

# Sexual differences in spatio-temporal interaction among badgers

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**Abstract.** I tested the following hypotheses of territorial polygyny on badgers (*Taxidea taxus*: Carnivora; Mustelidae): Competition among adult females for food should result in intrasexual territoriality, while male competition for females should result in larger territories that encompass multiple female territories. The sagebrush-grassland study area (Wyoming, USA) contained a depauperate terrestrial fauna with a dense badger population preying on high densities of ground squirrels (*Spermophilus armatus*). Implant telemetry generated locations for analysis of home range and spatio-temporal interaction. During the summer breeding season males doubled movement rates and nearly tripled home range areas to overlap those of females. Before and after the breeding season, males reduced their home ranges to sizes nearer those of stable female ranges ( $\bar{x} = 2.82 \text{ km}^2$ ). Unexpectedly, home range overlap between males and females was no different than intrasexual overlap. However, analysis of spatio-temporal interaction revealed that females spatially avoided one another, while males were spatially and temporally attracted to one another, similar to that of male-female interactions. Presumably, olfactory mechanisms allow resource tracking and lagged communication. Male-male territoriality was not viable, most likely because the high density of badgers, combined with the severely male-biased sex ratio (1.75:1), effectively increased intruder pressure – as a resource, receptive females were too mobile and spatially unpredictable within their home ranges. Consequently, males monitored and searched widely for relatively scarce females during the breeding season with the effect of attracting each other. Male mobility, home range size, and possibly aggression increased with age, suggesting age-related breeding tactics, although dominance could only be surmised. This and other studies suggest how the spatial, temporal, and dominance components of carnivore resource partitioning and sociality will be understood better by unraveling the interplay of olfactory processes, attributes of disparate resources (e.g., food vs. females), seasonality, and population density and age-sex structure.

**Key words:** Carnivores – Spatio-temporal interaction – Polygyny – Intraspecific competition – Home range

Observation of the pattern of polygyny in numerous species over varying population densities, sex ratios and habitats has led to the hypothesis that space use often differs between the sexes because reproductive success of males is affected more by mate supply and that of females more by habitat constraints. Males competing for females are often territorial whereas female space use is determined by habitat features such as food supply (reviews in Powell 1979; Wittenberger 1979; Schoener and Schoener 1982; Stamps 1983; Sandell 1989; Lott 1991). Schoener and Schoener (1980) proposed a general model of territoriality for the adult male of a polygynous species in which number of females was the resource to be maximized. It predicted that optimal male territory size should increase with an increase in female density, unless male intruder pressure also rose greatly (see also Schoener 1983). Their model and data suggested that adult males may generally exhibit more exclusive, contiguous home ranges than the other age-sex classes, with subadult males often engaging in a nonterritorial, transient strategy. Hixon (1987) extended this general theme of territorial polygyny to the case where both sexes are territorial and territories overlap intersexually, with female territoriality connected to predictable food supplies.

In this paper I examine intraspecific resource partitioning in a sexually dimorphic population of badgers. Although I follow the general theme of territorial polygyny which focuses on the spatial component of resource partitioning, I also analyze the role of spatial and temporal interaction in home range overlaps using a straightforward statistical analysis of space-time use (Minta 1992). This is the first study to provide inferences about the type and strength of interaction, which is then used to interpret access to prey by females and to mates by males.

## Study system and background natural history

The badger exhibits a solitary life style and simple social organization (reviews in Lindzey 1982; Messick 1987).

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Most females initiate breeding as yearlings, although a few may breed as early as 4 months after birth. Males are also capable of breeding as yearlings (age 16 months). Females are slow to enter estrus and are not synchronous, possibly due to age differences and induced ovulation via repeated multi-male stimulation (Milligan 1982). This results in a prolonged breeding season (Ewer 1973), peaking in late July and early August, although an individual female has a narrow window of fertility (about one day). Following a 6-month delayed implantation and 5-week gestation, 1–5 (mode  $\approx$  2 to 3) young are born around April 1 and raised solitarily by the female. The time from birth to dispersal appears to be 3–4 months, which coincides with the annual breeding peak. Extended torpor bouts occur during winter within northern latitudes. Adult males are 25–40% larger than the average 7-kg adult female.

The badger is morphologically specialized for digging for rodents, though its diet ranges from omnivory to extreme carnivory. Primarily nocturnal, badgers have poor vision but exceptional olfactory acuity. Olfactory communication is highly developed in badgers. In addition to urine and feces, scent glands allow long-lasting messages that operate in the sender's absence (reviews in Macdonald 1985; Gorman and Trowbridge 1989). Behavioral and olfactory systems of carnivores are capable of delivering information about the activity of individual conspecifics and the renewal rates of resources (Peters and Mech 1975; Harrington 1981; Olton et al. 1981; Henry 1986). Male badgers appear more territorial than females, but mutual avoidance may be the rule (see Lindzey 1982; Long and Killingley 1983).

My field work was centered in the northeast portion of the National Elk Refuge in southeast Jackson Hole, northwestern Wyoming, USA. The entire study area (100 km<sup>2</sup>), which included part of Grand Teton National Park and Teton National Forest, averages 2050 m elevation. Its foothills and lowlands are dominated by sagebrush (*Artemisia* spp.), other low shrubs, and grasses (e.g., *Poa*, *Agropyron*, *Stipa*), with flat to steep rolling topography consisting of hollows and rounded hills. The study area is markedly seasonal with long cold winters and a mean annual temperature of 0°C.

Semi-colonial Uinta ground squirrels (*Spermophilus armatus*) were very dense, on the order of 10 squirrels ha<sup>-1</sup> and 15 ha<sup>-1</sup> during two years of the study (Minta 1990). The biomass of ground squirrels was at least an order of a magnitude greater than estimated for all other prey species combined (*Peromyscus* spp., *Microtus* spp., *Thomomys talpoides*, *Eutamias minimus*, and seasonally abundant grasshopper-sized arthropods). Badgers in my study population were highly carnivorous, with ground squirrels comprising more than three quarters of their diet. The diet did not differ by sex (Minta 1990).

Post-dispersal density of badgers was  $\geq 2$  km<sup>-2</sup> in the central part of the study area (Minta and Mangel 1989). The density of badger locations was clearly correlated with the density of ground squirrels (Minta 1990; Minta et al. 1992). Ground squirrel habitat was distinguished by the distinct mosaic formed by topography, vegetation, and geologically recent soils. As a result, badgers primarily occupied the bottoms and gentler slopes of hollows (deep silt soils) and to a lesser extent the breaks and plateaus of

higher elevations (gravely soils). Based on 101 individuals captured, the adult sex ratio was 1.75 (M:F,  $n=77$ ) and 0.85 ( $n=24$ ) for juveniles. Badgers  $>4$  years of age were nearly all males (91%,  $n=32$ ). In contrast, 55% ( $n=69$ ) of badgers  $\leq 4$  years were female.

## Methods and statistical approaches

Badger movements were followed from May 1982 to August 1985 during 26 months of field work. We captured badgers with leg-hold traps, snares, nets, and neck nooses, and aged them by counting cementum annuli of an upper first premolar (Messick and Hornocker 1981). We surgically implanted badgers with intraperitoneal radiotransmitters (50 implantations of 42 different badgers). We located telemetered badgers using omnidirectional and hand-held antennas on foot, skis, snowshoes, all-terrain vehicles, snowmobiles, and aircraft. Precise locations were obtained with a truck-mounted, twin-yagi directional array (see Minta 1990 for details). Since badgers could be simultaneously tracked from multiple stations, locations of badgers having neighboring home ranges could be gathered within hours. This was important for purposes of analyzing temporal interaction because I considered locations from two badgers to be statistically "simultaneous" if obtained within a period of less than 48 h, although most were within 24 h (Minta 1990, 1992). I chose this window of simultaneity because most odors would last for at least 48 h.

Definition and calculation of location and its error conform to procedures summarized in White and Garrott (1990). During tests the mean bearing error was  $0.41^\circ \pm 0.87^\circ$  (90% error arc of  $1.74^\circ$ ). Under field conditions the error was most likely greater, though system alignment was continuously adjusted to achieve a mean bearing error near zero. To evaluate the degree of statistical independence of serial locations I applied a test of independence (Schoener 1981; Swihart and Slade 1985, 1986). Adhering to these tests for badgers would have left too few locations for analysis, therefore I used biological independence, whereby serial locations were separated by a major activity shift (Minta 1992 after Lair 1987).

Activity and movement of all adult badgers decreased precipitously during cold snaps and after heavy snowfalls in fall. Sustained low temperatures and snowpack accumulation from October through December corresponded to badgers entering prolonged torpor periods through March or April. Activity and movement increased in June and peaked during the height of the breeding season, late July to early August. Therefore the year was divided into three seasons for locational analysis: prebreeding (1 January–30 June), breeding (1 July–10 August), and postbreeding (11 August–31 December).

I used the harmonic mean method (Dixon and Chapman 1980) for representing the distribution of locations. Program McPAAL (Stüwe and Blohowiak 1985) produced plots and calculated areas (using a  $25 \times 25$  grid) within specified isopleths of the utilization distribution (Van Winkle 1975; Anderson 1982). I defined the isopleth containing 95% of an animal's locations as the home range boundary. I also computed the 30%, 60%, and 90% isopleths (core areas) to analyze the relative dispersion of locations by age, sex, and season. More seasonal than annual home ranges were calculated because some individuals were tracked for less than one year. Since hypotheses dealt with age-sex categories, I considered home range estimates from different years to be different samples.

Home range overlap and interaction is described by Minta (1992) and summarized here. I used 'mean potential interaction probability', or simply mean overlap, as a measure of home-range overlap (shared area) by two animals. For two animals,  $\alpha$  and  $\beta$ , mean overlap is the geometric mean of the product of the ratios of overlap size to annual home range size:

$$\text{Mean overlap} = \sqrt{p_{11}} = \sqrt{\frac{\text{Overlap}}{\text{Home range } \alpha} \cdot \frac{\text{Overlap}}{\text{Home range } \beta}},$$

where  $0 < \sqrt{p_{11}} \leq 1$ .

A mean overlap of 1 is calculated for two home ranges of identical size exhibiting 100% overlap. For analyzing interaction between two animals within home range overlap, the pair's association is reduced to binomial events forming a  $2 \times 2$  classification; each is either present or not in the shared area. Observed frequencies of presence and absence for each animal can be compared with expected frequencies based on two null hypotheses of spatially independent home range use by each animal relative to the other, and one null hypothesis of temporally independent home range use by the two animals. The temporal order of 'simultaneous' pairs of locations for the two animals can then be evaluated for a pattern of use regarding the area of overlap. An overall chi-square test ( $df=3$ ) is partitioned into spatial "main effects" and temporal "interaction", analogous to analysis of variance:  $\chi^2_{\text{tot}} = \chi^2_{A:\bar{A}} + \chi^2_{B:\bar{B}} + \chi^2_{\text{int}}$ . However, overall significance is not a precondition for examining the partitions because they are independent. Nominal significance is defined as  $p \leq 0.1$  for this model (a justifiable p-level in carnivore studies which are haunted by small sample sizes: see Minta 1992). The two main effects are each animal's purely spatial attraction to or avoidance of the shared area, denoted by the coefficients of association  $L_{A:\bar{A}}$  and  $L_{B:\bar{B}}$ . When interaction effects ( $L_{\text{int}}$ ) are significant, it is possible to interpret temporal attraction to or avoidance of the shared area. This temporal response is in terms of the pair's simultaneous versus solitary occupation of the shared area relative to overall home range use. I use 1984 data because the highest proportion of the estimated population (62.5%) were implanted that year (Minta and Mangel 1989).

To compare seasonal mobility, I used the same locations described for home range estimation. For comparison with other studies, the distance between a badger's successive locations was used to calculate its movement rate ( $\text{km day}^{-1}$ ). Values were transformed to  $\log_{10}(x+1)$  rates for calculation of means and 95% confidence intervals, then back-transformed for presentation of results (Sokal and Rohlf 1981).

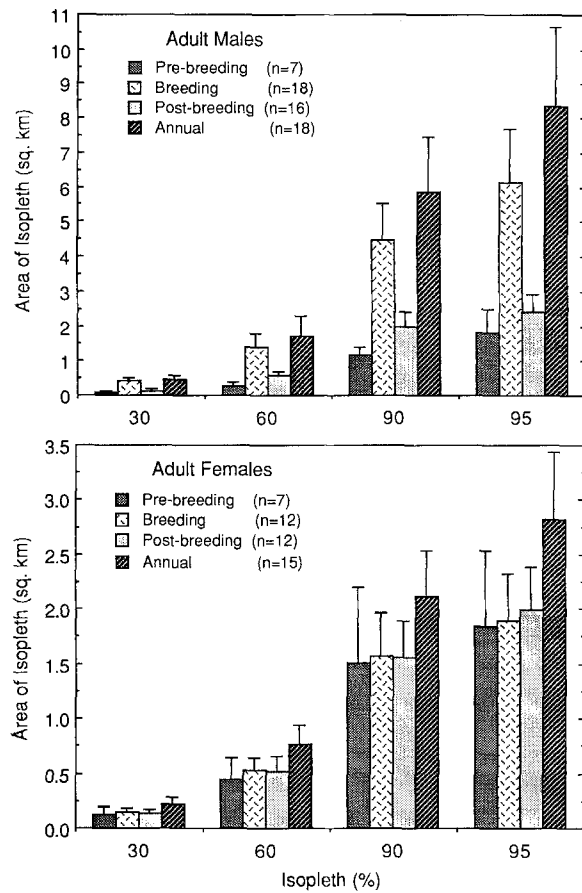
Recent wounds were examined on 90 different badgers during or immediately after the breeding season, so I knew all wounds were inflicted during the current breeding year. I applied a subjective index of wounding that ranged from zero (absence of wounds) to five (severest wounding observed during the study).

## Results

For badgers, conventional wisdom regarding territorial polygyny predicts that female territoriality maintains predictable, high quality habitat containing renewable patches of ground squirrels. In contrast with males, female competition for food should result in small, stable home ranges with little home range overlap. Males should treat females as the critical defendable resource and male-male competition should result in each male home range encompassing several smaller female home ranges. Since this scenario is most applicable to breeding adult resident carnivores (Ewer 1973; Powell 1979; Sandell 1989), I exclude juveniles from my analyses ( $< 1$  y).

### Home range analysis

Independent locations were used to calculate isopleths for 33 adults on an annual basis ( $\bar{x}=91.2$  locations,  $SD=36.1$ ), 14 adults for the prebreeding season ( $\bar{x}=34.6$ ,  $SD=12.8$ ), 30 adults for the breeding season ( $\bar{x}=37.9$ ,  $SD=15.0$ ), and 28 adults for the postbreeding season ( $\bar{x}=45.8$ ,  $SD=16.9$ ). Males ( $n=18$ ) averaged larger home ranges than females ( $n=15$ ) on an annual basis (Mann-Whitney  $Z=4.05$ ,  $p=0.0001$ , Fig. 1). But the sexes

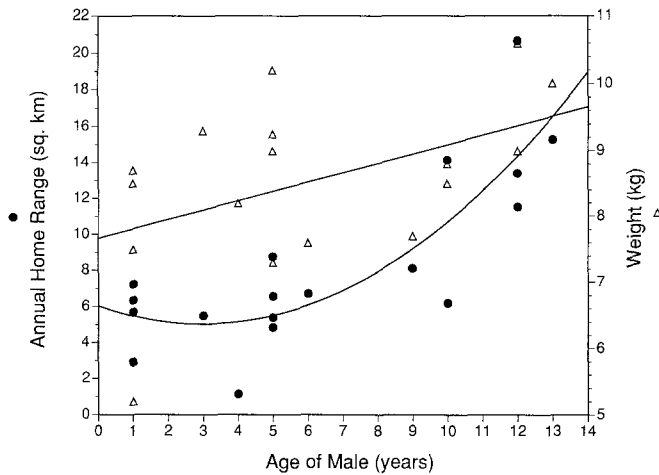


**Fig. 1.** Seasonal home range (95% isopleth) and core-area sizes for adult male badgers (upper graph) and females (lower graph) sampled between 1982 and 1984. Annual home range is plotted for comparison. Error bars are upper 95% confidence intervals

also differed in the way they concentrated use within core areas (i.e., 30:95, 60:95, and 90:95% isopleth ratios); females tended to use their home range more uniformly (flatter utilization distribution) or tended to be more restricted by home range boundaries (truncated distribution), or both (Minta 1990). Older adult males had larger annual home ranges than did younger males (Fig. 2;  $r_s=0.717$ ,  $Z=2.96$ ,  $p=0.003$ ) and generally weighed more than younger males (Fig. 2;  $r_s=0.462$ ,  $Z=1.91$ ,  $p=0.057$ ). The low variation in adult female ages did not permit an analogous analysis.

Home range size differences helps confirm the existence, but not the identity, of sexually dichotomous resource bases. Seasonal interactions should aid in their identification: 1) prior to and during the breeding period resident males should greatly increase their ranges and rates of movement to monitor females and maximize encounters with them; and 2) home range boundaries should be less rigid during the breeding season, male home ranges significantly less so than females. Outside the breeding season, male badgers should reduce their home range size as the critical resource shifts from females to prey.

Most of the difference between male and female annual home ranges was due to a large range expansion by



**Fig. 2.** Plot of adult male age versus annual home range size with a second-order polynomial least-squares curve fit ( $n=18$ ). Spearman rank correlation coefficient,  $r_s=0.717$ . Plot of adult age versus weight for same 18 males with linear fit ( $r_s=0.471$ )

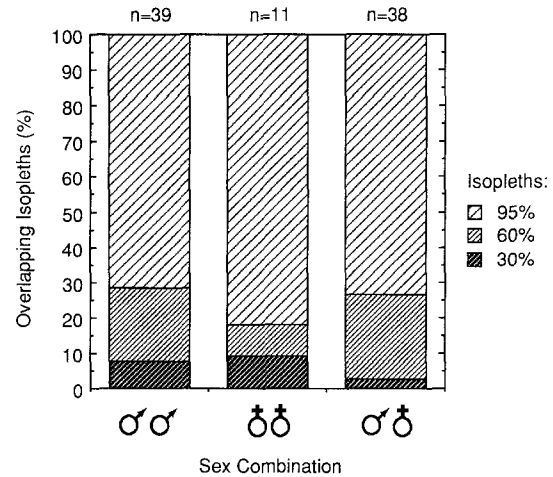
males during the breeding season (Fig. 1). The reported correlation between annual home range size and age of males (Fig. 2) was chiefly influenced by the relatively greater expansion of breeding ranges by older males. Note that this expansion of the 95% isopleth was proportionate across the 30, 60, and 90% isopleths during the breeding season, indicating an overall spatial expansion rather than a statistical effect from breeding forays beyond normal borders. Female home ranges did not vary predictably with season.

The size difference between male and female home ranges was highly significant during the breeding season ( $Z=4.06$ ,  $p=0.0001$ ). In contrast, there was little difference in home range sizes between the sexes during the prebreeding season, although if one examines all non-breeding season data (i.e. pre- and post-breeding records), there is still a tendency for males to exhibit larger home ranges than females ( $Z=2.10$ ,  $p=0.036$ ). Females did not exhibit such striking seasonal shifts in their patterns of space use – instead, their seasonal home range patterns basically reflected the annual patterns.

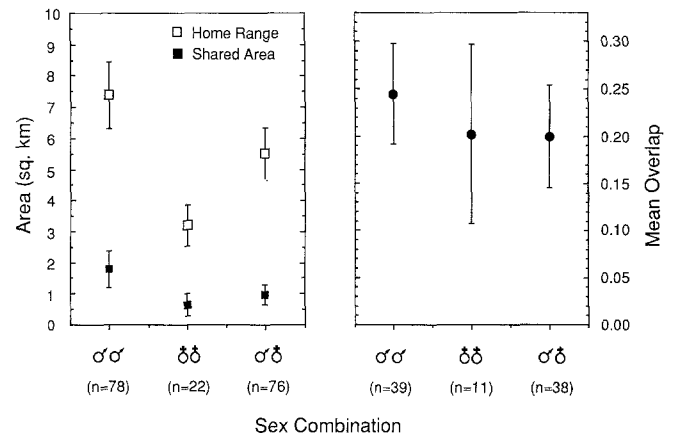
Badgers shifted the locations of their seasonal home ranges; otherwise the annual home range would have been equivalent to the largest seasonal home range (Fig. 1). For example, even though female seasonal ranges changed little in size, females shifted seasonal activity areas, contributing to a more dispersed pattern of locations on an annual basis. The roaming movement of males during the breeding season (see below) increased annual home range size. In addition, older males generally maintained non-breeding home ranges that were peripheral to areas occupied by female badgers year-round (lowlands with higher squirrel concentrations), and then expanded their ranges to include those areas during the breeding season.

#### Home range overlap

We expect reduced intersexual competition because critical resources are different for the sexes. Therefore resident



**Fig. 3.** The percent of isopleths that overlap for paired sex combinations, 1984



**Fig. 4.** Intra- and intersexual overlap of annual home ranges, 1984. Graph on left shows mean size of home range pairs and mean size of area of overlap for the different sex combinations. Note that sample sizes are twice for home range what they are for shared area because two different home ranges form one shared area. Graph on right shows mean overlap. Error bars are 95% confidence intervals

adults should exhibit significantly more spatial exclusion within than between sexes. This should produce differences in average home range overlap, if it is an adequate index of spatial exclusion. Occurrences of overlap between all pairs of annual home ranges; by sex and isopleth, are depicted in Fig. 3. I assigned a mean overlap of 1.0 to two exceptional cases, in each a male home range completely encompassed a much smaller female's home range. I hypothesized intrasexual overlap should occur less often than intersexual overlap. Contrary to this hypothesis, when examined in terms of isopleth size, none of the three sex combinations (male-male, female-female, male-female) in Fig. 3 are substantially different ( $3 \times 3$  table:  $\chi^2=2.13$ ,  $p=0.712$ ,  $df=4$ ). In addition, size of overlap areas and mean overlap between all pairs of adult annual home ranges do not support the idea that male-female overlap was greater than male-male or female-female overlap (Fig. 4 and Kruskal-Wallis  $H=1.934$ ,  $p=0.380$ , although

some data are dependent). Furthermore, the variances of the three overlap categories were unexpectedly homogeneous (Bartlett's  $\chi^2=0.090$ ,  $p=0.956$ ). However, using 60% core areas (not shown), male-male overlaps ( $\bar{x}=0.205$ ,  $SD=0.135$ ,  $n=9$ ) were less than male-female overlaps ( $\bar{x}=0.243$ ,  $SD=0.261$ ,  $n=9$ ). Only 1 female-female instance (0.398) was available, resulting in no significant differences among these categories (Kruskal-Wallis  $H=1.180$ ,  $p=0.555$ ).

### Mobility

One corollary of the hypothesis that males should exhibit expanded breeding ranges, is that males will increase their movement in order to monitor females via systematic coverage of their home ranges. Data support this hypothesis, with movement rates of males increasing during the breeding season, and being highest for older males (Fig. 5 based on 2,872 movements of adult badgers during 1984). Movement rates of females also increased during the breeding season, but to a lesser degree than for males. Because older females were so rare in the population, the data for that category is based on only two individuals that were intensively studied. Nevertheless, both older females moved at slower rates than younger females, the opposite trend of males. Mobility of younger badgers did not differ by sex outside the breeding season (Mann-Whitney  $Z=3.363$ ,  $p=0.0008$ ). Older males moved at a higher rate than younger males, both during the breeding season (Mann-Whitney  $Z=3.053$ ,  $p=0.002$ ) and outside the breeding season (Mann-Whitney  $Z=3.257$ ,  $p=0.001$ ).

### Spatio-temporal interaction

Patches of ground squirrels were stationary and renewed slowly relative to the badger's rate of detection (via olfaction) and response (mobility). This resource could be partitioned by females that occupy overlapping home ranges, but that tend to avoid shared space compared to the exclusive portion of their home ranges. If the avoidance was not correlated with the timing of other females' presence in the overlap, it would be expressed as "pure" spatial avoidance (that is, in the absence of any temporal interaction) (Minta 1992). On the other hand, a male badger's attraction to a female, a fast-moving resource relative to squirrel patches, as well as to its own mobility, would be expressed as temporal attraction if the male tracked the female. A male could increase encounters with females by virtue of timing – more frequently attracted to female overlaps during the females' presence, not to the space per se. Thus, when analyzing cumulative locations (and timings) within annual home range overlaps, badger interactions should be analyzed as a mixture of spatial and temporal responses, because members of a pair could respond differently to different resources, or differently to each other as resources.

The proportion of adult home range interactions classified as nonrandom was greater than those classified as random. Based on overall chi-square significance, nonrandom male-male associations (53.8%,  $n=39$ ) were

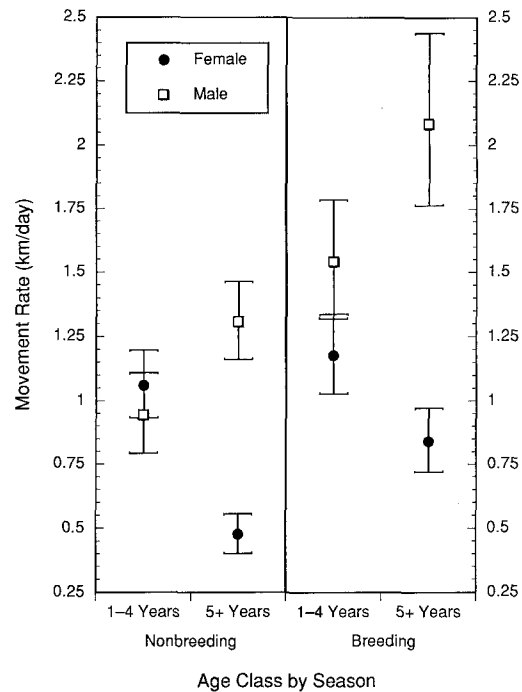
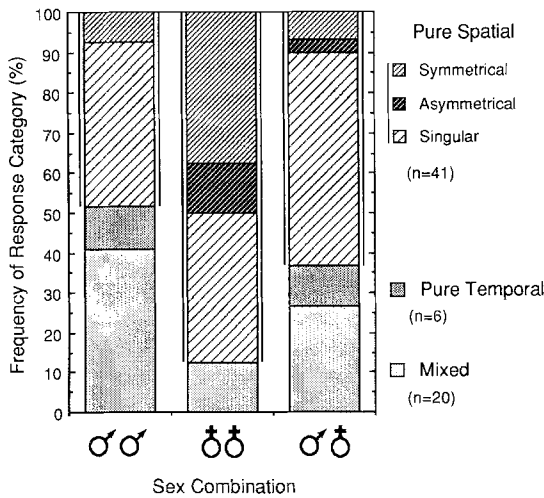


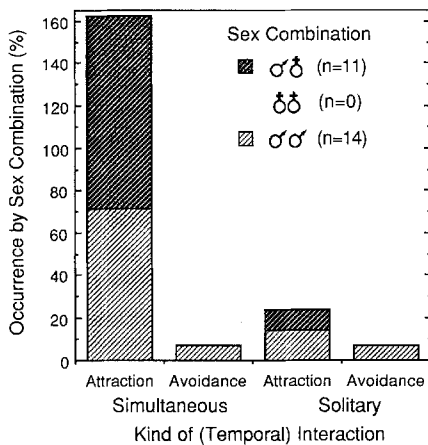
Fig. 5. Mean movement rates of younger and older badgers during nonbreeding and breeding portions of the year. Means and 95% confidence intervals were back-transformed from  $\log_{10}(x+1)$

fewer than nonrandom female-female (72.7%,  $n=11$ ) and male-female (71.1%,  $n=38$ ) associations.

When overall chi-square were partitioned into a pair's main effects (each member's pure spatial response) and temporal interaction, at least one significant chi-square partition occurred in 76.1% ( $n=88$ ) of all adult badger associations. Pure spatial association ( $L_{A:\bar{A}}$  or  $L_{B:\bar{B}}$ ) without significant temporal interaction occurred in 33.3% of male-male associations, in 63.6% of female-female associations, and in 55.3% of male-female associations. Temporal interaction ( $L_{ixn}$ ) was a significant response in 35.9% of male-male associations, 9.1% female-female associations, and 28.9% of male-female associations. Pure temporal responses (with no significant spatial effects) were uncommon, and most temporal responses were mixed with spatial responses within a pair. The relative proportion of pure and mixed responses is portrayed in Fig. 6 without regard to whether the response was one of attraction or avoidance. Note that pure spatial responses were further classified as symmetrical (both animals show the same response of attraction or avoidance), asymmetrical (animals show opposite responses), or singular (only one of the pair has any significant response). Significant temporal attraction/avoidance, whether pure or mixed with a spatial response, must be either simultaneous (synchronized so both are present or absent when overlap is used) or solitary (synchronized so one is present in overlap when the other is absent and vice versa). The occurrence by category for the kind of temporal interaction appears in Fig. 7. Simultaneous attraction was very common whereas both kinds of temporal avoidance were rare. Each member of a pair is capable of expressing a different combination of spatial and temporal attraction or



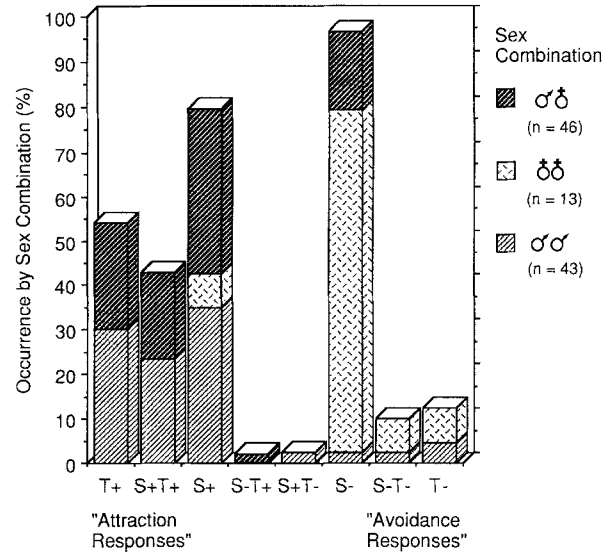
**Fig. 6.** Given that there is a significant chi-square partition, the proportion of responses that fall into one of three main categories: pure spatial, pure temporal, and mixed spatial temporal (spatial effects and temporal interaction within a pair). Note that the pure spatial response is also further broken down by type of association. See text for explanation



**Fig. 7.** Occurrence by sex combination for kind of temporal interaction based on significant  $\chi^2_{\text{in}}$  partition. The female-female category is excluded because there was only one occurrence of simultaneous avoidance

avoidance. The exact type of response, or combination of types, is pooled by sex category in Fig. 8. Females tended toward spatial avoidance, although the sample size is small. The type and frequency with which males were attracted to each other was similar to the frequency with which males were attracted to females.

Male-male and male-female associations might naturally result in some kind of attraction based solely on the tremendous expansion of male home ranges during the breeding season. This possibility is hard to evaluate because sample sizes did not permit analysis of pairwise interaction for seasonal home ranges, but we can test the following null hypothesis using the subset of simultaneous locations;  $R_B$ , the ratio of breeding season locations within overlaps to total annual locations in overlaps does not



**Fig. 8.** Occurrence by sex combination for specific type of spatio-temporal response along an attraction-avoidance gradient. When temporal interaction was significant both members of the pair expressed the same type of response (i.e., either temporal attraction, T+, or temporal avoidance, T-), but it may or may not be combined with a different spatial responses (S+, S-) depending on outcome of main (spatial) effects. For example, one individual within a pair may have a T- response while the other individual has a S-T- response

differ from  $R_T$ , the ratio of total breeding season locations to total annual locations. The observed comparisons are: male-male associations —  $R_B=0.619$  vs.  $R_T=0.482$  ( $Z=4.197$ ,  $p<0.0001$ ), female-female associations —  $R_B=0.540$  vs.  $R_T=0.425$  ( $Z=1.785$ ,  $p=0.074$ ), and male-female associations —  $R_B=0.654$  vs.  $R_T=0.452$  ( $Z=6.42$ ,  $p<0.0001$ ). For all three combinations of sex interaction, badgers occupied the overlapping areas of their home ranges more during the breeding season, though females did so with other females to a lesser degree.

#### Wounds as indicator of intraspecific strife

Scarring and wounding often give investigators a subjective idea of the degree of intraspecific strife in carnivore populations (so long as injuries rarely result in death [Schoener 1979]). Wounds and recent scars were present on 73% of all males ( $n=52$ ) and 50% of all females ( $n=38$ ). Degree of wounding was more severe on males than females ( $X^2=19.81$ ,  $df=5$ ,  $n=90$ ,  $p=0.001$ ). Scarring increased with age for females ( $r_s=0.403$ ,  $p=0.056$ ) and especially males ( $r_s=0.660$ ,  $p=0.0001$ ). As an indicator of trend only, males two years and older averaged 4 times the index value of juvenile males and 2.5 times the index value of females two years and older.

#### Discussion

Annual home ranges of females resembled territories: space use was stable and, despite the overlap among females, home ranges were characterized by spatial avoidance and solitary use of shared areas. Male home ranges

doubled or tripled in size during the breeding season, during which time they were attracted to females. Male-male interaction was also manifested as spatio-temporal attraction, either through correlated attraction of males to females, or because males were using each other to monitor and find females, or both. Males frequently tracked each other during the breeding season, and younger males were also detected in close proximity to older males that were consorting with females (Minta 1990).

Our results confirmed two of our expectations: (i) intrasexual territoriality for females, with small stable home ranges and (ii) larger male home ranges that expand during breeding season. However, contrary to our expectations males did not exhibit greater overlap with females than with other males. To understand these results one needs to look in more detail at how resources are detected and used, and the effect of age and social structure.

Mammals often divide up access to resources by staking out spatially nonoverlapping territories, by exhibiting overlapping habitat use but not at the same time, or by dominance hierarchies. Solitary mammals, particularly carnivores, share space both by timing their access with one another and, depending on the situation, by dominance (Leyhausen 1979; Hornocker et al. 1983; Sandell 1986, 1989; Minta 1992). Olfactory mechanisms provide long-lasting information for identifying age, sex, and individuals, which allows structured dominance, and for assessing the activity pattern and spatial proximity of others. With increasing spatial overlap, the temporal and dominance components of resource partitioning can assume a greater role than the spatial component (e.g., territoriality). Exact outcomes will depend on the relative stability of resources in space (e.g. stationary food vs. ranging mates) and time (rates of renewal and mobility), and the animal's ability to detect changes and respond to them (e.g., Wittenberger 1981; Wiens 1984).

In this study, critical resources (prey) for adult female badgers were stationary and predictable. Female badgers could gain solitary or even exclusive access to areas containing prey by tracking its own and other's past activity. Using the same cues, males could detect when females were near or in estrus. However, females became a "complicated" resource for male badgers during the breeding season because they were fast-moving targets which were also pursued by other contentious males. First, the high density of breeding males combined with the dispersion of relatively fewer females likely resulted in too much intruder pressure for territoriality (Schoener 1983). Second, female badgers on the Refuge were a highly mobile resource during the breeding season. Males could attempt to maximize breeding frequency by overlapping smaller female home ranges and by moving faster than females. An individual female's day-long estrus, but prolonged attraction to males (weeks), effectively made a female a very scarce, nonrenewable resource that was predictable at the seasonal scale, but much less predictable on a daily basis. Through olfaction, males were able to pinpoint approximate timing of fertility, but they could not predict where the female would be in her home range during estrus. A male sequestering a female that was not ready to breed would lose opportunities for monitoring and breeding other females. Thus, at the scale of the male's breeding

home range, a female may have appeared as an unpredictable, "renewable" resource (via her high mobility and her uncertain pattern of circulation through home range overlaps with males). This may explain why males moved at such high rates and appeared attracted to either sex during the breeding season.

When competition for females takes the form mainly of nonaggressive searching, then one expects a selective premium on such male traits as mobility, perceptiveness, and spatial memory (Trivers 1972; Thornhill and Alcock 1983; Schwagmeyer 1988). This may be the case with male badgers, since male badgers possessing higher mobility, better spatial learning, and greater abilities to track females may well acquire more mating opportunities (Gaulin and Fitzgerald 1986, 1989). Such males would also be more likely to efficiently monitor the status of multiple females and to be present when females were receptive, possibly resulting in a 'roaming' strategy (Erlinge and Sandell 1986, Sandell and Liberg 1992). Male badgers attempting to sequester a particular female for breeding exhibited male-male dominance, possibly as a function of age and size modified by 'prior rights' (Dunbar 1982; Erlinge et al. 1982; Sandell 1986; Korona 1991). We expect aging badgers to be more willing to engage in a serious fight (Packer and Pusey 1985; Korona 1991).

In conclusion, home range overlap did not differ within and between the sexes even though males greatly expanded their ranges during the breeding season. Home ranges and home range overlaps do not account for the temporal order of movements and therefore reveal little about animal interactions. For badgers, olfaction provides a mechanism for tracking resources and for the structured temporal interaction observed in this study. The key ingredients to understanding the unexpected overlap I observed among males seeking females are: high densities of males, patchy distribution of females connected to prey availability, and highly mobile females available for mating for only exceedingly brief time periods. Putting all these facets together, it seems that males could not monopolize and defend many particular females (since they would not know when those females would be in estrus, and intruder pressure would be high). Thus instead of a pattern of space use geared towards monopolizing resources, male badger space use is understood as a strategy for finding resources. Viewed in this light, males overlap in their habitat use because they are running around trying to find the same fleetingly available females and either scent-tracking females, cueing in on the same habitat features that are good predictors of females, or cueing in on the presence of other males as an indicator females are about.

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