The Ecology of Spatial Cognition

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49 PUBLICATIONS   **1,991** CITATIONS

64. Schenk, F. (1989) A homing procedure for studying spatial memory in immature and adult rodents, *J. Neurosci. Meth.* **26**, 249-258.
65. Schenk, F., Contant, B., and Grobéty, M.C. (1990) Angle and directionality affect rat's organization of visit sequences and spatial learning in modular mazes, *Learn. Motiv.* **21**, 164-189.
66. Schenk, F., Contant, B., and Werffeli, P. (1990) Intrahippocampal cholinergic grafts in aged rats compensate impairments in a radial maze and in a place learning task., *Exp. Brain Res.* **82**, 641-650.
67. Schenk, F. and Gafner, M. (1992) Spatial learning under limited access to visual landmarks, *Eur. J. Neurosci., Suppl.* **5**, 2315.
68. Schenk, F. and Gafner, M. (1993) Place learning in the absence of visual cues, *Eur. J. Neurosci., Suppl.* **6**.
69. Schenk, F. and Morris, R.G.M. (1985) Dissociation between components of spatial memory in rats after recovery from the effects of retrohippocampal lesions, *Exp. Brain Res.* **58** 11-28.
70. Sharp, P.E., Kubie, J.L., and Muller, R.U. (1990) Firing properties of hippocampal neurons in a visually symmetrical environment: contributions of multiple sensory cues and mnemonic processes, *J. Neurosci.* **10**, 3093-3105.
71. Sinden J.D., Hodges, H., and Gray, J.A. (in press) Neural transplant and recovery of cognitive function, *Behav. Brain Sci.*
72. Squire, L.R. (1992) Memory and the hippocampus: a synthesis from findings with rats and humans, *Psychol. Rev.* **99**, 195-231.
73. Strijkstra, A.M. and Bolhuis, J.J. (1987) Memory persistance of rats in a radial maze varies with training procedure, *Behav. Neural Biol.* **47**, 158-166.
74. Sutherland, R.J. and Dyck, R.H. (1983) Hippocampal and neocortical contributions to spatial learning and memory, *Neurosci. Abstract* **13** 189.9.
75. Suzuki, S.w, Augerinos, G., and Black, A.H. (1980) Stimulus control of spatial behavior on the eight-arm maze in rats, *Learn. Motiv.* **11**, 1-18.
76. Thinus-Blanc, C. (1987) *Cognitive Processes and Spatial Orientation in Animal and Man*, NATO Scientific Affairs Division, Dordrecht.
77. Thinus-Blanc, C. (in press) A model of animal spatial cognition, in H. Roitblat and J. A. Meyer (eds.), *Comparative Approach to Cognitive Science*, MIT Press, Cambridge (Mass.).
78. Wilkie, D.M. and Palfrey, R. (1987) A computer simulation model of rats' place navigation in the Morris water maze, *Behav. Res. Meth. Instr. Comp.* **19**, 400-403.
79. Whishaw, I.Q. (1991) Locale or taxon systems: no place for neophrenology? *Hippocampus* **1**, 272-274.

THE ECOLOGY OF SPATIAL COGNITION

Adaptive patterns of space use and hippocampal size in wild rodents

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"Just as the human body represents a whole museum of organs, each with a long evolutionary history, so we should expect to find that the mind is organized in a similar way. It can no more be a product without history than is the body in which it exists".

Carl Jung, *Man and His Symbols* (1964)

1. Introduction

To understand the brain and its function, it will be necessary to understand its evolutionary history. It is thus not surprising that one of most exciting developments in cognitive science is the interface between cognitive neuroscience and evolutionary biology. Certain areas of intersection may be more profitable than others, and in the present chapter, I will argue that one of the most important questions is the ecological and evolutionary significance of spatial cognition.

Spatial cognition is a major focus of cognitive neuroscience. Yet in the rush to understand spatial cognition in humans, more fundamental questions have often been left behind. For example, how did spatial cognition evolve? Why did spatial cognition evolve? What current ecological variables predict specializations in spatial cognition and its neural basis? A complete understanding of this ability will require multidisciplinary studies of the ecology, mechanism and function of spatial cognition.

What is the ecology of spatial cognition? Ironically, an animal's knowledge of the spatial distributions of resources is the cornerstone of behavioral ecology, the study of the "survival value of behavior" [40]. One of its basic tenets is that the spatial and temporal distribution of critical resources, such as food, refuge or mates, will determine the spatial dispersion and hence social organization behavior of animals competing for such resources [42]. This theory has predicted complex social and competitive interactions in a variety of animal species, both vertebrate and invertebrate, terrestrial and aquatic [40].

In short, an animal's knowledge of spatial distributions is critical to its survival and reproduction. To study the evolution of this cognitive trait requires knowledge both of its phylogenetic history and comparative studies of its current function. Comparative studies demand a diversity of species to be powerful and it is a happy coincidence that we have detailed knowledge of spatial cognition in a laboratory species, the Norwegian rat, which,

as a rodent, belongs to the most diverse order of mammals, the order Rodentia. Rodents have invaded most habitats on Earth and show an incredible diversity of lifestyles, both terrestrial, such as burrowing, running, gliding and climbing species, and aquatic. Rodents thus occupy a vast array of "spatial niches".

However, most rodents are solitary and nocturnal, taking in information largely via auditory and olfactory channels. What kind of spatial complexity do they experience? How is this related to their spatial learning ability and its neural basis? Because the laboratory rat has been the primary animal model for spatial cognition, it has also been the primary model for the neurophysiology of this ability. Decades of research on this topic has identified the important role of one forebrain structure in particular, the hippocampal complex or formation. Although the precise role of the hippocampus in spatial computations is hotly debated, its importance in integrating sensory information about cues in the environment into a geometric coordinate system, or cognitive map, is now widely accepted (see chapters by Nadel, and Schenk *et al.*, present volume).

Unfortunately, most of the work on spatial learning in rodents has been conducted under artificial conditions. Despite a sophisticated body of theory and physiological data on spatial computations in rodents, we are still largely ignorant of the context in which this ability has evolved. The purpose of the present chapter is to address this gap between theory and real world rodents, by presenting data on the ecology of space use, spatial learning ability and hippocampal size in a variety of rodent species.

2. Foraging and the Ecology of Spatial Learning

All mobile animals must track the spatial distribution of resources such as food, shelter and mates. However some species face greater challenges than others; for some species, resources may be more unpredictable in space and/or time, increasing the difficulty of remembering their location. For example, it is a robust finding that in primates, a frugivorous diet is associated with a larger brain size than is a folivorous diet [23]. At first, this makes intuitive sense: fruits are more sparsely and unpredictably distributed than leaves. Yet research on folivory has detailed the care with which foliovores must balance their intake of plant secondary chemicals, resulting in complex feeding strategies [77]. And if plants show individual differences in their production of protective chemicals [16], then foliovory would demand that a single, unchanging spatial distribution of trees must be learned; in other words, a "reference memory" task [48]. In contrast, frugivores also learn the spatial distribution of trees but face a heavier demand on their "working memory" [1]: for many frugivores, fruit ripens and either rots, drops or is taken by a competitor. Even if some trees characteristically produce better fruit, the important knowledge may be the spatiotemporal distribution: when were the fruits last checked, would more fruits have ripened by now, how many competitors have been in that area, etc.

2.1. THE CASE OF THE GRAY SQUIRREL

Such foraging decisions are faced not just by frugivorous primates but also by their temperate counterpart, seed-eating tree squirrels. On my field site in New Jersey, eastern gray squirrels (*Sciurus carolinensis*) foraged for seeds from a variety of tree species (three oaks (*Quercus*), three hickory (*Carya*) and one walnut (*Juglans*)). Hickory trees produced a seed high in lipids [24] and were the favored source of seeds to eat and cache, and nut quality varied consistently among individual trees within a species [26]. Thus a gray
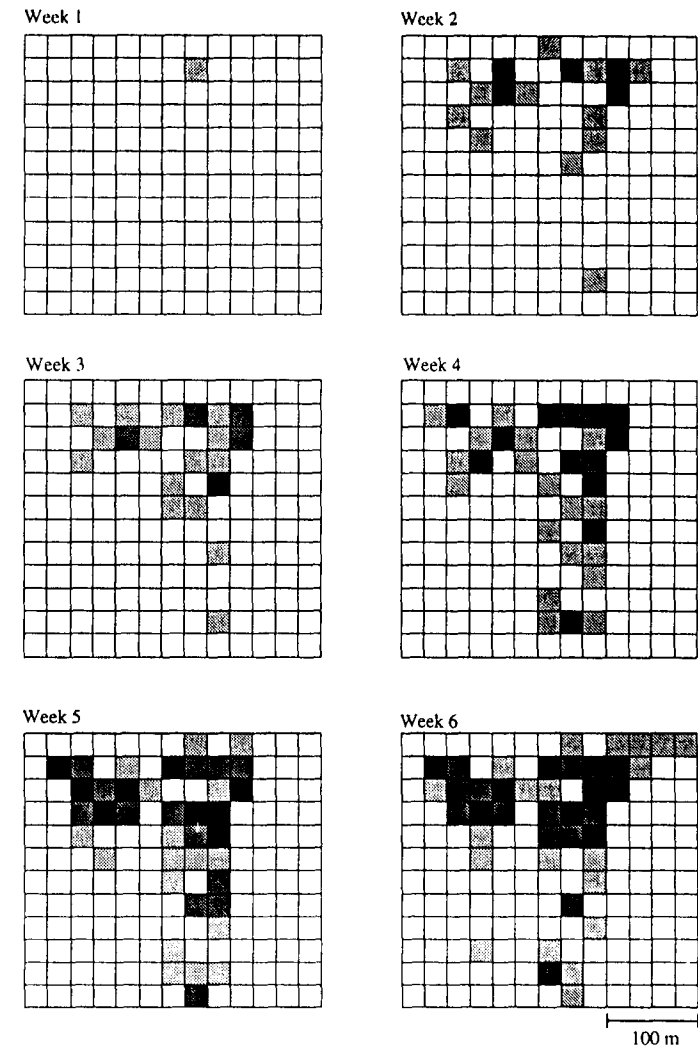

Figure 1. The spatiotemporal distribution of hickory trees showing evidence of use. Each map shows the cumulative activity of one week in 1984; each square represents a 25x25 m quadrant. The square's shading indicates the number of trees being used in that quadrant during each week (open = zero trees, light hatching = 1 tree; medium hatching = 2-3 trees; solid = 4-7 trees) (adapted from [26]).

squirrel, spending its life on a few hectares [15], faces the same reference memory task as the foliovore or frugivore: learning the location of the best food trees. But because of feeding competition, the actual spatial dispersion of seeds remains unpredictable. Figure 1 shows the change in spatial dispersion of food tree use over time on a site in New Jersey. Over three years, squirrels started the harvest in one small area then expanded their foraging ranges as the favorite trees were depleted.

Adding to the unpredictability of this resource is the temporal distribution of seeds. Oak and hickory tree species are "masting" species: individual trees produce a large crop at irregular intervals [52]. Thus a squirrel cannot predict the exact spatial distribution of food without carefully sampling the quality and density of nuts on a larger number of trees. And since this distribution changes daily, depending on the number of competitors, this task may require a large spatial memory capacity.

Many tree squirrel species face an even more challenging task: they scatter-hoard. Birds and mammals that scatter-hoard store all their food in small, undefended caches [46], though scatter-hoarding is best defined as the single deposition of food to a storage site [83]. This distinguishes it from the more familiar type of hoarding in rodents, larder hoarding, or multiple depositions to the same site. Thus scatter-hoarded, but not larder hoarded, food caches must be relocated at the time of consumption, which may be hours, days or months after they were first cached. Thus scatter-hoarders must find their food twice: first, when it is harvested and second, when the cache is retrieved.

This double challenge has resulted in specialized spatial memory abilities in scatter-hoarding birds (see chapters by Clayton and Krebs, and Shettleworth, present volume). Early work on marsh tits and black-capped chickadees additionally demonstrated that the birds were not finding caches by their odor [70]. In contrast, mammalian scatter-hoarders have long been assumed to rely exclusively on odor cues to relocate their caches, and to eschew the use of memory [75], despite the famed ability of laboratory rats in remembering the locations of scattered food items [54].

Gray squirrels are obligate food-storers, depending completely on their cached seeds for winter survival [78]. In addition, gray squirrels breed in mid-winter, and this fact may explain the strong correlation between adult female fecundity and the size of the hickory nut crop shown [51]. Thus a gray squirrel's ability to retrieve its caches, weeks or months after caching, not only dictates its survival but also its reproduction.

Gray squirrels frequently cache nuts in areas that adjoin or overlap with the caching areas of other squirrels [26]. Field studies have shown that tree squirrels can locate experimentally buried seeds by their odor [4, 74, 75, 78]. If they can also remember cache locations, gray squirrels would have a minimum repertoire of two retrieval strategies: trial-and-error search for cache odor, whether of their own or of other squirrels' caches, and memory for the locations of their own caches.

2.2. THE ROLE OF MEMORY IN CACHE RETRIEVAL

To find out whether gray squirrels can remember cache locations, I measured cache retrieval accuracy in captive gray squirrels, by comparing their success in retrieving nuts from caches that they had made, and caches other squirrels had made. If a squirrel remembers the locations of its caches, then it could retrieve more of its own caches than another squirrel's caches.

This proposition was tested on eight hand-reared male gray squirrels, caching and retrieving nuts in a large (5x10 m) outdoor arena. Squirrels were allowed to cache hazelnuts and then several days later, were re-released into the arena to find them again. During the delays, the original nuts were unearthed and, for the retrieval phase, new nuts were buried in their place. In addition, the number of caches was doubled, by adding 10 more caches to the original number; the locations of these caches had been chosen by other squirrels that
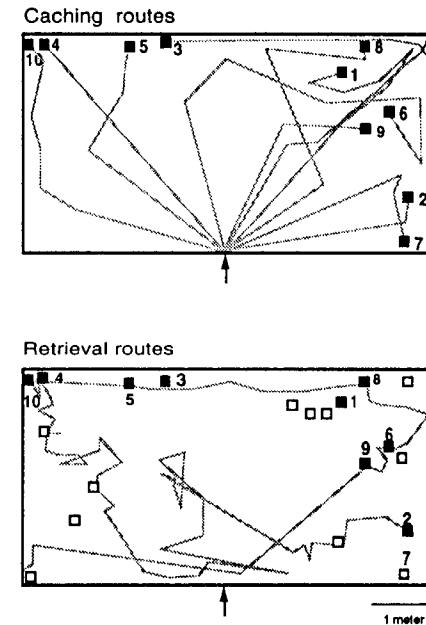

Figure 2. Schematic representation of caching and retrieval routes by the squirrel Alvin, after a delay of two days. Solid squares are Alvin's caches, open squares are the caches of other squirrels. Numbers refer to the sequence in which nuts were cached or retrieved, the arrow indicates the location of the observer and the source of hazelnuts (adapted from [30]).

week. Thus, the retrieval condition mimicked the situation faced by wild gray squirrels of looking for their own caches amongst a background of other squirrels' caches.

Although squirrels buried nuts in areas where other squirrels had also buried nuts, they retrieved significantly more nuts from their own cache sites than from the cache sites of other squirrels, even after delays of 4 or 12 days. This retrieval accuracy could not be explained by the squirrels' habitual use of the same areas: the ratio of own caches to other caches was greater than expected based on the availability of caches in the area searched during retrieval. A squirrel was also more likely to retrieve its own cache even when another squirrel's cache was closer to it or when a squirrel neglected to retrieve the cache closest to itself and instead dug up a more distant nut. Thus the results of this experiment clearly showed a bias of about 2:1 in favor of own caches. In addition, the path taken and the order in which caches were taken suggested the use of a cognitive map of the caches. Figure 2 shows the routes taken in one trial after a two day delay. Such an extreme difference in these routes suggest the use of a predetermined route based on a cognitive map of the caches. With such a map, a squirrel, having maximized cache dispersion and hence maximized the length of routes travelled during caching, could then minimize travel distance during retrieval [30]. It is an advantage of studying a walking scatter-hoarder, such as a squirrel, that these travel routes can be more easily measured than the routes followed by a scatter-hoarder caching in three dimensions, such as a bird.

This experiment demonstrated that a gray squirrel could use two simultaneous retrieval strategies: olfactory trial and error search and memory of specific locations. In some ways, this is not surprising, given the natural history of the gray squirrel. First, vision plays an important role in their behavior. Gray squirrels are diurnal, have good color vision and use visual signals to communicate. Thus visuospatial memory should play an important role in its foraging. Second, gray squirrels scatter-hoard thousands of nuts in a short period of time, and must recover them months later, often from underneath a deep snow cover [26, 78]. Snow reduces the transmission of olfactory cues and makes trial and error search much more energetically costly. However, a memory for a hidden cache site that is defined by its position relative to large, permanent landmarks, such as trees, would not be disrupted by such seasonal changes in microhabitat.

However just because a mammal makes adaptive use of visuospatial memory to relocate caches does not mean it is has a specialized ability to do so; this is the distinction between adaptive use and adaptive specialization first raised by Rozin and later applied by Sherry to the case of food-storers [68, 70]. First, it is necessary to find out if this ability is general or limited to obligate scatter-hoarders such as the gray squirrel. For example, many rodent species are nocturnal, not diurnal, and some scatter-hoarders forage, cache and retrieve their caches throughout the year, not with month-long delays. These scatter-hoarders are perhaps more typical and less likely to rely on memory; the scatter-hoarding gray squirrel could be the one exception to the mammalian rule.

2.3. THE CASE OF THE KANGAROO RAT

A more typical scatter-hoarder is the Merriam's kangaroo rat *(Dipodomys merriami)*. Like all kangaroo rats, Merriam's is a nocturnal, solitary desert granivore [64]. What is the spatial ecology of a scatter-hoarding kangaroo rat? How are their resources distributed in space and time? The ecological determinants of space use patterns have been well studied in several species, including Merriam's kangaroo rat. Kangaroo rats differ from other desert rodents in their ability to use bipedal locomotion to move at high speeds [50]. Perhaps for this reason, kangaroo rats are able to forage in the open areas of the desert, relying on their speed and specialized low frequency hearing to detect and avoid predators [79, 84]. Kangaroo rats collect the tiny seeds produced by desert shrubs and annuals into external, fur-lined cheek pouches. Most of these plants produce tiny, wind-dispersed seeds that must be sifted from the sand, though higher concentrations may accumulate in certain areas [65]. Thus seeds are distributed unpredictably in time and space and, depending on the microhabitat, a kangaroo rat may have to forage over wide areas. Although many kangaroo rats larder hoard, Merriam's kangaroo rats scatter-hoard seeds in small surface caches [7]. Their caching areas are not defended yet their ability to retrieve their caches is critical for survival.

Not only do Merriam's kangaroo rats not defend a central larder, they do not even have a central burrow. Instead, they use a series of temporary dwellings, or "day burrows", where they spend the day. At night, kangaroo rats forage from trips from the day burrow or from other burrows. Foraging bouts may keep a kangaroo rat in the center of its foraging range throughout the night, but it will return to its day burrow at the end of its activity bout [2, 3].

Can Merriam's kangaroo rats rely solely on their memory for cache locations for cache retrieval? I addressed this question with a second study of memory for cache locations, this time using male and female Merriam's kangaroo rats that had been trapped as adults in the
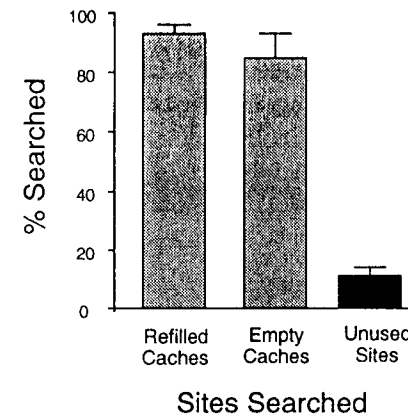

Figure 3. Cache retrieval accuracy in Merriam kangaroo rats. The bars indicate the percentage of cups searched from three different categories: cups which had been used for caching and contained seeds, cups which had been used for caching but had been emptied and cups which had not been used for caching.

field. The goal of this experiment was to remove odor as a possible cue for cache location. Kangaroo rats cached sunflower seeds in sand-filled cups in a small arena (1 x 2 m) and then were allowed to retrieve their caches 24 h later. I removed odor cues first, by washing all the surfaces before retrieval, and second, by replacing only half the number of original caches. By observing their subsequent search of cups, I could compare the probability of searching in cups that did or did not contain seeds. As cups without seeds offered no other clue to cache history than location, the kangaroo rats' search of these cups indicated their spatial memory of the location. Thus, this experiment differed from the squirrel experiment in several ways: caches were reduced, not doubled, and odor cues were removed.

Despite these differences, kangaroo rats appeared to be using the same retrieval strategy as squirrels: they searched the sites in which they had cached 24 h earlier. They were, in fact, equally likely to search cups with or without seeds, and were very unlikely to search cups where they had not cached earlier, as shown in Figure 3. In addition, a closer examination of the "errors" revealed that the non-cache cups tended to be located near cache cups and were more likely to be visited after all the caches had been emptied. Thus rather than errors, this may have been a targeted retrieval strategy [27].

Thus, like squirrels, kangaroo rats can retrieve caches accurately using their memory of specific locations. In contrast to the squirrel experiment, this experiment also showed that odor cues from the cache are not necessary for accurate retrieval by a mammalian scatter-hoarder, as is also true for birds. Despite differences in their sensory capabilities, scatter-hoarding birds and mammals may have the same need for increased spatial memory capacity in order to maximize the efficiency of cache retrieval.

3. Adaptive Significance of Memory

These results are important in setting the stage for an ecological analysis of spatial memory in food-storers. What is the adaptive significance of this ability? What are the benefits of using memory to retrieve caches? And finally, what does a mammalian scatter-hoarder really remember? As in birds (see chapters by Clayton and Krebs, and Shettleworth, present volume), it could remember where it has cached, where it has retrieved caches, or, perhaps most importantly, where it has failed to retrieve caches, i.e., where its caches have been pilfered.
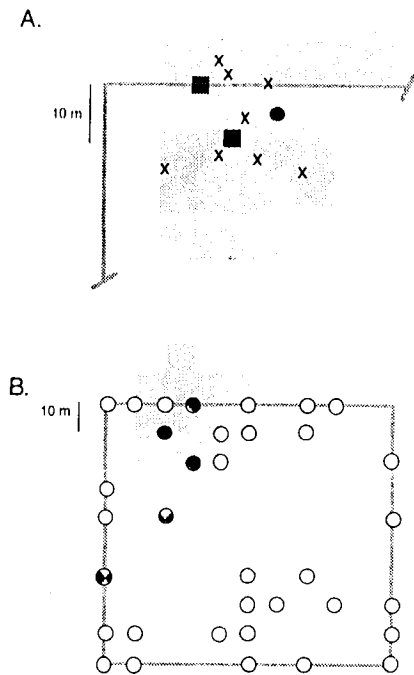
Figure 4. The cache distribution and subsequent pilfering of caches in one focal individual, Female HL1. A) The solid circle indicates her current day burrow, the filled square indicate provisioning sites, and X's indicate caches. Light hatched areas indicate her movements prior to provisioning. B) Circles indicates trap sites. Filled circles indicate that the trapped animal showed evidence of dye in its bolus. Solid circle the trap site of the provisioned kangaroo rat, female HL1; the hatched circle indicates the trap sites of other individuals with dye traces (2 other kangaroo rats, 1 pocket mouse, 1 cactus mouse), and open circles are trapped individuals who did not show traces of dye.

3.1. CACHE PILFERING AND SPATIAL MEMORY

The loss of caches to pilfering competitors is obviously an important driving force behind food-storing behavior [80]. Without pilferers, foragers would have little reason to store food; they should either not store food at all but leave it where they found it or, at most, store their caches in one easily accessible location. Martin Daly, Margo Wilson and I have begun field studies to document such costs of pilfering. We have devised a simple method to track the fate of caches: applying vital dyes to provisioned bait. The dyes are taken in with the food and pass out in the fecal bolus within 24 h, or more importantly, whenever the animal eats again from the cached, dyed food. Using this "pulse-chase" design, we target an individually radio-tagged kangaroo rat, give it a specific quantity of dyed bait and then monitor the appearance of dye in the entire rodent community over a given period of days (Fig. 4).

The dye method has allowed us to follow the fate of caches and derive minimum estimates of pilfering risk. The first experiments on kangaroo rats, in an assemblage of four other granivorous species (species of *Chaetodipus*, *Perognathus*, and two species of *Pero-*
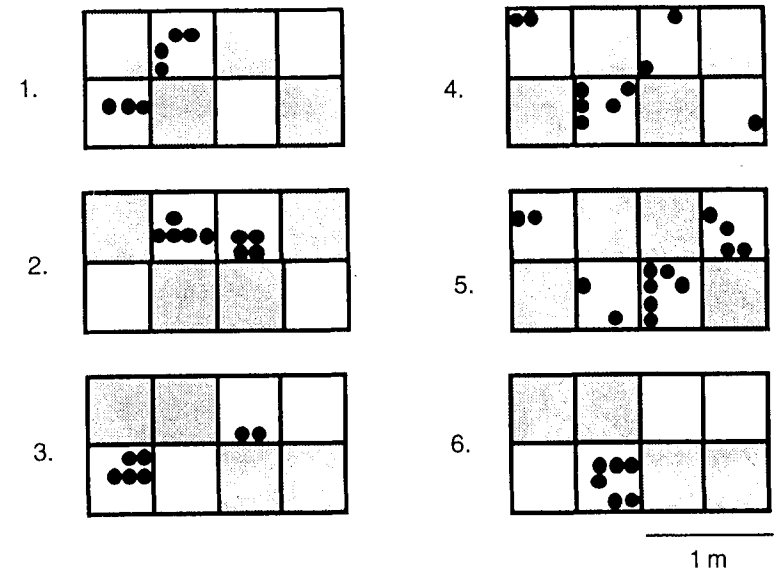

Figure 5. The distributions of caches produced in six consecutive trials by one kangaroo rat (male 613). Open squares indicate plates that contained a regular array of 16 sand-filled cups for caching; solid squares indicate areas of the arena without sand cups for caching. Filled circles indicate cache locations (adapted from [27]).

myscus) yielded the following results. First, a kangaroo rat's caches can be pilfered by up to three of four other species, in addition to predations by other kangaroo rats. Second, pilfering kangaroo rats are often neighbors, and finally, caches are more likely to be pilfered in areas where animals are at a high density. Thus in our study site, evidence from the dyed caches of animals living in areas with fewer neighbors, were less likely to appear in the boluses of other individuals.

The dye tracking method, albeit crude, confirms that pilfering presents real costs to scatter-hoarders. Perhaps the main weapon a kangaroo rat can muster in its war against the pilferers is its spatial memory of caches. Memory for cache locations can allow it to play the shell game with the pilferers and win, by arranging its caches in unpredictable arrays. It is clear that the use of memory should and does have immediate benefits in kangaroo rats. Figure 5 shows the cache distribution of one male in the memory experiment. I then allowed other kangaroo rats the opportunity to pilfer these caches. Given the same 24 h period of food deprivation and search time, the cache owner of the caches found 31% more caches than did the pilferers [27].

Thus, it is clear that Merriam's kangaroo rats may face stiff competition from cache pilferers. Because they do not defend cache sites, their main defense against such pilfering is increasing the unpredictability of cache locations or decreasing their density, as we have shown using artificial caches [7]. However, the more unpredictable the cache array, the more difficult it should be to remember individual cache sites. Thus, how an animal place its caches should be a trade-off between the costs of loss to pilferage and cost of an increased used of spatial memory.
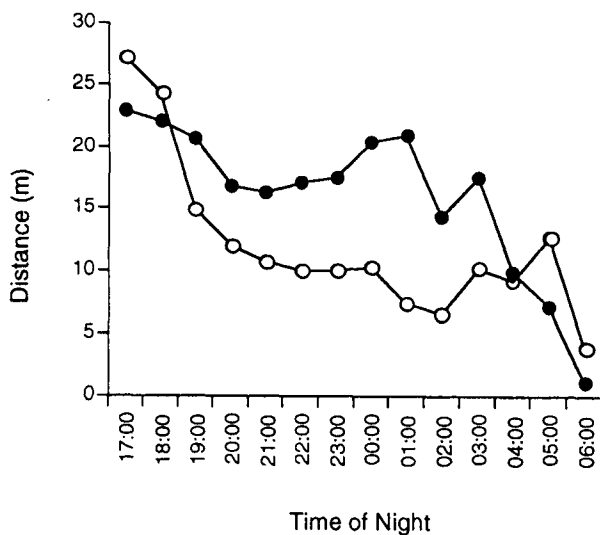
Figure 6. Aboveground activity as revealed by kangaroo rats' mean distance from their day burrow at scheduled hourly radiotransmitter fixes, according to moon phase. Data are pooled for 179 individuals tracked between 1980 and 1990 on the deep Canyon site, and are from dates within 3 weeks of the winter solstice; sunset occurred within the hour before the 1700 radio fix and sunrise within the hour after 0600 radio fix (adapted from [6]).

3.2. PREDATION AND SPACE USE

Among the most conspicous adaptation of kangaroo rats to their niche are their anti-predator adaptations, i.e., fast locomotion and ability to detect predators by sound [79, 84]. Thus kangaroo rats specialize in foraging under the constraints of constant predation risk, further shaping the spatial cognitive task they face. They must not only remember where their caches are, where their pilfering neighbors are and even where the caches of their pilfering neighbors are, but where and when it is safe to forage, cache and to retrieve caches.

On our study site in Southern California (Deep Canyon Desert Research Station), Merriam's kangaroo rats face a panoply of predators. We have documented predation by coyote (*Canis latrans*), great horned owl (*Bubo virginianus*), northern shrike (*Lanius ludovicianus*) and four species of snakes (3 rattlesnakes, 1 gopher snake) [8]. We have documented one response in detail: the avoidance of activity under bright moonlight. This is a well described phenomenon: nocturnal desert rodents are less active under high light conditions of the full moon [43, 61]. However, our results, based on data from 156 radiotagged kangaroo rats tracked between 1980 and 1992 on the Deep Canyon site, show that kangaroo rats are exquisitely sensitive to time of risk. We found that avoidance of activity is modulated hour by hour, that the pattern reverses under dark moon conditions [6] and that changes in activity influence not only their risk of predation but also their risk to certain species of predator [8]. As seen in Fig. 6, during the full moon, kangaroo rats concentrate their aboveground activity during the crepuscular periods. The opposite pattern is seen during the new moon, the darkest period of the lunar cycle: kangaroo rat activity peaks at midnight [6].

In addition, kangaroo rats may have to keep track of the place of risk. Our long-term monitoring of kangaroo rats show that predation events are not independent; a cluster of predations by a certain type of predator, such as Great Horned Owl, suggests predators move through desert concentrating on local areas. Although this raises interesting questions about the spatial cognitive ability of owls as they search for kangaroo rats (especially as owls on our site often scatter-hoard kangaroo rats after they have been killed!), it also suggests such patterns are predictable, and thus can be learned by resident kangaroo rats. Current research in my laboratory is addressing these questions.

Thus, it is clear that the risk of predation must continually act to reduce aboveground activity. Our evidence for this comes from the radiotracking records of animals that were subsequently taken by predators. Our standard data on movements consists of hourly radio-fixes, which yields mean movement between fixes. Records collected between 1980 and 1990 on 50 predation events, allowed us to compare the movements of 44 recent predation victims with other kangaroo rats tracked simultaneously but escaping predation. The comparison supports the hypothesis that activity is costly: victims had moved significantly greater distances between radio fixes than their contemporaries at the time of their death [8].

3.3. SEX DIFFERENCES IN SPACE USE

If activity increases the risk of predation, why are some kangaroo rats more active? One of the main predictors of activity is reproductive condition. Both males and females increase the rates of movement in their home range during the breeding season [2], and this is correlated with increased predation. However, there is also a sex difference in the change of activity level and hence in the risk of predation. Males show significant increases in the rate of movement relative to females, and this is correlated with a correspondingly high rate of predation. Why do males incur higher risk? In kangaroo rats, it appears that familiarity breeds not contempt but receptivity to mate. Male kangaroo rats increase visitation to neighboring females and such increased visitation appears to positively influence female mate choice [62, 63].

3.4. SEX DIFFERENCES IN SPATIAL LEARNING

Such sex differences in space use are typical in polygynous mammalian species. Females generally have small, localized ranges, while range expansion is an important tactic used by polygamous males to maximize the number of potential mates [82]. Thus, in these systems, mobility confers greater reproductive benefits on males than on females. This leads to inequality of space use during the breeding season and thus under polygamy, the two sexes experience divergent selective pressures for spatial ability. Under polygyny, males should profit more than females from any increase in spatial skills that could facilitate mobility. The process of acquiring mates might include: locating and remembering the burrows of females, monitoring their state of receptivity by olfactory investigation, leaving scent marks at regular intervals such that familiarity is increased - all of these tasks could require a significant commitment to spatial learning.

However, such sex differences in space use are absent in species with monogamous mating systems [57]. In monogamous species, the sexes exhibit convergent reproductive strategies. They exploit the environment in similar ways and thus express similar patterns of space use (Fig. 7). Gaulin and FitzGerald [20, 22] predicted that such differences in space
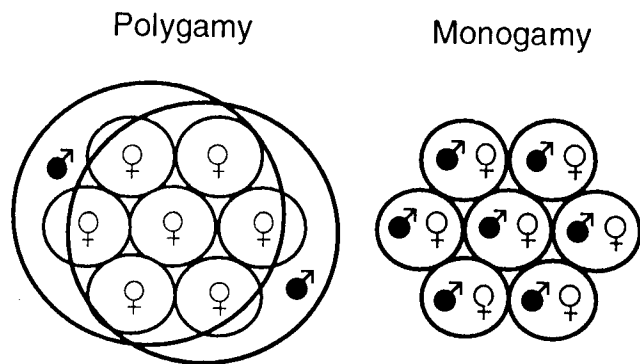
Polygamy   Monogamy

Figure 7. Schematic diagram of space use in mammalian species with different mating systems. Under polygamy, male home-ranges encompass several smaller female ranges; under monogamy, males and females share a joint home-range or territory.

use would result in the presence of sex differences in spatial learning in polygamous species, and the absence of such differences in monogamous species. They tested this hypothesis with several species of voles, rodents in the genus *Microtus*, a genus which displays nearly the entire range of mammalian mating systems, from promiscuity to monogamy [55]. Thus in polygamous species, such as the meadow vole (*M. pennsylvanicus*), breeding males may range over areas four to five times greater than those of breeding females. This sex difference in range size is absent among immature meadow voles and among adults outside the breeding season, indicating that range expansion is a sexually selected male reproductive tactic. Monogamous vole species, such as pine (*M. pinetorum*) and prairie voles (*M. ochrogaster*), lack such sex differences in ranging behavior, regardless of age or reproductive condition. As predicted, voles of polygamous species exhibited strong sex differences in spatial ability; in contrast, monogamous vole species, tested under identical conditions, lacked such sex differences (reviewed in [19]). The hypothesis that sexual selection can predict patterns of spatial learning ability, also offered an explanation for previous observations of sex differences in spatial learning in laboratory rats, a domesticate of polygynous ancestry [14].

3.5. SEX-SPECIFIC SPATIAL ABILITIES

The difference between males and females appears to result from two sex-specific specializations in spatial learning: navigational ability and memory for object location. Navigational ability has been conceptualized as the ability to form cognitive maps, from which an animal may construct novel routes to locations, or construct routes based on partial arrays of landmarks [81]. This is an oversimplification, of course, of an important concept which has been and continues to be discussed at many levels of analysis [18, 53, 60] (see chapter by Schenk *et al.*, present volume). However, for present purposes it is this type of spatial ability that is required for locating and remembering the locations of ephemeral resources, such as receptive females. In the laboratory, such navigational abilities have been assayed by performance on mazes, such as the symmetrical maze [12]; the radial arm maze [54], and the water maze [47]. Superior acquisition of these tasks have been demonstrated

in males from several polygamous species [12, 22, 86] similar pattern has been observed in our own species [38].

In contrast, polygamous females show different specializations in spatial learning. Females appear to attend instead to more fine-grained spatial details of an environment, such as the appearance and location of visual landmarks. In laboratory rats, if such landmarks are altered, female performance shows much greater disruption than male performance [86].

Such specialization in female spatial learning has also been demonstrated in humans [72] and desert kangaroo rats. Kangaroo rats were trained to locate a hidden plastic token which, if found, resulted in a food reward. Using similar methods to studies of laboratory rats, the arena was rotated to disrupt performance; as predicted female performance was more disrupted than that of males by such rotations [42].

4. Brain Allocation and the Hippocampus

Other contributors to this volume will have addressed questions of hippocampal structure, function, genetics and development in detail (see chapters by Clayton and Krebs, and Shettleworth, present volume). Thus I will pass lightly over these topics and concentrate instead on simple patterns of hippocampal size in wild rodents and their ecological and evolutionary significance.

The first suggestion that the size of the hippocampus could be correlated with natural patterns of spatial behavior came from studies of passerine birds [5, 41, 71]. The extraordinary result that food-storing species have proportionately larger hippocampal formations than species that do not store food opened up a new field: neuroethological studies of spatial cognition. Yet our knowledge of hippocampal function was still limited to studies of laboratory rodents, raised and tested under simple laboratory conditions. The following studies are a first attempt to bridge this gap between the neurophysiology of spatial cognition in the lab rodent and the role of spatial cognition in the behavior of wild rodents.

Size, of course, is a crude measure of brain allocation. However, it is a basic principle of brain evolution that increased function is reflected in increased complexity of its neural basis. Although this has recently been questioned [66, 67], it is still a conservative and useful starting point with which to think about brain evolution. Thus, given the caveat that the notion of "bigger is better" is always an assumption to be tested (see also chapter by Deacon, present volume), we can ask questions about the relative allocation of brain to functional subunits. In the case of the hippocampal formation, we assume that certain species will need more detailed cognitive maps or a greater storage capacity for spatial data or even a faster coding and/or retrieval of spatial information. All of these conditions might be sufficient selective pressure to change the allocation of brain space to increased investment in the hippocampal formation (or, as I will refer to the Ammon's horn and dentate gyrus in the rest of this chapter, the hippocampus). As discussed elsewhere in this volume, the size of the hippocampal formation in songbirds is correlated with food-storing behavior.

Thus, one would predict that differences in space use predict differences in hippocampal size; i.e., rodents that must track unpredictable spatial distributions of critical resources should have proportionately larger hippocampi (see chapter by Clayton and Krebs, and Shettleworth, present volume).

4.1. HIPPOCAMPAL SIZE IN FOOD-STORING RODENTS

The first question one might ask is whether, like birds, food-storing rodents have relatively larger hippocampi than rodent species that do not store food. However, because most rodent food-storers use only a single larder [83], such a *"cognitive niche"* would not demand adaptive specializations or even the use of spatial memory. Thus species using the common strategy of larder hoarding should be predicted to have less allocation to hippocampus than closely related species using a memory-intensive strategy such as scatter-hoarding.

In collaboration with Wayne Spencer, I tested this hypothesis by comparing relative hippocampal volume in Merriam's kangaroo rats and bannertail kangaroo rats (*D. spectabilis*). These species are sympatric throughout much of their range and although their diets and mating systems are similar, they differ dramatically in their method of food-storage. As discussed earlier, Merriam's kangaroo rats store seeds in scattered locations and use spatial memory to relocate these caches [27] whereas bannertail kangaroo rats return food to one central cache, which they defend. Bannertails are larger than Merriam's and defend small, productive territories from which they harvest seeds, using a series of trails which emanate from a centrally located burrow [36, 64]. Merriam's, in contrast, forage over larger areas and do not maintain a permanent home burrow [3]. Together, these differences in behavior suggest that Merriam's kangaroo rats experience greater selection pressure on the ability to map spatial relationships among new food sources or to remember the precise locations of food caches.

We trapped wild adult male kangaroo rats from these species during the breeding season on sites near Portal, Arizona: Merriam's, bannertails and Ord's (*D. ordii*). Much less is known of the ecology of Ord's kangaroo rats, despite a wide geographical distribution [64]. However, Schroder [69] measured home range utilization in all three Portal species of kangaroo rat, and found that Ord's home range was intermediate in size between Merriam's and bannertails. Thus we also measured hippocampal volume in Ord's kangaroo rats, with the prediction that it might also be intermediate in size. Finally, although these species differ in foraging tactics, they all have the same mating system. Thus, bannertails are also polygynous, and males increase their space use dramatically during the breeding season [62]. This predicts that in addition to the species differences in hippocampal size, predicted by home range size and food-storing behavior, we would also see differences in hippocampal size between males and females.

Hippocampal volume was measured using standard histological techniques: perfusion with buffered formalin, sectioning of frozen tissue and staining for Nissl substance with cresyl violet. Hippocampal areas were then digitized from projected images of serial sections, and used to calculate volume of hippocampus. Whole brain volume was estimated from brain weight to produce a measure of relative hippocampal size. Because of species differences in brain weight, a ratio of observed hippocampal size to expected hippocampal size was calculated based on the relationship between hippocampal volume and brain volume from a large sample of small mammals [76]; details of this method can be found in [31]. Sex differences in hippocampal volume, however, were analyzed using an analysis of covariance, as recommended by [57].

As predicted, patterns of natural space use correlated with hippocampal size within and between species. Relative hippocampal volume was significantly greater in Merriam's
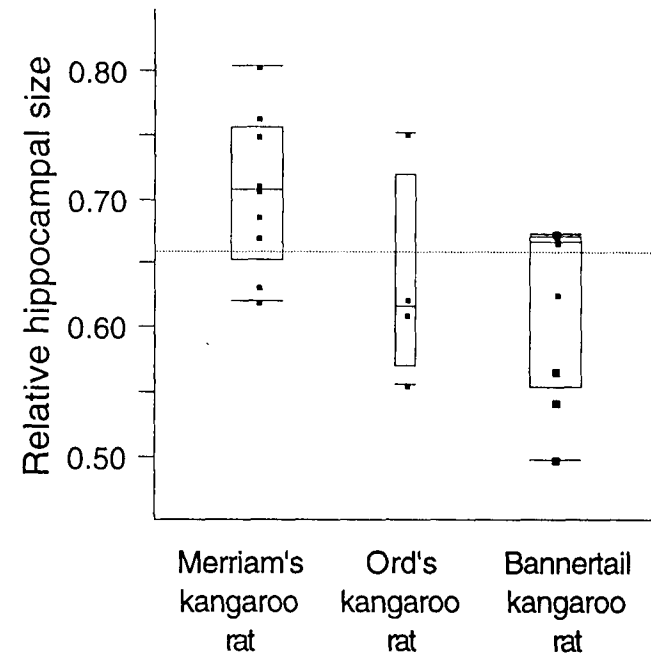

Figure 8. Relative hippocampal size in three species of kangaroo rats: Merriam's (n = 5 males, 4 females), Ord's (n = 4 males) and Bannertail (n = 5 males, 4 females). Relative hippocampal size was calculated from the ratio of observed hippocampal volume to expected hippocampal volume in a small mammal of equivalent brain volume (for more details see [31]). Box plots represent the 25%, 50% and 75% quantiles for each species; horizontal lines indicate the 10% and 90% quantiles (adapted from [31]).

kangaroo rat than in bannertails. 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 hippocampal size (Fig. 8). However, because we had no data on female Ord's, we limited our statistical comparisons to pairwise comparisons of relative hippocampal size among males. There were no significant differences between male Ord's kangaroo rats and male bannertail kangaroo rat in relative hippocampal size, however Ord's kangaroo rats did have significantly smaller hippocampi than Merriam's kangaroo rat [31].

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 [83]. Mean home ranges (weighted Jennrich-Turner areas [35]) for *Dipodomys*, published in [69] are: Merriam's, 1.79 ha; Ord's, 1.28 ha; and Bannertails, 0.13 ha. Thus, species ranking by home range size roughly correlates with species ranking by relative hippocampal size (Fig. 8). Home range size itself is only a rough measure of space use; more precise measures of space use patterns, such as the number of new foraging sites visited in a foraging bout, may yield better correlations with hippocampal size [73].
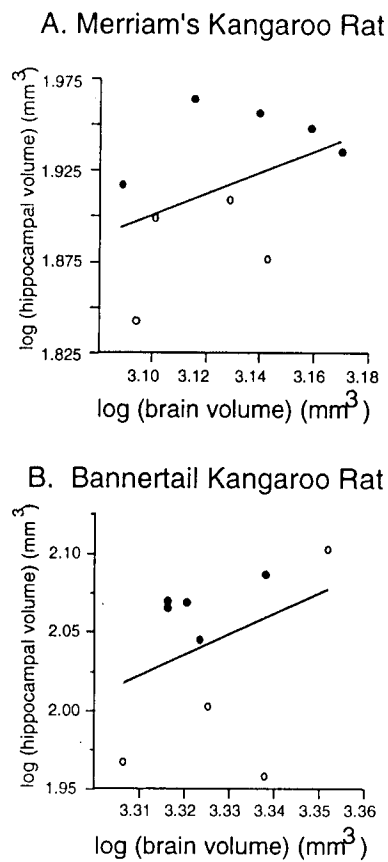
A. Merriam's Kangaroo Rat

B. Bannertail Kangaroo Rat

Figure 9. Sex differences in hippocampal size in kangaroo rats. Points represent individual males (filled circle) and females (open circle). Sample sizes were 5 males, 4 females for each species (adapted from [31]).

4.2. SEX DIFFERENCES IN HIPPOCAMPAL SIZE

As expected, males have larger hippocampi than females in both Merriam's kangaroo rat and bannertails [31] (Fig. 9). These patterns suggest that, as in passerine birds, hippocampal size is partially determined by the cognitive demands of foraging, and as in voles, is partially determined by the cognitive demands imposed by the mating system.

Since most mammalian species are polygynous, like the kangaroo rats, and are thus sexually dimorphic in their use of space, hippocampal size should be dimorphic in most species. Moreover, hippocampal size should be sexually dimorphic in polygynous species and monomorphic in monogamous species. This, in fact, is the case. Polygynous male meadow voles, trapped as adults during the breeding season, have significantly larger hippocampi, relative to the size of the whole brain, than conspecific females. There is, in contrast, no sexual dimorphism in hippocampal size in monogamous pine voles [29] (Fig. 10).
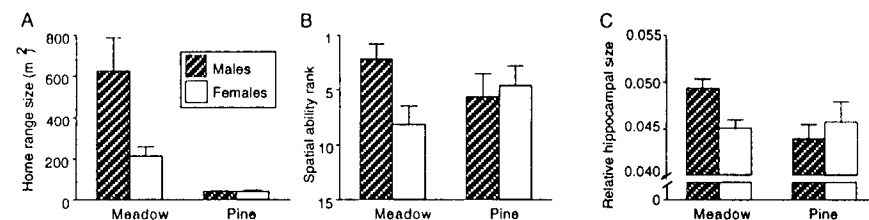
Figure 10. A and B) Sex differences in spatial abilities, and C) relative hippocampal size (in proportion to the volume of the entire brain) in breeding adult voles. Sample sizes were 10 individuals of each sex in each species.

4.3. SEASONAL MODULATION OF SEX DIFFERENCES

In addition, sex differences in patterns of space use are seasonal. Polygamous meadow voles show marked seasonal changes in social system and space use [21, 44]. Male home ranges in the winter decrease to a size similar to that of nonbreeding males or females, accompanied by an increase in social tolerance and the formation of mixed sex and lineage groups [44].

These behavioral changes are correlated with changes in brain structure. Under natural conditions, voles show large seasonal fluctuations in cranial volume and brain weight [13, 88, 90]. These measures reach a maximum during the summer breeding season and a minimum in winter. The structural changes appear to be triggered by photoperiod, i.e. the number of daylight hours. In the laboratory, meadow voles males reared under summer photoperiod (14 h daylight) had heavier brains than males reared under winter photoperiod (10 h daylight) [9, 10]. Rearing photoperiod had no effect on normal females, although females masculinized with neonatal testosterone injections also showed this effect of photoperiod on adult brain size [85]. Photoperiod thus appears to be the proximate cue triggering changes in brain mass, and the response appears to be sexually dimorphic.

Such drastic changes in spatial and social ecology, accompanied by gross changes in brain volume, might be expected to effect changes in spatial learning ability. With my collaborators, I have evidence that such changes occur in two species of polygamous voles, the meadow vole and the montane vole (*M. montanus*), a species that shows sex differences in natural space use [32, 33, 34]. The idea that sex differences in spatial learning are modulated by photoperiod were tested in two ways. First, montane voles were raised on winter or summer photoperiods and tested on the Morris water maze [47], a task which yields consistent sex differences in laboratory-reared meadow voles [37], and in wild montane voles (Jacobs, unpublished data). However, the male advantage in spatial navigation to a hidden goal was only present in animals reared under the long photoperiod, simulating the summer breeding season [28]. This has also been shown in deer mice (*Peromyscus maniculatus*): only mice reared under long (i.e., summer) day lengths show sex differences in spatial learning, with a male advantage. However such differences were absent in mice reared and tested in short (i.e., winter) day lengths [17].

Because there is no evidence of seasonal changes in learning under natural conditions or in wild voles, my collaborators and I also reexamined existing data on spatial learning ability in wild-caught meadow voles. In this previously published study [22], meadow voles were captured during natural short days (early December) and were then housed in the

laboratory under long day conditions (14 h daylight). Voles were then tested at regular intervals over a period of several months on a series of seven symmetrical mazes [12]. Such an exposure to increased photoperiod produces predictable increases in brain and body weights in this species, and this response is more pronounced in males [10]. As predicted, these winter-caught voles showed no sex difference initially, however a male superiority in task acquisition did develop after several weeks in the artificially lengthened photoperiod [28].

Thus despite differences in species and methodology, there is increasing evidence that spatial learning ability is predictably correlated with photoperiod. Indeed, photoperiod appears to be an important determinant of sex differences in spatial learning and may be a widespread phenomenon. In addition to the wild rodent species, photoperiodic modulation of radial arm maze performance has been reported in laboratory rats [11], and there are even reports of seasonal cycles in spatial learning ability in men; spatial ability is inversely related to seasonal cycles in the level of circulating testosterone [39].

What is the evidence for changes in the hippocampus? Photoperiod appears to be the proximate cue triggering changes in brain mass. Two lines of evidence suggest that photoperiod may also be responsible for seasonal changes in hippocampal structure. First, in the Siberian trapping studies, Yaskin reported that the size of the hippocampus relative to the whole brain increased greatly between winter and spring sampling periods. Moreover, he noted that males had much larger hippocampi than females in the spring, but not the winter sample [88, 89].

Other convincing evidence comes from a study of the hippocampus of hibernating Siberian ground squirrels [58, 59]. These studies show that the onset of hibernation is accompanied by severe reduction in the length and density of dendritic arbors of pyramidal cells in the CA3 region of the hippocampus. Yet within 2 h of awakening from hibernation, the pyramidal cells have regenerated the dendritic arbors and established new synapses. This example of seasonal degeneration and regrowth is remarkable for the extremely rapid rates of morphological change observed, and demonstrates that the hippocampus is capable of responding quickly to environmental cues, such as light and temperature. In summary, although the trapping data are open to other interpretations, these data in conjunction with the data on hibernating squirrels suggest that seasonal changes in hippocampal structure do occur and could be of surprising magnitude.

4.4. FUTURE DIRECTIONS

In order for a trait to evolve, there must be heritable variation among individuals, competition for limited resources and finally, successful competition must result in increased fitness. It is striking that the chapters in the present volume have provided most of the evidence necessary for the study of the evolution of one cognitive trait in particular, spatial navigation and its neural basis. First, there are the genetic studies of hippocampal structure, which demonstrate that not only is there a strong relationship between mossy fiber tract volume and spatial ability, but such traits are highly heritable (see chapters by Crusio, Lipp and Wolfer, and Schwegler and Lipp, present volume). The present chapter reviews evidence that under natural conditions a rodent's spatial ability is necessary to compete for limited resources, such as food caches and mates. Finally, I have found that patterns of hippocampal size are predicted from an individuals competitive situation, suggesting that

such variation in trait expression could be precisely adapted to meet such challenges. The next step is to apply the methods that have been so successful in the genetic study of hippocampal structure (visualization of the mossy fiber tract with the Timm's stain and quantification of the volume of hippocampal components using stereology; see chapter by Madeira and Andrade, present volume) to studies of wild rodents. I have currently begun such studies to examine species and sex differences in the volume of the mossy fiber tracts and hippocampal subcomponents.

Yet the final, and perhaps most difficult step is the demonstration that differential trait expression results in differential fitness. If we could provide evidence for this in the case, for example, of spatial navigation then we would have completed the evolutionary puzzle: we would have a cognitive trait, with an identified neural basis, whose enhanced expression increases an individual's ability to compete for scarce resources, which itself is both variable and highly heritable and whose expression varies predictably among individuals facing different environmental challenges.

This final piece of the jigsaw puzzle may be difficult, yet not impossible, to collect. Field studies of sex differences in spatial ability in rodents could supply the missing link, by using hormonal manipulations. In laboratory rats, navigational ability is determined by the early hormonal environment of the neonate [87]. Thus hormonal manipulations at this critical period could be used to bias the spatial abilities of males within cohorts. This technique has already been used to manipulate dispersal behavior in Belding's ground squirrels [25]; the same techniques could be applied to other rodent species. This, in combination with field telemetry and DNA fingerprinting studies (see chapter by Arnold, present volume), could produce correlations between space use, spatial learning, hippocampal size and mating success of males.

Finally, such comprehensive studies could address the question of the origin of individual differences, and the role of developmental feedback, as has been shown in the effects of experience on hippocampal size in marsh tits (see chapter by Clayton and Krebs, present volume). Sex differences in the structure of hippocampal components are even more likely to be the result of an interaction between genotype and environment, with such interactions mediated by gonadal and adrenal hormones [45]. Similarly, seasonal changes in the level of pineal hormones may trigger concurrent changes in hormones that control hippocampal neurogenesis and cell death and lead to the observed differences in space use and spatial learning. Such differences might even be open to genetic analysis, as photoresponsivity in voles varies among individuals and appears to be genetically mediated [49]. I hope to address several of these questions with my research over the next few years.

5. Conclusions

In conclusion, understanding the function and mechanisms of spatial cognition may be a critical step towards understanding how a specialized learning ability evolves to solve the specific cognitive tasks set by a specific ecological niche, i.e., by the species's *cognitive niche*. The current volume is an example of how this goal can be achieved through the integration of approaches, from the ecology of space use to the cellular structure of the hippocampus. Such integration can lead us to a new synthesis of evolutionary biology and cognitive neuroscience, which, in combination with quantitative genetics and cellular neuroscience, may lead to new understanding of hippocampal and brain function.

References

1. Baddeley, A. (1981) The concept of working memory: A view of its current state and probably future development, *Cognition* 10, 17-23.
2. Behrends, P., Daly, M., and Wilson, M.I. (1986) Aboveground activity of Merriam's kangaroo rats *(Dipodomys merriami)* in relation to sex and reproduction, *Behaviour* 96, 210-226.
3. Behrends, P., Daly, M., and Wilson, M.I. (1986) Range use patterns and spatial relationships of Merriam's kangaroo rats *(Dipodomys merriami)*, *Behaviour* 96, 187-209.
4. Cahalane, V.H. (1942) Caching and recovery of food by the western fox squirrel, *J. Wildl. Manag.* 6, 338-352.
5. Canady, R.A., Kroodsma, D.E., and Nottebohm, F. (1984) Population differences in complexity of a learned skill are correlated with the brain space involved, *Proc. Natl. Acad. Sci. USA* 81, 6232-6234.
6. Daly, M., Behrends, P.R., Wilson, M.I., and Jacobs, L.F. (1992) Behavioural modulation of predation risk: moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, *Dipodomys merriami*, *Anim. Behav.* 44, 1-9.
7. Daly, M., Jacobs, L.F., and Wilson, M.I. (1992) Scatter-hoarding by kangaroo rats *(Dipodomys merriami)* and pilferage from their caches, *Behav. Ecol.* 3, 102-111.
8. Daly, M., Wilson M., Behrends, P.R., and Jacobs, L.F. (1990) Characteristics of kangaroo rats, *Dipodomys merriami*, associated with differential predation risk, *Anim. Behav.* 40, 380-389.
9. Dark, J., Dark, K.A., and Zucker, I. (1987) Long day lengths increase brain weight and DNA content in the meadow vole, *Microtus pennsylvanicus*, *Brain Res.* 409, 302-307.
10. Dark, J., Spears, N., Whaling, C.S., Wade, G.N., Meyer, J.S., and Zucker, I. (1990) Long day lengths promote brain growth in meadow voles, *Dev. Brain Res.* 53, 264-269.
11. Davachi, L., Williams, C.L., Hinton, S.C., and Meck, W.H. (1992) Photoperiodic regulation of testes size and spatial memory function in the albino rat: Organizational and activational effects, *Soc. Neurosci. Abstr.* 18, 708.
12. Davenport, J., Hagquist, W., and Rankin, G. (1970) The symmetrical maze: An automated closed field test series for rats, *Behav. Res. Meth. Instrument* 2, 112-118.
13. Dehnel, A. (1949) Studies on the genus *Sorex* L, *Ann. Univ. M. Curie-Sklodowska, Sect. C.* 4, 17-102.
14. Dewsbury, D.A. (1981) An exercise in the prediction of monogamy in the field from laboratory data on 42 species of muroid rodents, *Biologist* 63, 138-162.
15. Doebel, J.H. and McGinnes, B. S. (1974) Home range and activity of a gray squirrel population, *J. Wildl. Manag.* 38, 80-867.
16. Freeland, W.J. and Janzen, D.H. (1974) Strategies in herbivory by mammals: the role of plant secondary compounds, *Am. Nat.* 108, 269-289.
17. Galea, L.A.M., Kavaliers, M., Ossenkopp, K.P., Innes D., and Hargreaves, E.L. (1994) Sexually-dimorphic spatial learning varies seasonally in two populations of deer mice, *Brain Res.* 635, 18-26.
18. Gallistel, C.R. (1990) *The Organization of Learning*, MIT Press, Cambridge (Mass.).
19. Gaulin, S.J.C. (1992) Evolution of sex differences in spatial ability, *Yearbook Phys. Anthropol.* 35, 125-151.
20. Gaulin, S.J.C. and FitzGerald, R.W. (1986) Sex differences in spatial ability: An evolutionary hypothesis and test, *Am. Nat.* 127, 74-88.
21. Gaulin, S.J.C. and FitzGerald, R.W. (1988) Home range size as a predictor of mating system in *Microtus*, *J. Mammal.* 69, 311-319.
22. Gaulin, S.J.C. and FitzGerald, R.W (1989) Sexual selection for spatial-learning ability, *Anim. Behav.* 37, 322-331.
23. Harvey, P.H. and Krebs, J.R. (1990) Comparing brains, *Science* 249, 140-146.
24. Havera, S.P. and Smith, K.E. (1979) A nutritional comparison of selected fox squirrel foods, *J. Wildl. Manag.* 43, 691-703.
25. Holecamp, K.E., Smale, L., Simpson, H.B., and Holekamp, N.A. (1984) Hormonal influences on natal dispersal in free-living Belding's ground squirrels *(Spermophilus beldingi)*, *Horm. Behav.* 18, 465-483.
26. Jacobs, L.F. (1987) Food-storing decisions in the grey squirrel *(Sciurus carolinensis)*, Ph.D. Thesis, Princeton University.
27. Jacobs, L.F. (1992) Memory for cache locations in Merriam's kangaroo rats, *Anim. Behav.* 43, 585-593.
28. Jacobs, L.F., Gaulin, S.J.C., and Rowsemitt, C.R.(submitted) Seasonal modulation of sex differences in spatial learning ability in two species of voles, *Behav. Proc.*
29. Jacobs, L.F., Gaulin, S.J.C., Sherry, D.F., and Hoffman, G.E. (1990) Evolution of spatial cognition: Sex-specific patterns of spatial behavior predict hippocampal size, *Proc. Natl. Acad. Sci. USA.* 87, 6349-6352.
30. Jacobs, L.F. and Liman, E.R. (1991) Grey squirrels remember the locations of buried nuts, *Anim. Behav.* 41, 103-110.
31. Jacobs, L.F. and Spencer, W. (1994) Natural space-use patterns and hippocampal size in kangaroo rats, *Brain Behav. Evol.* 44, 125-132.
32. Jannett, F.J.Jr. (1978) The density-dependent formation of extended maternal families of the montane vole, *Microtus montanus nanus*, *Behav. Ecol. Sociobiol.* 3, 245-263.
33. Jannett, F.J.Jr. (1980) Social dynamics of the montane vole, *Microtus montanus*, as a paradigm, *Biologist*, 62, 3-19.
34. Jannett, F.J.Jr. (1981) Sex ratios in high density populations of the montane vole, *Microtus montanus*, and the behavior of territorial males, *Behav. Ecol. Sociobiol.* 8, 297-307.
35. Jennrich, J.I. and Turner, F.B (1969) Measurements of noncircular home range, *J. Theor. Biol.* 22, 227-237.
36. Jones, W.T. (1984) Natal philopatry in bannertail kangaroo rats, *Behav. Ecol. Sociobiol.* 15, 151-155.
37. Kavaliers, M., Eckel, L.A., and Ossenkopp, K.P. (1993) Brief exposure to 60 Hz magnetic fields improves sexually dimorphic spatial learning ability in the meadow vole, Microtus pennsylvanicus, *J. Comp. Physiol. A.Sens. Neural Behav. Physiol.* 173, 241-248.
38. Kimura, D. (1992) Sex differences in the brain, *Sci. Am.* 267, 118-125.
39. Kimura, D. and Toussaint, C. (1991) Sex differences in cognitive function vary with the season, *Soc. Neurosci. Abstr.* 17, 868.
40. Krebs, J.R. and Davies, N.B. (1993) *An Introduction to Behavioural Ecology*, Blackwell Scientific Publications, Oxford.
41. Krebs, J.R., Sherry D.F, Healey, S.D., Perry, V.H., and Vaccarino, A.L. (1989) Hippocampal specialization of food-storing birds, *Proc. Natl. Acad. Sci. USA* 86, 1388-1392.
42. Langley, C.M. (1994) Spatial memory in the desert kangaroo rat *(Dipodomys deserti)*, *J. Comp. Psych.* 108, 3-14.
43. Longland, W.S. (1994) Effects of artificial bush canopies and illumination on seed patch selection by heteromyid rodents, *Am. Midl. Nat.* 132, 82-90.
44. Madison, D.M. and McShea, W.J. (1987) Seasonal changes in reproductive tolerance, spacing and social organization in meadow voles: A microtine model, *Amer. Zool.* 27, 899-908.
45. McEwen, B.S., Coirini, H., Westlind-Danielson, A., Frankfurt, M., Gould, E., Schumacher, M., and Wooley, C. (1991) Steroid hormones as mediators of neural plasticity, *J. Steroid. Biochem. Molec. Biol.* 39, 223-232.
46. Morris, D. (1962) The behaviour of the green acouchi *(Myoprocta pratti)* with special reference to scatter-hoarding, *Proc. Zool. Soc. Lond.* 139, 701-732.
47. Morris, R.G.M. (1984) Development of a water-maze procedure for studying spatial learning in the rat, *J. Neurosci. Methods.* 11, 47-60.
48. Morris, R.G.M., Garrud, P., Rawlins, J.N.P., and O'Keefe, J. (1982) Place navigation impaired in rats with hippocampal lesions, *Nature* 297, 681-863.
49. Nelson, R.J. (1987) Photoperiod-nonresponsive morphs: a possible variable in microtine population-density fluctuations, *Am. Nat.* 130, 350-369.
50. Nikolai, J.C. and Bramble, D.M.(1983) Morphological structure and function in desert heteromyid rodents, *Great Basin Nat. Mem. (Biology of Desert Rodents)* 7, 44-64.
51. Nixon, C.M., McClain, M.W., and Donohoe, R.W. (1975) Effects of hunting and mast crops on a squirrel population, *J. Wildl. Manag.* 39, 1-25.
52. Nixon, C.M., McClain, M.W., and Hansen, L.P. (1980) Six years of hickory seed yields in southeastern Ohio, *J. Wildl. Manag.* 44, 534-539.
53. O'Keefe, J. and Nadel, L. (1978) *The Hippocampus as a Cognitive Map*, Oxford University Press, Oxford.
54. Olton, D.S. and Samuelson, R.J. (1976) Remembrance of places past: Spatial memory in rats, *J. Exp. Psychol. Anim. Behav. Processes* 2, 97-116.
55. Ostfeld, R.S. (1990) The ecology of territoriality in small mammals, *Trends Ecol. Evol.* 5, 411-415.
56. Ostfeld, R.S. (1985) Limiting resources and territoritoriality in microtine rodents, *Am. Nat.* 126, 1-15.
57. Packard, G.C. and Boardman, T.J. (1990) The misuse of ratios to scale physiological data that vary allometrically with body size, in M.E. Feder, A.F. Bennett, W.W. Burggren, and R.B. Huey (eds.), *New Directions in Ecological Physiology*. Cambridge University Press, Cambridge, pp. 216-239.
58. Popov, V.I. and Bocharova, L.S. (1992) Hibernation-induced structural changes in synaptic contacts between mossy fibres and hippocampal pyramidal neurons, *Neuroscience.* 48, 53-62.
59. Popov, V.I., Bocharova, L.S., and Bragin, A.G. (1992) Repeated changes of dendritic morphology in the hippocampus of ground squirrels in the course of hibernation, *Neuroscience* 48, 45-51.
60. Poucet, B. (1993) Spatial cognitive maps in animals: new hypotheses on their structure and nerual mechanisms, *Psychol. Rev.* 100, 163-182.

61. Price, M.V., Waser, N.M., and Bass, T.A. (1984) Effects of moonlight on microhabitat use by desert rodents, *J. Mammal.* **65**, 353-356.

62. Randall, J.A. (1991) Mating strategies of a nocturnal desert rodent (*Dipodomys spectabilis*), *Behav. Ecol. Sociobiol.* **28**, 215-220.

63. Randall, J.A. (1991) Sandbathing to establish familiarity in the Merriam's kangaroo rat, *Dipodomys merriami*, *Anim. Behav.* **41**, 267-276.

64. Randall, J.A. (1993) Behavioural adaptations of desert rodents (Heteromyidae), *Anim. Behav.* **45**, 263-287.

65. Reichmann, O.J. and Oberstein, D. (1977) Selection of seed distribution types by *Dipodomys merriami* and *Perognathus amplus*, *Ecology*, **58**, 636-643.

66. Roth, G., Blanke, J., and Wake, D.B. (1994) Cell size predicts morphological complexity in the brains of frogs and salamanders, *Proc. Natl. Acad. Sci. USA*. **91**, 4796-4800.

67. Roth, G., Nishikawa, K.C., Naujoks-Manteuffel, C., Schmidt, A., and Wake, D.B. (1993) Paedomorphosis and simplification in the nervous system of salamanders, *Brain. Behav. Evol.* **42**, 137-170.

68. Rozin, P. and Kalat, J.W. (1971) Specific hungers and poison avoidance as adaptive specializations of learning, *Psychol. Rev.* **78**, 459-486.

69. Schroder, G.D. (1987) Mechanisms for coexistence among three species of *Dipodomys*: Habitat selection as an alternative, *Ecology* **68**, 1071-1083.

70. Sherry, D.F. (1985) Food storage by birds and mammals, *Adv. Study. Behav.* **15**, 153-188.

71. Sherry, D.F., Vaccarino, A.L., Buckenham, K., and Herz, R.S. (1989) The hippocampal complex of food-storing birds, *Brain Behav. Ecol.* **34**, 308-317.

72. Silverman, I. and Eals, M. (1992) Sex differences in spatial abilities: evolutionary theory and data, in J. Barkow, L. Cosmides, and J. Tooby (eds.), *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*, Oxford University Press, New York, pp.487-503.

73. Spencer, W.D. (1992) Space in the lives of vertebrates: on the ecology and psychology of space use, Ph.D. Thesis, University of Arizona.

74. Stapanian, M.A. and Smith, C.C. (1978) A model for seed scatterhoarding: coevolution of fox squirrels and black walnuts, *Ecology* **59**, 884-896.

75. Stapanian, M.A. and Smith, C.C. (1984) Density-dependent survival of scatterhoarded nuts: an experimental approach, *Ecology* **65**, 1387-1396.

76. Stephan, H., Frahm, H., and Baron, G. (1981) New and revised data on volumes of brain structures in insectivores and primates, *Folia Primatol.* **35**, 1-29.

77. Strier, K.B. (1992) Ateline adaptations: behavioral strategies and ecological constraints, *Am. J. Phys. Anthro.* **88**, 515-524.

78. Thompson, D.C. and Thompson, P.S. (1980) Food habits and caching behavior of urban grey squirrels, *Can. J. Zool.* **58**, 701-710.

79. Thompson, S.D. (1982) Microhabitat utilization and foraging behaviour of bipedal and quadrupedal heteromyid rodents, *Ecology*, **63**, 1303-1312.

80. Tinbergen, N., Impekoven, M., and Franck, D. (1967) An experiment on spacing-out as a defence against predation, *Behaviour*, **28**, 307-321.

81. Tolman, E.C. (1948) Cognitive maps in rats and men, *Psychol. Rev.* **55**, 189-208.

82. Trivers, R.L. (1972) Parental investment and sexual selection, in B. Campbell (ed.) *Sexual Selection and the Descent of Man: 1871-1971*, Aldine, Chicago, pp.136-179.

83. Vander Wall, S.B. (1990) Parental investment and sexual selection, in *Food Hoarding in Animals*, University of Chicago Press, Chicago.

84. Webster, D.B. and Webster, M. (1971) Adaptive value of hearing and vision in kangaroo rat predator avoidance, *Brain Behav. Evol.* **4**, 310-322.

85. Whaling, C.S., Zucker, I., Wade, G.N., and Dark, J. (1990) Sexual dimorphism in brain weight of meadow voles: role of gonadal hormones, *Develop. Brain Res.* **53**, 270-275.

86. Williams, C.L., Barnett, A.M., and Meck, W.H. (1990) Organizational effects of early gonadal secretions on sexual differentiation in spatial memory, *Behav. Neurosci.* **104**, 84-97.

87. Williams, C.L. and Meck, W.H.(1991) The organizational effects of gonadal steroids on sexually dimorphic spatial ability, *Psychoneuroendocrinology* **16**, 155-176.

88. Yaskin, V.A. (1984) Seasonal changes in brain morphology in small mammals, *Carnegie Mus. Nat. Hist. Spec. Publ.* **10**, 183-193.

89. Yaskin, V.A. (1988) Seasonal and annual variability in brain growth features in narrow-skulled voles (*Microtus gregalis*), *Zool. Zhur.* **68**, 438-447.

90. Yaskin, V.A. (1989) Seasonal changes in brain and cranium size in small mammals, *J. Gen. Biol. (Zhurnal Obshcheybiologii)* **50**, 470-480.