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Natural Space-Use Patterns and Hippocampal Size in Kangaroo Rats

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Key Words
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Kangaroo rat, *Dipodomys*
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Sexual selection

Abstract
The size of the hippocampus, a forebrain structure that processes spatial information, correlates with the need to relocate food caches by passerine birds and with sex-specific patterns of space use in microtine rodents. The influences on hippocampal anatomy of sexual selection within species, and natural selection between species, have not yet been studied in concert, however. Here we report that natural space-use patterns predict hippocampal size within and between two species of kangaroo rats *(Dipodomys)*. Differences in foraging behavior suggest that Merriam's kangaroo rats *(D. merriami)* require better spatial abilities than bannertail kangaroo rats *(D. spectabilis)*. Sex-specific differences in mating strategy suggest that males of both species require more spatial ability than females. As predicted, hippocampal size (relative to brain size) is larger in Merriam's than in bannertail kangaroo rats, and males have larger hippocampi than females in both species. Males of a third species *(D. ordii)* also have smaller hippocampi than Merriam's kangaroo rat males, despite being similar to Merriam's in brain and body size. These results suggest that both natural and sexual selection affect the relative size and perhaps function of mammalian hippocampi. They also reassert that measures of functional subunits of the brain reveal more about brain evolution than measures of total brain size.

Introduction

Most mobile animals must determine and remember the spatial locations of critical resources. The hippocampal complex or formation, a forebrain structure in birds and mammals, is essential for integrating sensory information about cues in the environment into a geometric coordinate system, or cognitive map [O'Keefe and Nadel, 1978; Bingman et al., 1989]. This is not its entire role: the hippocampus does not mediate all types of spatial learning [Olton, 1982], and it is involved in some types of non-spatial learning [Cave and Squire, 1991; Eichenbaum et al., 1991]. However, an intact hippocampus is necessary for mapping spatial relationships in novel environments and using such relationships for navigation [Nadel, 1991; O'Keefe, 1991; Sutherland and Rudy, 1991]. Laboratory rats with hippo-

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campal damage are unable to form mental maps of their environment and hence cannot navigate to points in space using partial arrays of landmarks [Morris et al., 1982].

Hippocampal size has been found to correlate with suspected selection pressures on spatial abilities among species of passerine birds and within species of microtine rodents. Passerine birds that store food in scattered locations have a larger hippocampal complex than species that do not, indicating that natural selection for foraging efficiency, via the ability to remember cache locations, affects the size of this structure [Krebs et al., 1989; Sherry et al., 1989]. Even species that do not store food, however, may need to track the spatial distribution of resources, such as the location of mates. Microtine rodent species show sex differences in home range size, which is related to sex differences in mate searching behavior. Such natural measures of spatial ability are likewise correlated with sex differences in spatial learning ability [Gaulin and FitzGerald, 1986]. Finally, these behavioral dimorphisms predict the presence or absence of sex differences in hippocampal size [Jacobs et al., 1990]. This suggests that sexual selection, in addition to natural selection, may also lead to increases in hippocampal size.

Thus, there is evidence that at least two selective pressures, natural selection for foraging ability in passerine birds, and sexual selection for increased access to mates in microtine rodents, can lead to increases in hippocampal size. This suggests an interesting question: could we detect the effects of two selective forces, natural selection and sexual selection, operating simultaneously on hippocampal size? We present affirmative evidence that both mechanisms may affect the evolution of hippocampal size in wild rodents of the genus *Dipodomys*.

We measured relative hippocampal volume in Merriam's kangaroo rats *(D. merriami)* and bannertail kangaroo rats *(D. spectabilis)*. Merriam's kangaroo rats store seeds in scattered locations and use spatial memory to relocate these caches [Jacobs, 1992], whereas bannertail kangaroo rats return food to one central cache, which they defend [Schroder, 1979; Randall, 1984; Randall, 1993]. Although bannertails are larger than Merriam's (table I), their home ranges are smaller [Behrends et al., 1986a; Schroder, 1987]. Bannertail kangaroo rats are highly philopatric, usually spending their entire adult lives in a single burrow, and exploit rich food sources via obvious trails radiating out from the burrow [Schroder, 1979]. Merriam's kangaroo rats wander more widely while exploiting sparser patches of loose seeds, use trails less frequently, and shift burrow locations often [Behrends et al., 1986a, 1986b; Jones, 1989]. Together, these differences in foraging behavior suggest that Merriam's kangaroo rats experience greater selection pressure on the ability to map spatial relationships in novel areas and to remember many locations with precision. In accordance with Jerison's principle of proper mass in brain evolution [Jerison, 1973], we predicted that Merriam's kangaroo rats should have larger hippocampi, relative to total brain size, than do bannertails.

Although these species differ in foraging tactics, they have the same mating system. Males are polygynous, ranging widely during the breeding season to locate receptive females, which are more sedentary [Behrends et al., 1986a, 1986b; Randall, 1991]. Thus we predicted for both species that males should have larger hippocampi than females.

Materials and Methods

We collected adult kangaroo rats (table I) in Sherman live traps during the breeding season (March, 1989) near Portal, Arizona. The trapping transects were adjacent to sites where the behavior of both Merriam's and bannertail kangaroo rats have been studied intensively [Jones, 1984, 1989; Zeng and Brown, 1987; Randall, 1991]. All animals were trapped in the same habitat, with different species or sexes sometimes collected in the same trap on different nights. All males were in reproductive condition, i.e., with testes fully descended into the scrotum.

In addition to the Merriam's and bannertail kangaroo rats that we captured, Dr. Peter Waser donated four male Ord's kangaroo rats *(D. ordii)*, captured at the same time and place as the other species. These males were also in breeding condition. We had no a priori hypotheses regarding hippocampal anatomy in this species. Little is known about its food-hoarding behavior or if it exhibits sex differences in space use; its home range is intermediate in size to that of *D. merriami* and *D. spectabilis* [Schroder, 1987]. Nevertheless, we recorded the same brain measurements on Ord's males as for the other specimens, in order to derive hypotheses about this species' spatial behavior based on its brain anatomy.

We anesthetized kangaroo rats by intraperitoneal injection of sodium pentobarbitol (40 mg/kg of body weight) and recorded standard body measurements. Animals were then transcardially perfused with physiological saline followed by 10% buffered formalin solution. We dissected the brain from the skull in the field and placed it in formalin. In the laboratory, brains were uniformly trimmed caudal to cerebellum, weighed, postfixed in formalin and embedded in 0.05% gelatin and 30% egg albumin. The embedded tissue was then transferred to 15% and then 30% sucrose in phosphate buffer before sectioning. Frozen sections were cut in the horizontal plane at 80-μm intervals; every fourth section was mounted and stained for Nissl substance with cresyl violet. We traced the boundaries of the hippocampus (dentate gyrus and Ammon's horn) at ×14 magnification with a projection microscope, confirming boundaries at higher magnification when necessary. All slides were coded so that the tracing author was naive to the sex of the animal. Because bannertail kangaroo rat brains were much larger than brains from the smaller species, we could not avoid recognizing these brains. However, we adhered to strict criteria for hippocampal boundaries, making it unlikely that the knowledge of which species was being traced biased our measurements. In addition,

Table 1. Summary statistics for study specimens (mean ± SE)

Group	N	Body weight (g)	Brain weight (g)	Hippocampal volume (mm^3)	Relative brain size	Relative hippocampal volume
D. merriami						
Male	5	48.2±1.4	1.41±0.05	88.3±1.7	0.029±0.001	0.065±0.002
Female	4	42.0±2.4	1.36±0.04	76.5±2.5	0.033±0.002	0.058±0.002
All	9	45.4±1.6	1.39±0.03	83.1±2.5	0.031±0.001	0.062±0.002
D. spectabilis						
Male	5	130.2±2.9	2.18±0.02	117.2±1.8	0.017±0.005	0.056±0.001
Female	4	109.5±13.0	2.22±0.05	102.9±8.3	0.021±0.002	0.048±0.003
All	9	121.0±6.6	2.20±0.02	110.9±4.3	0.019±0.001	0.052±0.002
D. ordii						
Male	4	48.0±2.3	1.45±0.031	77.5±4.4	0.030±0.001	0.055±0.003

the brains of Merriam's and Ord's kangaroo rats were indistinguishable.

Hippocampal area was measured from serial sections of whole brain. We calculated the volume between sequential sections using the formula for the volume of a truncated cone [Sherry et al., 1989] and summed these for total hippocampal volume. Total brain volume was converted from brain weight by using brain specific gravity [Stephan, 1960].

The measurement of interest is relative hippocampal size. When the reference variable, e.g., brain size, does not vary between groups, ratios (e.g., hippocampal volume divided by brain volume) can be used in statistical comparisons. However, when there are differences in brain size between species or between males and females within a species, relative hippocampal size cannot be accurately assessed with such a ratio [Packard and Boardman, 1990]. Instead, the preferred method for intergroup comparisons is analysis of covariance (ANCOVA), which removes the effect of brain size on hippocampal size. However, this method assumes that the range of values for the reference variable, e.g., brain volume, overlaps between groups. This assumption holds for the intraspecific comparisons between males and females in both Merriam's and bannertail kangaroo rats, and was therefore used to compare hippocampal size between the sexes within each species. However, this method could not correct for the effect of brain size in the comparison between Merriam's (average brain weight = 1.39 g) and bannertails (average brain weight = 2.20 g). Instead, the observed hippocampal volume for each animal was compared to the expected hippocampal volume for a given brain volume. Expected hippocampal volume was calculated from the relationship between the hippocampus and brain size in published data on insectivore species [Stephan et al., 1981]. This is a unique data set on hippocampal size in small mammals, comprising 28 species from 7 insectivore families (sample size per species averaged 2.0, and ranged from 1 to 5). Insectivores are relatively similar to kangaroo rats in that they are small, terrestrial and nocturnal, and their prey is distributed in similar spatial patterns. We also included the two species of elephant shrews (*Elephantulus fuscipes* and *Rhynchocyon stuhlmanni*) from this data set, although elephant shrews have now been placed in their own order, Macroscelidae [Nowak, 1991]. Their data were included in the analysis, however, as elephant shrews are also ecologically similar to kangaroo rats. The species means for heteromyids were calculated from data collected in the present study and also data from one additional heteromyid species, the long-tailed pocket mouse (*Chaetodipus formosus*) (n = 1 female). This specimen was prepared using the same methods as for the kangaroo rats.

Based on the data from insectivores and elephant shrews, the equation describing the relationship between hippocampal size and brain size is:

$$\log(\text{hippocampal volume}) = 0.906\,(\log(\text{brain volume})) - 0.762$$

This equation was used to calculate expected hippocampal volume in each individual kangaroo rat from its observed brain volume, using the formula:

$$\text{Expected hippocampal volume} = (10^{-0.762})\,(\text{brain volume}^{0.906})$$

Deviation from the expected allometric relationship between hippocampal volume and brain volume was estimated by calculating the ratio between expected hippocampal volume and observed hippocampal volume. Species differences in this ratio, hereafter referred to as relative hippocampal size, were then analyzed using a one-way analysis of variance.

The original research reported here was performed under guidelines established by the National Institutes of Health and by the University of Utah Institutional Animal Care and Use Committee.

Results

The relationship between hippocampal volume and brain volume in small mammals, based on data from this and other studies, is shown in figure 1. The equation derived from the data on four heteromyid species was similar to that derived for the insectivores, viz., log (hippocampal volume) = 0.825 (log (brain volume)) − 0.691. Such a relationship, based on four species, of which three are conge-

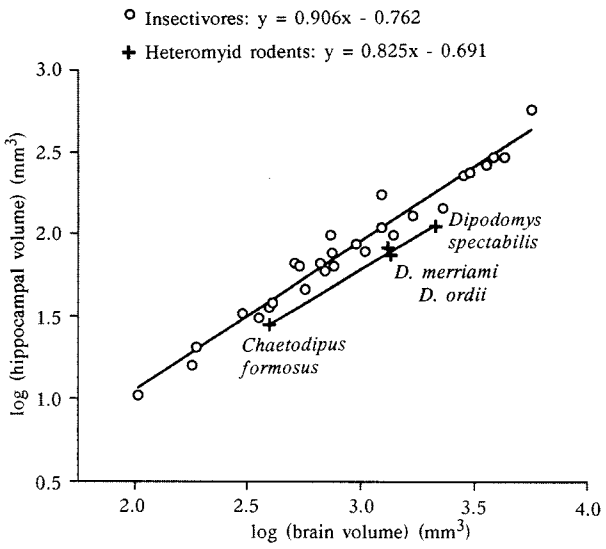

Fig. 1. The relationship between hippocampal volume and brain volume in insectivores (n = 28 species from 7 families) and heteromyid rodents (n = 4 species from the family Heteromyidae). Points represent mean values for each species; insectivores are represented by open circles and rodents by crosses.

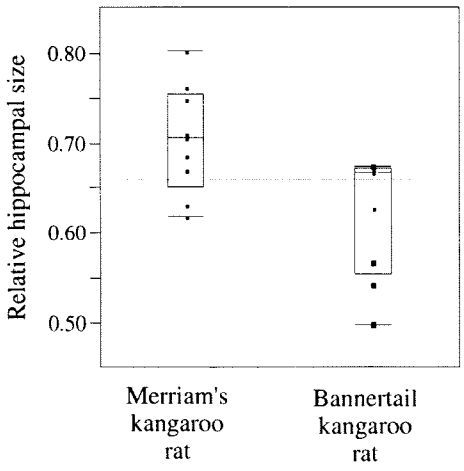

Fig. 2. Relative hippocampal size in Merriam's and bannertail kangaroo rats. Relative size was calculated from the ratio of observed hippocampal volume to expected hippocampal volume for a small mammal of equivalent brain volume. Box plots represent the 25%, 50% and 75% quantiles for each species; horizontal lines indicate the 10% and 90% quantiles.

ners, can only be considered preliminary. However, the similarity suggests that hippocampal allometry was comparable in the reference group – the insectivores – and in the group under study, the heteromyid rodents.

Using this relationship to correct for the effect of brain volume on hippocampal volume, we found that relative hippocampal size was significantly greater in Merriam's kangaroo rats than in bannertail rats (ANOVA; $F = 7.89$, $df = 1$, $p = 0.0126$) (fig. 2). The figure shows the variation in relative hippocampal size within each species. Thus, as predicted, the wide-ranging, scatter-hoarding species had a relatively larger hippocampus than the more sedentary, larder-hoarding species.

Also as predicted, both species showed sex differences in hippocampal size (fig. 3A, B). In both species, males had significantly larger hippocampi than did females, after correction was made for the effect of brain size (ANCOVA; Merriam's: $F = 11.41$, $df = 1$, $p = 0.0149$; bannertail: $F = 8.89$, $df = 1$, $p = 0.0246$). The linear regression of hippocampal volume on brain volume shows that some groups were more variable than others in this relationship. For example, in bannertails, the individual with the absolutely largest whole brain and hippocampus was female, not male. Many other factors influence sexual dimorphisms in the brain [Arnold and Breedlove, 1985; Gaulin and Hoffman, 1987], however, so it is not surprising to find this much variability.

We had predicted these patterns for relative hippocampal size, but we did not expect differences in relative brain size. To determine whether these hypothesized selection pressures also affect the size of the whole brain, we calculated the regression of log brain weight versus log body weight for the genus *Dipodomys*, using data for males of seven species [from Hafner and Hafner, 1984], which yielded a scaling exponent of 0.46± 0.09 SE. The exponent defining the slope between males of *D. merriami* and *D. spectabilis* is 0.44 (our data) or 0.49 [data from Hafner and Hafner, 1984], neither of which differs significantly from the genus slope. A slope calculated from our data combining sexes is 0.47, which is likewise no different from the genus slope. Thus, we found no significant departures in total brain size for our species from the established allometric relationship for the genus. Similarly, there are no within-species sex differences in relative brain size, although there is a trend towards larger brains in female bannertails (table 1).

Adding our sample of Ord's kangaroo rats to the analysis lent further support to the hypothesis that hippocampal size is related to patterns of natural space use. Ord's kangaroo rats appeared to be intermediate to the other species in

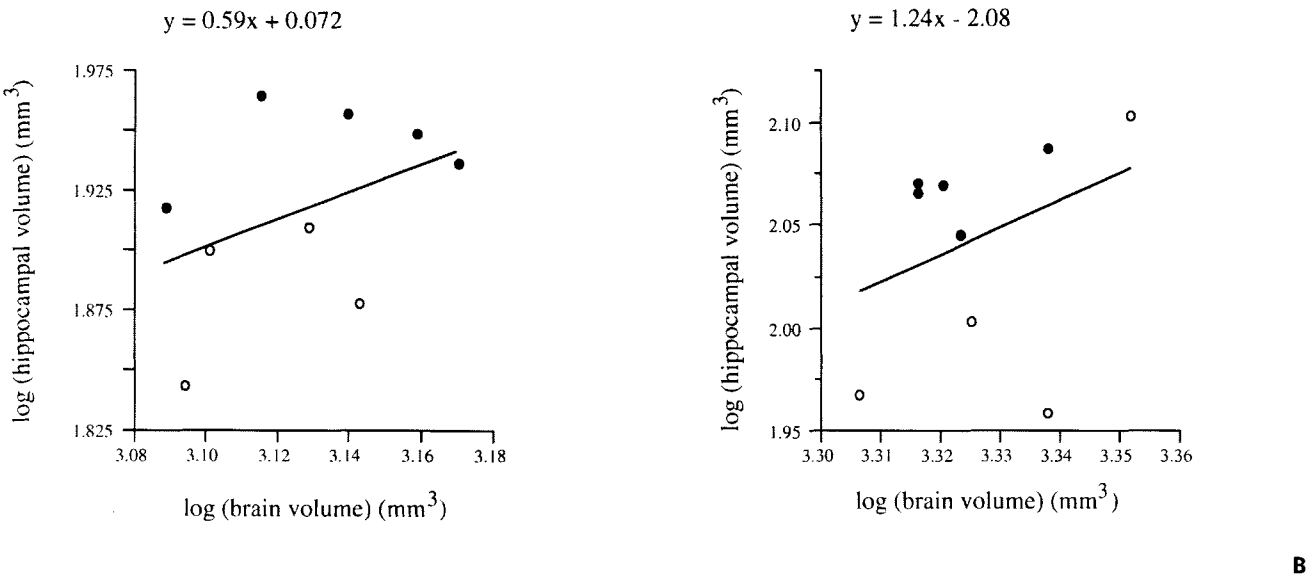

Fig. 3. Sex differences in hippocampal size in kangaroo rats. Points represent individual males (filled circle) and females (open circle); lines represent linear regressions. **A** Merriam's kangaroo rat. **B** Bannertail kangaroo rat.

hippocampal size (fig. 4). However, because we had no data on female Ord's, we limited our statistical comparisons to pairwise comparisons of relative hippocampal size among males. A one-way ANOVA yielded no significant differences between male Ord's kangaroo rats and male bannertail kangaroo rats in relative hippocampal size ($F = 1.21$, $df = 1$, $p = 0.307$). In contrast, Ord's kangaroo rats did have significantly smaller hippocampi than Merriam's kangaroo rats ($F = 5.64$, $df = 1$, $p = 0.0491$). Because these species do not differ in brain size, this species difference was reanalyzed and confirmed with ANCOVA ($F = 7.07$, $df = 1$, $p = 0.038$).

These results suggest that it is not just the spatial distribution of food caches per se that correlates with hippocampal size. Scatter hoarding species do not usually defend territories, but roam more widely and thus have larger home ranges [Vander Wall, 1990]. Mean home ranges (weighted Jennrich-Turner areas [Jennrich and Turner, 1969]) for *Dipodomys*, published in Schroder [1987] are: *D. merriami*, 1.79 ha ($n = 5$ males, 1 female); *D. ordii*, 1.28 ha ($n = 5$ males, 1 female); and *D. spectabilis*, 0.13 ha ($n = 1$ male, 3 females). Thus, species ranking by home range size roughly correlates with species ranking by relative hippocampal size (fig. 4). Home range size itself is only a rough measure of space use; more precise measures of space use

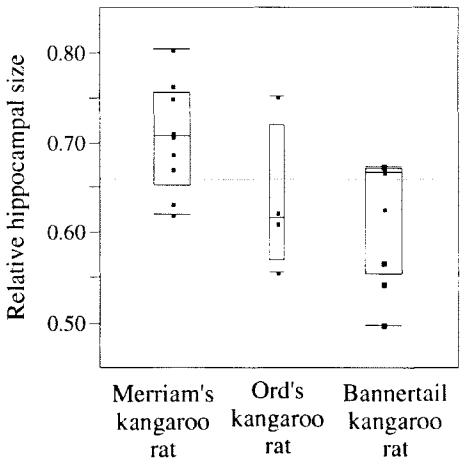

Fig. 4. Relative hippocampal size in three species of kangaroo rats. Relative size was calculated from the ratio of observed hippocampal volume to expected hippocampal volume for a small mammal of equivalent brain volume. Box plots represent the 25%, 50% and 75% quantiles for each species; horizontal lines indicate the 10% and 90% quantiles. The relative width of the box represents sample size per species ($n = 9, 4, 9$).

patterns, such as the number of new foraging sites visited in a foraging bout, may yield better correlations with hippocampal size [Spencer, 1992]. We must emphasize, however, that our interpretation of data from Ord's kangaroo rats is speculative, as we had no a priori predictions about this species.

Discussion

The size of the hippocampus has been correlated with requirements for spatial memory in birds [Krebs et al., 1989; Sherry et al., 1989] and spatial learning ability in rodents [Lipp et al., 1987; Jacobs et al., 1990]. This study presents further evidence that ecological demands on spatial abilities affect hippocampal size. Our findings suggest that species in the genus *Dipodomys* may have evolved special adaptations in the hippocampus, according to their need for spatial information processing. They also suggest that two mechanisms, natural selection for foraging behavior and sexual selection for increased efficiency in locating mates, may simultaneously act upon hippocampal size in kangaroo rats. Finally, we found that total brain size did not vary significantly among study groups, indicating that it is too gross a measure to correlate with behavioral differences in these animals.

A species difference in hippocampal size was predicted from patterns of space use and hoarding behavior. As predicted, the hippocampus of the wide-ranging, scatter-hoarding Merriam's kangaroo rat was significantly larger than that of its more sedentary and larder-hoarding congener, the bannertail kangaroo rat. Although our original hypothesis had only predicted this difference, hippocampal size in the Ord's kangaroo rat may also be related to patterns of natural space use. Despite the similarity in brain and body size between Ord's and Merriam's, hippocampal size was smaller in Ord's, as is the size of its home range in areas where it is sympatric with Merriam's [Schroder, 1987]. There are no published accounts of hoarding behavior, or the use of memory to retrieve food caches in Ord's kangaroo rats, however, so we can only speculate that this species is less dependent on spatial memory for cache retrieval than is Merriam's kangaroo rat. Field observations of caching behavior by Ord's kangaroo rats in Utah documented both scatter hoarding and larder hoarding [M. Daly, P. Behrends, M. Wilson and L. Jacobs, unpubl. data]. While these observations are preliminary, they suggest that the need for spatial processing in Ord's kangaroo rats may be more similar to that of bannertail kangaroo rats; i.e., they may be predominantly larder-hoarders. However, Ord's kangaroo rat has a large geographic range, and it is possible that the behavior of individuals in Utah is not related to the observed patterns of hippocampal size measured in Arizona individuals. Future experiments comparing the spatial learning ability of all three species on the same tasks could test the implications of the neuroanatomical pattern presented here.

Evidence to date indicates that sexual dimorphism in hippocampal size may be a typical phenomenon in polygamous mammals. In addition to the two heteromyid rodent species examined here, hippocampal size was found to be sexually dimorphic in the polygamous meadow vole, although not in the monogamous pine vole [Jacobs et al., 1990]. However, sex differences in hippocampal size have yet to be studied in other species, including the laboratory rat. This is surprising, given the ample evidence for sex differences in spatial learning in this species [Joseph et al., 1978; Williams et al., 1990]. However, spatial learning has previously been considered a nonreproductive behavior [Beatty, 1979], and therefore it was not expected that its neural basis was sexually dimorphic, in contrast to expectations regarding brain areas more directly associated with reproductive behaviors [Arnold, 1984]. We predict that dimorphism in hippocampal size will continue to be found in polygamous species, such as the laboratory rat [Dewsbury, 1981], and will prove to be the predominant pattern in mammals, most of which are polygamous [Daly and Wilson, 1983].

The first sexual dimorphism in hippocampal size in birds has recently been reported by Sherry et al. [1993]. This study reports a sexual dimorphism in hippocampal size in the nest-parasitic brown-headed cowbird *(Molothrus ater)*. In this species, females must locate the nests of host species, and thus they appear to have a greater demand for spatial memory than males; females also have a larger hippocampus than males. In contrast, hippocampal size was not sexually dimorphic in icterid species with mating systems where males and females face similar spatial demands. It is intriguing that sexual dimorphisms in hippocampal size can be found in such disparate taxa as mammals and birds, and that the direction of the sex difference is not absolute but must be predicted from the spatial ecology of the species. Such results are yet another example of the emerging pattern of the relationship between hippocampal size and the spatial distribution of resources [Sherry et al., 1992; Spencer, 1992].

The patterns of relative hippocampal size described here have important implications. First, it appears that hippocampal size responds to the ensemble of demands on spatial abilities, rather than to any single element. The home ranges and movement patterns of male and female kanga-

roo rats are similar during much of the year, but males have larger hippocampi, apparently owing to their distinctly different spatial behavior during the breeding season. And, although scatter-hoarding bird species have larger hippocampi than non-hoarders [Krebs et al., 1989; Sherry et al., 1989], male and female Merriam's kangaroo rats differ in hippocampal size despite similar food-caching behavior.

Thus relative hippocampal size appears to be correlated with the special function of the hippocampus, which is not just spatial memory but specifically the cognitive integration of locations to form a map of allocentric space. Such maps may contain information about locations of food caches, receptive females, or any other environmental attributes, and the need for maps of greater richness, complexity, or magnitude may select for a larger hippocampus.

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