive success.

The role of female behavior in shaping reproductive competition among males was not addressed in this study. The locations of females' burrows provided an unambiguous means of assigning females to male areas, but individual females did not restrict their activity to the area defended by a single male, and most females interacted with multiple males before and on the day of estrus (Lacey, 1991). Although receptive females interacted most frequently with the male on whose area they resided (Lacey, 1991), females appeared to have the opportunity to assess different prospective mates and, potentially, to influence the number and order of males with which they mated. The behavior of female California and Richardson's ground squirrels has been shown to change on the day of estrus in ways that appear to increase contact with potential mates (e.g., increased area of female activity; Boellstorff et al., 1994; Michener and McLean, 1996), suggesting that females may play a critical role in determining the copulatory and fertilization success of males. The behavior of female *S. parryii plesius* and its effects on male reproductive success will be examined in greater detail in a future publication.

Interspecific variation in ground squirrel mating systems

The relationship between territorial defense and fertilization success reported here has important implications for interspecific differences in ground squirrel mating systems. In particular, patterns of male fertilization success may help explain why reproductive competition in some species of *Spermophilus* is highly spatially defined (i.e., territorial; Dobson, 1984; Schwagmeyer, 1990), whereas other species show no evidence of site-specific defense of potential mates. Although both ecological and phylogenetic correlates for this behavioral difference have been considered (e.g., Dobson, 1984; Schwagmeyer, 1990), none has been found to provide a robust explanation for the observed variation in male site-specificity during the mating period.

Previous efforts to explain variation in ground squirrel mating systems have not considered the roles of sperm precedence and differential fertilization success in shaping patterns of reproductive competition. Although multiple mating by females appears to be common among ground squirrels (Boellstorff et al., 1994; Murie, 1995; Lacey et al., 1997; Michener and McLean, 1996; Schwagmeyer, 1990; Sherman, 1989), patterns of fertilization success vary markedly among species (Foltz and Schwagmeyer, 1989; Lacey et al., 1997; Sherman, 1989). These differences may contribute to interspecific variation in male behavior by creating asymmetries in the reproductive benefits received from copulations. For example, for species in which multiple paternity of litters is common (e.g., *S. beldingi*: Hanken and Sherman, 1981; *S. tridecemlineatus*: Foltz and Schwagmeyer, 1989), a comparatively large proportion of copulations will yield offspring, and thus males should behave in ways that allow them to mate with as many females as possible. In contrast, for species in which paternity is more restricted (e.g., *S. parryii plesius*: Lacey et al., 1997), males should adopt behaviors that increase their chances of achieving the few genetically effective copulations available; increased site specificity of male activity, including defense of a specific subset of females, may represent one response to this challenge.

This argument assumes that fertilization success is determined, at least in part, by factors other than male behavior. This assumption seems to be met in *S. parryii plesius,* in which variation in male copulatory behavior has no effect on paternity (Lacey et al., 1997). Differences in male behavior, however, have been shown to influence fertilization success in other ground squirrel species (Foltz and Schwagmeyer, 1989; Schwagmeyer and Foltz, 1990; Sherman, 1989), making it more difficult to identify causal relationships between probability of fertilization and copulatory behavior. The factors affecting sperm precedence and fertilization success are complex, and detailed physiological studies of ground squirrels are needed to determine precisely how paternity is controlled (Davies, 1991). Nevertheless, the striking differences in paternity and reproductive competition outlined here suggest that sperm precedence may be an important determinant of male behavior.

Parallels with extrapair fertilizations in birds

Relationships between territoriality and male fertilization success have been examined for a number of other mammals, many of which are species in which individuals form discrete social groups and adults of both sexes defend a common territory (e.g., dwarf mongooses: Rood, 1983; alpine marmots: Goossens et al., 1998; black-tailed prairie dogs: Hoogland, 1985; chimpanzees: Goodall, 1986). In these societies, reproductive success is often shared among the males within a group, but extragroup copulations appear to be rare (e.g., Arnold, 1990; Keane et al., 1994; but see Goossens et al., 1998; Hoogland, 1995; Morin et al., 1994). Because such groups are frequently composed of close relatives (e.g., Rood, 1983; Hoogland, 1995; Goosens et al., 1998), even males that do not sire young may gain limited reproductive success via inclusive fitness benefits. In contrast, male *S. parryii plesius* are not group-living, and neighboring males are unlikely to be related (Lacey, 1991). As a result, young that are sired by reproductive competitors yield no fitness benefits to resident males.

In this regard, reproductive competition among male *S. parryii plesius* more closely resembles that in avian species in which individual males actively attempt to deter extrapair copulations by the female(s) residing on their territory (e.g., Birkhead and Møller, 1992; Langmore, 1996; Tobias and Seddon, 2000). Although arctic ground squirrels do not form a distinct intersexual bond comparable to that found in many birds, males in both types of systems face the common challenge of preventing genetically effective copulations by reproductive competitors. Male reproductive success in a number of avian species appears to be associated with territory ownership (e.g., Currie et al., 1999; Gibbs et al., 1990; Sundberg, 1994), although, as in the present study, defense of a portion of the habitat is not always effective in preventing nonresident males from siring young.

Several recent studies of male reproductive competition and fertilization success in birds have partitioned the general phenomenon of territorial defense into a number of more specific aspects of male behavior such as patrolling territory boundaries, vocal advertisement of territory ownership, and changes in territory size in response to female receptivity (Langmore, 1996; Rodrigues, 1998; Tobias and Seddon, 2000). The specific aspects of male behavior most closely associated with reproductive success vary among species (e.g., Gil et al., 1999; cf. Tobias and Seddon, 2000), but one common theme of these studies is that traditional views of mating territories as fixed entities capable of deterring reproductive competitors are overly simplistic. Clearly, defense of a portion of the habitat represents only one of the suite of behaviors that males in these species use to prevent reproductive competitors from gaining access to receptive females. Our findings from arctic ground squirrels suggest that the same is true of territoriality in mammalian species. Thus, rather than regarding territoriality as a comprehensive description of male reproductive behavior, future studies of avian and mammalian mating systems will benefit by viewing territorial defense as only one of the many axes along which males compete for access to reproductive partners.

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