Sexual selection for spatial-learning ability

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Abstract. Sex differences in spatial learning have been thought to be universal among mammals, but their adaptive significance has been neglected. Spatial-learning skills are hypothesized to evolve in proportion to navigational demands, and it is predicted that sex differences in spatial ability will evolve only in species where range expansion contributes differentially to the reproductive success of males and females. This prediction was tested via field studies of ranging behaviour and laboratory studies of spatial ability in two congeneric rodent species whose mating systems differ. Radiotelemetric studies showed that, in a polygynous species (meadow voles, Microtus pennsylvanicus), males expanded their ranges only during the breeding season and only when they attained full reproductive status. Females showed neither response. This suggests that range expansion was a male reproductive tactic. In contrast, a monogamous congener (prairie voles, M. ochrogaster) showed no sex differences in ranging, regardless of reproductive status. This probably reflects the relative inability of monogamous males and females to benefit from increased exposure to members of the opposite sex. When subsequently tested in a series of seven symmetrical mazes, subjects from the field studies exhibited the predicted sex-by-species patterns of spatial ability: only meadow voles showed consistent male superiority on these spatial tasks.

Sex differences in the ability to solve spatial problems are among the most reliable of human sex differences (Maccoby & Jacklin 1974; Harris 1978; McGee 1979; Wittig & Petersen 1979). Tests of spatial ability are diverse, but all require the mental manipulation of spatial data. Each test yields a characteristic male advantage: on some tests the male–female differential is slight, but on others the average man performs a full standard deviation above the average woman (e.g. Wilson & Vandenberg 1978; see Fig. 4 in Linn & Petersen 1985). Factor-analytic studies suggest two or three components to spatial ability, but such data-reduction techniques leave the male advantage intact, and meta-analytic approaches confirm its validity (McGee 1982; Rosenthal & Rubin 1982; Linn & Pulos 1983; Linn & Petersen 1985). Sex differences in spatial ability are not restricted to Homo sapiens. In both wild and laboratory rodents, males consistently outperform females on spatial tasks such as maze learning (e.g. McNemar & Stone 1952; Barrett & Ray 1970; Joseph et al. 1978). The apparent generality of this sex difference invites explanation.

Psychologists have explored the ontogenetic bases of sex differences in spatial ability. For example, androgens elevate spatial ability in humans and laboratory rodents and thus are a proximate cause of such sex differences (Dawson et al. 1973, 1975; Stewart et al. 1975; Joseph et al. 1978; Buchsbaum & Henkin 1980; Hier & Crowley 1982; Rovet & Netley 1982; Rosnick et al. 1986; Gaulin & Hoffman 1988). But regardless of what developmental pathways influence spatial ability, a complete analysis would explain why selection has differentially favoured spatial ability in the two sexes.

Sexual selection theory (Bateman 1949; Williams 1966; Trivers 1972; Wade 1979) provides a general model for the evolution of sex differences in morphology, physiology and behaviour. Briefly, the strength of disruptive selection (moving male and female phenotypes apart) depends on the ratio of male to female variance in reproductive success. When this variance ratio is near unity, disruptive selection will be weak. Otherwise, competition for mates will be more intense in the sex with higher variance in reproductive success, causing disruptive selection for the traits most useful in this competition. Monogamous mating systems tend to produce variance ratios around unity and are thus characterized by minimal sex differences; polygamous systems produce variance ratios that can deviate markedly from unity and thus foster the evolution of sexual dimorphism.

We postulate that selection should favour spatial
ability in proportion to the amount of spatial data an animal must process in its normal movements, and suggest that (in non-migratory species) home range size is a useful proxy measure for this amount of spatial data. If this postulate is correct, disruptive selection for spatial ability should be limited to species with dimorphic ranging patterns.

In polygynous mating systems, males are expected to evolve reproductive tactics that augment their share of matings (Bateman 1949). In some forms of polygyny, males compete by ranging widely in search of mates but females are relatively sedentary (Trivers 1972; Charles-Dominique 1977; Gaulin & FitzGerald 1988). Where these species exhibit discrete breeding seasons, male ranges typically contract, removing the sex difference during the non-reproductive phase (Stamps 1977; Farentinos 1979; Webster & Brooks 1981). The fact that range expansion is limited to reproductive males argues that it is a consequence of the differential competition for mates that drives sexual selection in polygynous species. In contrast, selective pressure for range expansion by males would be absent or greatly reduced in monogamous species, where a male's reproductive success is linked to that of a single female. Thus, monogamous species are characterized by isomorphic male and female ranges, regardless of reproductive activity (Brown 1966; Chivers 1974; Kleiman 1977; FitzGerald & Madison 1983; Gaulin & FitzGerald 1988).

Spatial ability has been examined previously in Homo sapiens and several wild and domestic rodents. All are at least mildly polygynous or of polygynous ancestry (Murdock 1967; Martin & May 1980; Dewsbury 1981), and, as discussed above, all show a male advantage on spatial tests. These data are in agreement with our evolutionary hypothesis, but the hypothesis can only be tested by examining whether monogamous species also exhibit sex differences in spatial ability.

A previous study (Gaulin & FitzGerald 1986) supports the proposed hypothesis by providing data on range size and sunburst-maze performance for males and females of two congeneric rodent species (meadow voles, Microtus pennsylvanicus, and pine voles, M. pinetorum) that differ in mating system. In the polygynous species, males had larger ranges and performed better in the maze, whereas in the monogamous species there were no sex differences in either range size or maze performance. The present study uses multiple measures of both range size and spatial ability, a different spatial task and a different monogamous species to test the generality of our previous findings.

**METHODS**

We evaluated the range sizes and maze-learning abilities of males and females in two congeneric rodent species whose mating systems differ. Meadow voles are polygynous; females have relatively small ranges and males travel much more widely, competing to encompass many female ranges within their own (Getz 1961; Madison 1980a, b). Prairie voles, Microtus ochrogaster, are relatively monogamous; mated pairs share a range from which each member excludes same-sex conspecifics and within which they jointly rear offspring (Getz & Carter 1980; Getz & Hoffman 1986). Extraneous variables often confound cross-species comparisons, but our use of congeners minimizes this problem.

**Field Methods**

Because reproductive tactics may vary among populations of a single species (e.g. Fricke 1980), we chose not to rely on previous accounts of ranging patterns in meadow and prairie voles. Instead we used radiotelemetry to study the movement patterns of individual males and females of these two species in their natural habitats. In 1986, three field telemetry studies were conducted, two on meadow voles and one on prairie voles. Two summer studies provided breeding-season data. During May and June, we studied 47 prairie voles on the Jasper County Prairie Chicken Reserve, near Newton IL. During July and August, 43 meadow voles were telemetered near Colyer Lake in Centre County, PA. Finally, in November, 35 meadow voles were telemetered near Murrysville, PA, to provide post-breeding data.

Our methods were identical in all three studies. We surveyed an approximately 0.5-ha study grid and marked north–south and east–west grid lines at 8-m intervals. During all subsequent phases of field research, observers walked only on these grid lines. Two small Sherman-style live-traps were
placed at each grid intersection and the entire grid was censused over a 3-day period. Each captured vole was classified by sex, age-class and reproductive status and uniquely toe clipped for subsequent identification. We classified all animals weighing more than 39 g as adult, and all animals with adult pelage but weighing less than 39 g as subadult. Males were classified as reproductive only if their testes were consistently in a scrotal position; females were considered to be reproductive if they were pregnant or lactating at any time during their period of field study.

Following the census, all adult voles and selected subadults received intraperitoneal transmitter implants (AVM Instrument or Custom Electronics) under metafane anaesthesia (Pittman-Moore). Transmitter implants averaged 6% of preoperative body weight. Data collection began 3 days after surgery. At 5-day intervals, we conducted a 24-h telemetry session followed by an 8-h live-trapping session. During the telemetry sessions, a pair of observers with portable radios (AVM Instrument or Custom Electronics) and hand-held yagi aerials (AF Agtronics) used triangulation to record each subject’s position once every 2 h. We recorded all positional data to the nearest 1 m, the limit of accuracy and reliability of our methods. During the trapping sessions we checked the identification, sex, weight and reproductive status of all captured voles. Each study involved five such telemetry and trapping sessions spread over approximately 1 month.

We used a minimum-convex-polygon algorithm (MCPAAL, National Zoological Park) to compute two measures of range size for each subject: mean daily range and total home range. We computed daily (24-h) ranges by applying the algorithm to the data from a single telemetry session. Repeating this for each telemetry session, we then computed the arithmetic mean daily range for each subject, our first measure of range size. The second measure, total home range, was computed by applying this same algorithm to a subject’s pooled positional data from all telemetry sessions. The two measures tap different aspects of ranging behaviour. For example, an individual might exploit a small area in any given 24-h period, but its total home range might nevertheless be large, depending on the extent to which it exploited separate areas on successive days. Both measures of range size were subjected to analysis of variance techniques (Dixon 1985) to test for differences related to species, sex or reproductive status. All P-values are reported in the conservative, two-tailed form.

**Laboratory Methods**

After the field studies, subjects were transported to our laboratory in Pittsburgh for spatial-ability testing. There they were maintained on a light:dark 14:10-h cycle and housed in 28 × 18 × 13-cm plastic cages with water bottles and Sanicel bedding. Except when food-deprived prior to training and testing, subjects were fed rabbit chow (Purina) and fresh apple ad libitum.

Spatial ability was evaluated in a series of seven automated, symmetrical mazes (Fig. 1) of a type previously shown to yield sex differences in laboratory rats (Davenport et al. 1970). Although our hypothesis is based on the postulated evolutionary consequences of searching for mates, 45-mg food pellets (Bioserve) were used as positive reinforcers in these experiments. Mates could not be used as rewards because sexual selection theory predicts that motivation would then have been unequal between the sexes of the (polygynous) meadow vole, but equal in males and females of the (monogamous) prairie vole. This sex-by-species pattern of motivation would, by itself, tend to yield superior male performance in meadow voles and minimal differences between the two sexes of prairie voles. Because this is precisely the pattern of results predicted by our hypothesis, we had to rule out this alternative explanation by choosing a reward (food) that would be more evenly motivating across groups. To equalize motivation in our design, all subjects were food-deprived (but not water-deprived) beginning 24 h before each of their training and testing sessions. Given the number of subjects and the time required for testing and maze reconstruction, a typical subject received food ad libitum on 12 of every 13 days.

The apparatus used in these experiments has two important advantages. First, because data were collected and logged automatically they are free of the effects of experimenter fatigue and bias. Second, symmetrical mazes minimize the amount of presumably disruptive handling because the subject runs a series of uninterrupted shuttles. This is especially important when dealing with wild as opposed to domesticated subjects.

Prior to testing, each subject was placed in one of
Gaulin & FitzGerald: Spatial-learning ability

Figure 1. Diagrams of the mazes. A detailed diagram of maze T-3 is shown. All mazes had symmetrically opposite goal-boxes at G and infra-red photocells to report the movement of the subjects. Areas marked E were monitored by photocells which, if activated, incremented the error count. Voles reportedly do not see infra-red but, as a precaution, each maze had an equal number of error and correct photocells, the latter shown only for maze T-3. Automated feeders (not shown) gave rewards only after complete traverses of the maze. The computer program is available on request.

Table 1. Mean range size (±se) for males and females of two meadow vole populations

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>Home range (m²)</th>
<th>Mean 24-h range (m²)</th>
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</thead>
<tbody>
<tr>
<td>Breeding population</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Females</td>
<td>22</td>
<td>157.4±26.1</td>
<td>64.0±10.4</td>
</tr>
<tr>
<td>Males</td>
<td>21</td>
<td>694.6±211.5</td>
<td>198.6±41.9</td>
</tr>
<tr>
<td>Non-breeding population</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Females</td>
<td>18</td>
<td>145.5±29.3</td>
<td>70.9±18.6</td>
</tr>
<tr>
<td>Males</td>
<td>17</td>
<td>204.9±42.7</td>
<td>84.8±17.5</td>
</tr>
</tbody>
</table>

In each spatial-ability test, a subject was placed in one of the two symmetrically opposite goal-boxes and its identification number was logged into the goal-boxes and food pellets were delivered at 30-s intervals. Next, each subject was placed in one goal-box and allowed to explore an unpartitioned version of the apparatus. In this second pre-training phase, food pellets were delivered each time the subject crossed the central arena to the opposite goal-box. This parallels the reward schedule used in testing (see below), but with no maze to be learned. When each subject had received these two types of pre-training, spatial-ability testing began.
Table II. Mean range size (±se) for reproductive and non-reproductive males and females of two breeding vole populations

<table>
<thead>
<tr>
<th></th>
<th>Home range (m²)</th>
<th>Mean 24-h range (m²)</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td></td>
</tr>
<tr>
<td><strong>Males</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Meadow voles*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reproductive</td>
<td>12</td>
<td>1124.8 ± 321.1</td>
</tr>
<tr>
<td>Non-reproductive</td>
<td>9</td>
<td>1211.2 ± 10.3</td>
</tr>
<tr>
<td>Prairie voles</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reproductive</td>
<td>18</td>
<td>270.1 ± 67.5</td>
</tr>
<tr>
<td>Non-reproductive</td>
<td>3</td>
<td>322.5 ± 224.7</td>
</tr>
<tr>
<td><strong>Females</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Meadow voles*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reproductive</td>
<td>8</td>
<td>162.8 ± 38.1</td>
</tr>
<tr>
<td>Non-reproductive</td>
<td>14</td>
<td>154.3 ± 35.7</td>
</tr>
<tr>
<td>Prairie voles</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reproductive</td>
<td>11</td>
<td>192.4 ± 33.6</td>
</tr>
<tr>
<td>Non-reproductive</td>
<td>15</td>
<td>176.6 ± 34.4</td>
</tr>
</tbody>
</table>

* Only the breeding (Colyer) population of meadow voles is included.

To guard against possible sampling biases (e.g. did toxin-exposed animals exhibit abnormal learning patterns; were those who ran the entire series of mazes a non-random sample?), data were analysed in two different ways. The first type of analysis was restricted to the 38 subjects that did run all seven mazes. This analysis consisted of a repeated-measures analysis of variance with the square root of total errors as the dependent variable, and three independent variables: sex and species were treated as 'between factors' and maze was a 'within factor' (repeated measure) yielding a 2 x 2 x 7 design. A square root transformation was applied to total errors to eliminate an unacceptable positive correlation between the 28 cell means and their standard deviations that characterized the raw data (Fig. 2). For the second type of analysis we included all the obtained spatial-ability measures for each subject, regardless of whether the subject had run all seven mazes. Analysis of variance is sometimes used for such data sets but the usual approach of substituting the mean score when a subject missed a particular maze artificially deflates the variance, thus distorting inferential techniques that depend on variance. Instead, we used Fisher's exact test to assess whether the number of mazes on which the average male performed better than the average female differed by species. All P-values are reported in the conservative, two-tailed form.

**RESULTS**

**Field Data**

During the breeding season, at least half of the adult females in each species were either pregnant or lactating, and all adult males had scrotal testes and were thus potentially breeding. In contrast, by late autumn, 67% of the adult females in the Murrysville population showed no signs of reproductive activity; only a single female was pregnant and five were still lactating, presumably for their last litters of the season. Similarly, most of the adult males in the Murrysville population showed testicular regression, only 30% still having scrotal testes.

There were minimal differences in body weight between the species and sexes. Prairie vole females
Figure 2. Total number (±SE) of errors per maze, by species and sex (a: meadow voles; b: prairie voles; ■: males; □: females). Mazes are arranged along the x-axis in order of presentation. Sample sizes are given below the bar; only those subjects that ran all seven mazes are included. See text for inferential statistics.

Averaged 46.3 g (±1.8 SE, N = 26); males averaged 45.6 g (±1.5, N = 21). Meadow vole females averaged 44.7 g (±1.0, N = 40); males averaged 44.9 g (±1.8, N = 38). Two-way analysis of variance indicated no significant effects for species, sex or the interaction (F < 0.6, P > 0.4).

Meadow voles showed patterns of range size that were dependent on both sex and reproductive activity. The range sizes of male meadow voles differed dramatically between the Colyer (breeding) and Murrysville (post-breeding) populations; in contrast, the range sizes of females in these two populations were virtually identical (Table I). When data were grouped by population and sex, two-way analyses of variance showed significant population-by-sex interactions for total home range (F = 4.76, P = 0.040) and for mean 24-h range (F = 5.85, P < 0.021). These interactions indicate that reproductive activity had no systematic influence on female range size, whereas male ranges expanded markedly during the breeding season.

Controlling for seasonality by considering only the Colyer (breeding) population of meadow voles and the Jasper County (breeding) population of prairie voles clarifies the differences between these polygynous and monogamous congeners. Reproductive males (those with scrotal testes) had ranges an order of magnitude larger than did non-reproductive males among meadow voles, whereas differences in range size between reproductive and non-reproductive males were trivial in prairie voles (Table II). When subjected to two-way analyses of variance by species and reproductive status, male range sizes showed significant species-by-status interactions for total home range (F = 7.58, P = 0.016) and for mean 24-h range (F = 11.78, P = 0.019). Thus, males in a polygynous species expanded their ranges on attaining reproductive status, but males in a monogamous species did not.

Female range sizes showed a strikingly different pattern (Table II). Two-way analyses of variance by species and reproductive status showed no significant main or interaction effects for either measure of range size (F < 0.50, P > 0.40). Thus, in both species, female range size was very stable across the reproductive transition.
Figure 3. Total number (± SE) of errors per maze, by species and sex (a: meadow voles; b: prairie voles; ■: males; □: females). Notation as in Fig. 2. All subjects are included regardless of whether they ran all seven mazes. See text for inferential statistics.

**Laboratory Data**

Spatial ability measures for the 38 subjects that ran all seven mazes (Fig. 2) were subjected to a repeated measures analysis of variance. The analysis examined three main effects (species, sex and maze) and four interaction effects; of these seven, only two were significant. A significant maze effect \((F = 90.96, P < 0.000)\) indicated that some mazes were more difficult than others. More importantly, a significant sex-by-species interaction \((F = 5.40, P = 0.026)\) conformed precisely to the predictions of our model: males outperformed females only in the polygynous species. Sex alone did not have a significant effect on maze performance across species \((F = 1.27, P = 0.268)\), supporting our expectation that sex differences in spatial ability should not be universal. Maze did not interact significantly \((F < 1.95, P > 0.075)\) with species, sex, or the combination; this suggested that the mazes were measuring the same parameter across all groups, thus providing unbiased comparisons.

Spatial-ability measures for all subjects, regardless of whether they ran the full series of seven mazes, are presented in Fig. 3. Among meadow voles, males averaged fewer errors than did females on all seven mazes; among prairie voles, males averaged fewer errors on three mazes and females averaged fewer errors on the remaining four mazes. This distribution \((7.0/3.4)\) deviates significantly from chance expectations \((P = 0.035, \text{Fisher's exact test})\).

**DISCUSSION**

Body size is a key determinant of range size (McNab 1963; Geist 1974), but in species such as prairie and meadow voles that lack size dimorphism, factors other than body size must be invoked to explain sex differences in ranging behaviour. Any surplus ranging behaviour presumably entails energetic (and perhaps risk) costs that should be avoided in the absence of compensa-
tory benefits. Sexual selection theory suggests a possible compensatory fitness benefit from additional matings, but this compensatory benefit would typically be limited to reproductively active males of polygynous species.

In breeding populations of the polygynous meadow vole, adult males have much larger ranges than do adult females, but sex differences in ranging are not apparent among non-reproductive subadults. Outside the breeding season, adult male ranges contract dramatically, although female ranges remain stable. In contrast, the monogamous prairie vole exhibits no sex differences in ranging patterns, even among breeding adults. These data from congeneric species support the idea that sexual selection influences range size: range expansion is limited to the single category of individuals (breeding males of a polygynous species) most likely to benefit from increased exposure to mates.

The principal threat to the validity of this comparison involves the possibility that differences between the Colyer and Murrysville meadow vole populations are not wholly the consequence of seasonal differences in reproductive activity. There may be environmental differences (e.g. food supply or predator density) that encourage divergent ranging behaviour at these two sites. Both internal and external evidence argue against this interpretation. Any habitat differences should affect females as well as males, but both measures of female range size are remarkably invariant between these two sites (Table 1). In addition, two other field studies have detailed seasonal changes in meadow vole ranging behaviour, and both report a major contraction in male ranges, but not female ranges, outside the breeding season (Webster & Brooks 1981; Madison et al. 1984). Thus, while this possible alternative explanation cannot be completely discounted, it seems unlikely.

Having demonstrated that home range size depends on both sex and mating system, we sought a parallel relationship between spatial ability and these sex-by-mating-system patterns of range size. Among meadow voles, the average male consistently outperformed the average female. This result is not surprising because it agrees with the large literature documenting male superiority on such tasks. The striking result is that identical methods failed to yield a similar pattern of sex differences in an equally large sample of congeneric prairie voles. This novel finding was predicted a priori from a consideration of sexual selection theory.

Because a series of factors may covary with mating system, alternative post hoc hypotheses could be generated to explain these results. Any serious contender should involve a plausible causal link, such as that between range size and the demand for spatial skills. Developmental explanations are possible but they offer a different level of analysis rather than mutually exclusive causal models. For example, it could be argued that the experience of exploiting larger ranges in the field allowed male meadow voles to outperform female conspecifics on the maze tasks. The lack of differential experience would, in this view, also account for the lack of differential maze performance by male and female prairie voles. But unless this developmental model can explain why male meadow voles range more widely and why ranging experience should have a lasting effect on cognition, it in no way undermines the idea that sexual selection is the ultimate cause of sex differences in spatial ability. Moreover, much work with laboratory rats indicates that sex differences in spatial learning reliably emerge in the absence of any opportunity for differential experience (McNemar & Stone 1932; Barrett & Ray 1970; Dawson et al. 1973, 1975; Stewart et al. 1975; Joseph et al. 1978).

It is important to consider if differential motivation, rather than differential spatial ability, could have produced this pattern of results. This would be a reasonable alternative hypothesis only if there were a sex bias in motivation that was restricted to meadow voles. However, the lack of any species or sex differences in body weight, combined with the constant deprivation period, should have served to equalize motivation across groups.

These results, as well as our previous work (Gaulin & FitzGerald 1986), support the validity of our model and its assumptions. We tentatively conclude that spatial-learning skills, such as those assessed in our mazes, evolved as a navigational adaptation. Moreover, sex differences in such spatial skills are to be expected only in species where the sexes reap differential reproductive benefits from range expansion. Where selective pressure for range expansion affects the sexes equally, sex differences in spatial ability will be minimal.

Many researchers have shown that sexual selection can influence behaviour. The resultant behavioural sex differences presumably depend on underlying psychological or cognitive sex differences. Unfortunately, the effects of sexual selection on cognition have seldom been directly demon-
strated, and when they are, the links to behaviour tend to be poorly specified. This research attempts to clarify the influence of sexual selection on a functionally linked cognitive and behavioural system.

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