

Research report

Sexually dimorphic spatial learning varies seasonally in two populations of deer mice

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Abstract

Spatial learning in photoperiodically induced breeding (reproductive) and non-breeding (non-reproductive) adult male and female deer mice (*Peromyscus maniculatus*) was examined in a Morris water-maze task. Sexually mature, adult male and female deer mice that were derived from either a mainland population (*P. m. arctimisce*) or an island population (*P. m. angustus*) were required to learn the spatial position of a hidden, submerged platform in a water maze. Deer mice were tested either during the breeding season (summer; long day photoperiod) or during the non-breeding season (winter; short day photoperiod) with a total of six blocks of four trials conducted in a single day. Retention was tested with two probe trials which occurred one and three days after acquisition. During the breeding season male spatial task acquisition was superior to female spatial task acquisition for both populations. In contrast, during the non-breeding season there were no significant sex differences in spatial acquisition for either population. This change in sexually dimorphic spatial learning was due to female spatial-performance decreasing from non-breeding season to the breeding season and male spatial-performance increasing over the same period. Both populations displayed similar seasonal variations in sexually dimorphic water-maze task performance. There were, however, overall population differences in water-maze task performance that were related to the ecology of the mice, with the insular mice displaying shorter latencies to reach the hidden platform than did the mainland deer mice. It is suggested that changes in the levels of sex hormones which vary across the season in deer mice may account for the seasonal fluctuations in spatial acquisition in both populations and that these changes differentially influence the spatial learning of male and female mice.

Key words: Sex difference; Spatial learning; Water maze; Deer mouse; Sex hormone; Seasonal difference; Reproductive status; Breeding and non-breeding

1. Introduction

Sex differences in spatial ability favoring males have been well documented across species [15,18,41]. In adult laboratory rodents sex differences favoring males are typically seen during performance of relatively complicated spatial learning tasks such as the Morris water maze or the radial-arm maze when a subset of arms are baited [13,29,40,41]. Gonadal hormone levels in utero appear to mediate the expression of sexually dimorphic spatial ability in both humans [18] and laboratory rodents [29,41]. There is also some evidence to

suggest that gonadal hormone levels in the adult may influence the spatial performance of humans and perhaps rodents [17,22,33,34].

Gaulin and Fitzgerald [14] proposed and tested, an evolutionary theory of sexually dimorphic spatial learning based on the different reproductive tactics of the sexes in two species of microtine rodents. In the polygynous species of microtine rodent, the meadow vole (*Microtus pennsylvanicus*), males range widely during the breeding season to gain access to mates, while females hold territories. In contrast, in the monogamous prairie vole, (*Microtus ochrogaster*), pair-bonds are generally formed during the breeding season and these pairs cohabit a single territory. Gaulin and Fitzgerald [14] hypothesized that in the polygynous species sexually dimorphic spatial learning evolved in

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response to the increased spatial requirements of the widely ranging polygynous males, while in the monogamous species there was little selection pressure for the evolution of sexually dimorphic spatial learning. Both vole species were tested during the breeding season with the results indicating that both the home range size and rank performance on a number of spatial food mazes were sexually dimorphic favoring males only in the polygynous meadow voles. However, in the monogamous prairie voles, no significant sex differences in either home range size or spatial learning were evident between breeding males and females.

Many murid rodents, including a variety of species of voles and mice, are seasonal breeders. In the wild seasonal breeders display an annual pattern of reproduction, such that there is a season associated with reproduction (usually summer) and a season associated with an inhibition of reproduction (usually winter) [6,11,37,44]. Thus, across the seasons the reproductive tactics and associated behaviors change. For example, the sexually dimorphic range size in the meadow vole appears to depend on the breeding season, since there is no evidence of sex differences in home-range size during the non-breeding season [23]. There are a number of factors including temperature, food availability and, most predominately photoperiod, that are associated with the change of seasons and may serve as cues for changes in reproductively related functions [5,7,27].

Deer mice, *Peromyscus maniculatus*, are a polygynous, non-microtine (cericetinae) rodent that also display seasonal changes in reproductive, physiological and behavioral functions [1,2,5,6,7,23,24,30,31,38,44]. Sexually dimorphic home-range size has been found to vary similarly across the seasons in both deer mice and meadow voles [23,36,42]. In males, testes weight and plasma testosterone also vary across the season, such that under long-day cycles the testes weight (and testosterone) increases and under short-day cycles testes weight significantly decreases [4,5,9,27,31,35,37]. Similarly, females are cyclic during the breeding season but become acyclic with corresponding reduced gonadal hormone levels during the short-day, non-breeding season [3,32,37].

Thus, across the seasons in deer mice reproductive tactics, sexually dimorphic home-range size, testosterone levels in males and presumably estrogen levels in females, are changing. These are the same behavioral and endocrinological variables that are thought to be associated with and/or mediate the expression of sexually dimorphic spatial learning. This suggests that sexually dimorphic spatial learning may vary across the season in deer mice. In the laboratory, deer mice are photoperiodically induced breeders and have been shown to use daylength as a cue for the expression of seasonal changes in various reproductive parameters [8,9,27]. Accordingly, in the present study we examined

the spatial learning performance of photoperiodically induced breeding (reproductive) and non-breeding (non-reproductive) adult male and female deer mice in a version of the Morris water-maze task [25]. In addition, since deer mice from various habitats and geographic areas have been shown to differ in a number of behavioral, ecological and neurochemical factors [19,21,28], we examined the spatial learning performance in two different populations (subspecies) of deer mice. One population was derived from a dry mainland area while the other population was derived from a moist marine island area. Some of these data have previously been presented in abstract form [20].

2. Materials and methods

2.1. Subjects

Adult male and female deer mice were housed in mixed-sex pairs according to population (*Peromyscus maniculatus angustus* and *P. m. artemisiae*) with Purina Rat Chow and water available ad libitum. All mice were sexually mature (2–12 months of age; age was counterbalanced between groups) and 20–30 g in weight. *P.m. angustus* (island population) were derived from a population originally found on a moist island (Moresby Island, 48° north latitude, 127° west longitude and approximately 5 km² of area), lying in the Gulf Islands between southern mainland of British Columbia and Vancouver Island in Canada. *P.m. artemisiae* (mainland population) were derived from a population present in the relatively arid interior of British Columbia near Kamloops (50° 45' north latitude, 120° 30' west longitude). Additional characteristics of these wild and laboratory populations have been described elsewhere [19,21,28,32].

Reproductive deer mice (breeding; males scrotal, females cyclic) were maintained under a reproductively stimulatory, long-day photoperiod (16 h light/8 h dark cycle) in the summer. The reproductive deer mice are referred to in the text as 'breeding' (long-day). Non-reproductive deer mice (males non-scrotal, females reproductively quiescent) were maintained on a reproductively inhibitory, short-day photoperiod (10 h light/14 h dark) in the winter. The non-reproductive deer mice are referred to in the text as 'non-breeding' (short-day). Reproductive deer mice were tested during the summer and non-reproductive deer mice were tested during the winter. All of the mice were maintained in an air-conditioned room at a temperature of 21°C ± 2°C with 50% ± 10% relative humidity. Thus, the primary cue to the seasonal change was the length of time the lights were on [9,27].

2.2. Apparatus

The water maze was a black circular plastic pool, 110 cm in diameter and 30 cm high. The maze was filled with tap water (20–22°C) to a depth of approximately 14 cm. The hidden escape-platform (7 cm in diameter) was submerged approximately 1.0 cm below the water and was placed in a fixed position 15 cm from the edge of the pool. Powdered milk was added to the water to render it opaque and ensure that the platform was invisible to the deer mice.

Swimming ability was assessed separately using a glass aquarium (60 cm long, 37.5 cm wide, 45 cm high) with a visible wire-mesh platform (25 cm × 31.5 cm) fixed at one end of the aquarium. The aquarium was filled with tap water (20–22°C) to a depth of 30 cm, such that the wire mesh platform was visible at one end. The ambient light in the testing rooms was at a 'normal' room level.

2.3. Experimental procedure

There were two tasks in this experiment: a spatial learning task (water-maze) and a swimming ability task (aquarium).

Water-maze task. There were two phases to this learning task: an acquisition phase and a retention phase. A between-subjects design was used with $n = 16$ per population per season, with eight different males and females for a total of 64 animals.

Acquisition phase. From early morning to midday, individual mice were released into the maze from one of four equally spaced starting points (A–D) around the circular maze. Each mouse received six blocks of four trials over one day with the release points within trials randomized between blocks. The intertrial interval during each block was approximately 45 s and the blocks were separated by approximately 30 min. During each trial, each mouse was given 60 s to find the fixed platform. If a mouse found the platform, it was allowed to remain on the platform for 15 s. If a mouse failed to find the platform within the 60-s limit, it was placed on the platform for 15 s. During the interblock interval deer mice were held in their home cages with food and water available. Breeding deer mice were tested during the month of July, while the non-breeding deer mice were tested during the month of January. Testes position and vaginal smear data were collected during the first day of testing.

Retention phase. On the day after the acquisition phase, the first probe trial was conducted. A second probe trial was conducted three days after the acquisition day. During each probe trial the platform was removed and the animal was allowed to swim for 60 s in the maze. The time spent in the quadrant which had previously contained the platform was recorded. All animals were released from the starting point that was opposite to the quadrant which had previously contained the platform. Ambient light levels and spatial cues were constant between and among the summer and winter testing conditions.

Swimming Ability Test. The Swimming Ability Test, originally described by Vanderwolf [39], was conducted only during the breeding season. There were six subjects per group ($n = 12$ for both populations; $n = 6$ males, $n = 6$ females) for the swimming ability task. Subjects were individually released at one end of the aquarium and time taken to 'escape' to the visible platform (located at the opposite end of the aquarium) was recorded. Each animal received two blocks of five trials. After each subject had climbed onto the platform, the subject was allowed to remain on the platform for 10 s. There was an intertrial interval of 45 s and an interblock interval of approximately 30 min.

All of the trials were videotaped for analysis of swim speed. Swim speed was determined for the first trial in

the first block only in order to avoid any possible biases in subsequent trials of fatigue or learning on swim speed. Swim speed was calculated from the distance travelled using a digitizing program (Java, Jandel Scientific, Corte Madera, CA).

Data analysis. The water-maze acquisition data were analyzed using a repeated-measures analysis of variance (ANOVA) procedure. Latency to reach the hidden platform was the dependent variable with sex (male, female), population (mainland, island), and season (breeding, non-breeding) as the between-subjects factors and blocks of trials (average of each block of four trials, six blocks in all) as the within-subject factor.

The water-maze probe trials were analyzed using a repeated-measures ANOVA on time spent in each quadrant with sex (male, female), population (mainland, island) and season (breeding, non-breeding) as the between-subjects factors and quadrant (1–4) and probe trial as the within-subjects factors.

Swimming ability was assessed with two dependent variables: latency to reach a visible platform and swim speed. Each dependent variable was analyzed separately using a repeated-measures ANOVA with sex (male, female) and population (mainland, island) as the between-subjects factors and block (1–2) and trial (1–5) as the within-subjects factors.

All hypothesis tests used a significance level of $\alpha = 0.05$ and post-hoc comparisons used the Tukey's procedure.

3. Results

3.1. Water-maze task

Acquisition phase. An ANOVA for the data from the first trial was conducted in order to determine if there were preexisting biases towards finding the platform. No significant main effects or interactions were obtained.

The repeated-measures ANOVA on latency to reach the hidden platform for all trials revealed a significant four-way interaction of sex, season, population and block ($F_{5,280} = 3.65$, $P = 0.003$). The three-way interactions of sex by season by block ($F_{5,280} = 19.62$, $P < 0.001$) and sex by season by population were also significant ($F_{1,56} = 4.45$, $P = .039$). All two-way interactions and main effects were also significant.

Season. An analysis of the simple main effects of population revealed that both populations had a significant season by sex by block effect (island: $F_{5,140} = 11.27$, $P < 0.001$; mainland: $F_{5,140} = 12.2$, $P < 0.001$). All other main effects and interactions for both populations were significant. Post-hoc testing revealed that during the breeding season there were significant sex differences favoring males in each population for all

blocks. During the non-breeding season, no sex differences in latency to reach platform were found in the mainland population, except during Block 6 where males had significantly shorter latencies than did females. In the island population, however, females had significantly shorter latencies than males in Block 2 and 3 during the non-breeding season. Fig. 1 illustrates the group mean performance across all blocks for the island population during the breeding season and non-breeding seasons. Fig. 2 illustrates the group mean spatial performance for the mainland population during the breeding and the non-breeding seasons.

Since there was a significant difference between the sexes in the first block during the breeding season for both populations, the performance during the first block is illustrated in Fig. 3 for the island population and Fig. 4 for the mainland population.

Population. Female island mice displayed better task acquisition than did female mainland mice, displaying significantly shorter latencies to reach the hidden plat-

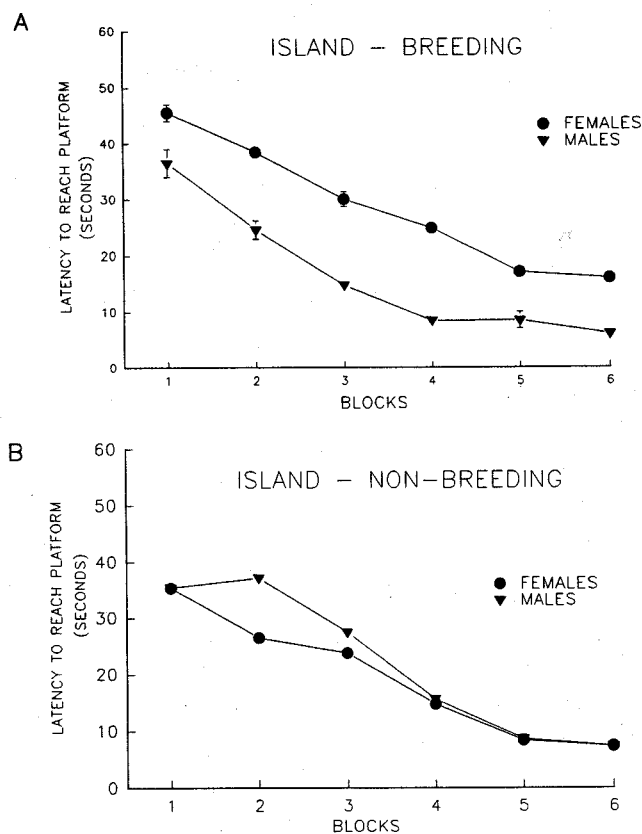


Fig. 1. A represents the group mean latencies to reach the hidden platform across all blocks for the island population of deer mice during the breeding season ($n = 8$ for males; $n = 8$ for females). B represents the group mean latencies to reach the hidden platform across blocks for the island population of deer mice during the non-breeding season ($n = 8$ for males; $n = 8$ for females). Different groups of animals were run in the different seasons. Error bars represent the standard error of the mean, if error bars do not appear to be present they are embedded in the symbol.

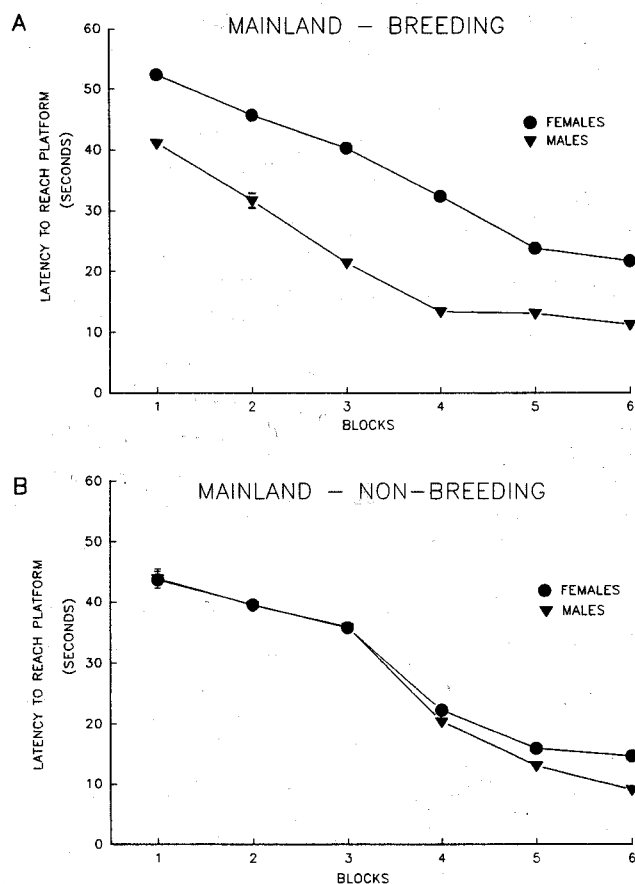


Fig. 2. A represents the group mean latencies to reach the hidden platform across all blocks for the mainland population of deer mice during the breeding season ($n = 8$ for males; $n = 8$ for females). B represents the group mean latencies to reach the hidden platform across blocks for the mainland population of deer mice during the non-breeding season ($n = 8$ for males; $n = 8$ for females). Different groups of animals were run in the different seasons. Error bars represent the standard error of the mean, if error bars do not appear to be present they are embedded in the symbol.

form ($P < 0.05$) than did female mainland deer mice during the breeding season (all blocks) and non-breeding season (except Block 2). Male island mice also displayed better acquisition in the water maze ($P < 0.05$) than male mainland deer mice during the breeding season (except Block 5) and during the non-breeding season (except Blocks 2 and 6).

Sex. Females of both populations displayed significantly better task acquisition during the non-breeding season compared to the breeding season for all blocks. Males of both populations, showed the opposite effect, performing significantly better during the breeding season than during the non-breeding season for Blocks 2–4.

Retention phase

The repeated-measures ANOVA revealed a significant three-way interaction of season by sex by probe-

test ($F_{1,56} = 15.61$, $P < 0.001$). There were also significant main effects of population ($F_{1,56} = 14.77$, $P < 0.001$), sex ($F_{1,56} = 319.27$, $P < 0.001$) and probe ($F_{1,56} = 4.39$, $P = 0.041$) and significant interactions of sex by season ($F_{1,56} = 88.98$, $P < 0.001$) and season by probe-test ($F_{1,56} = 9.89$, $P = 0.003$). During the first probe test males of both populations displayed better task retention than did females during the breeding season, spending significantly more time in the quadrant that had previously contained the platform (simple main effect of sex: $P < 0.001$ for breeding season). There was no significant difference between males and females in the non-breeding season (simple main effect of sex: $P = 0.113$ for non-breeding season). However, during the second probe test males displayed better

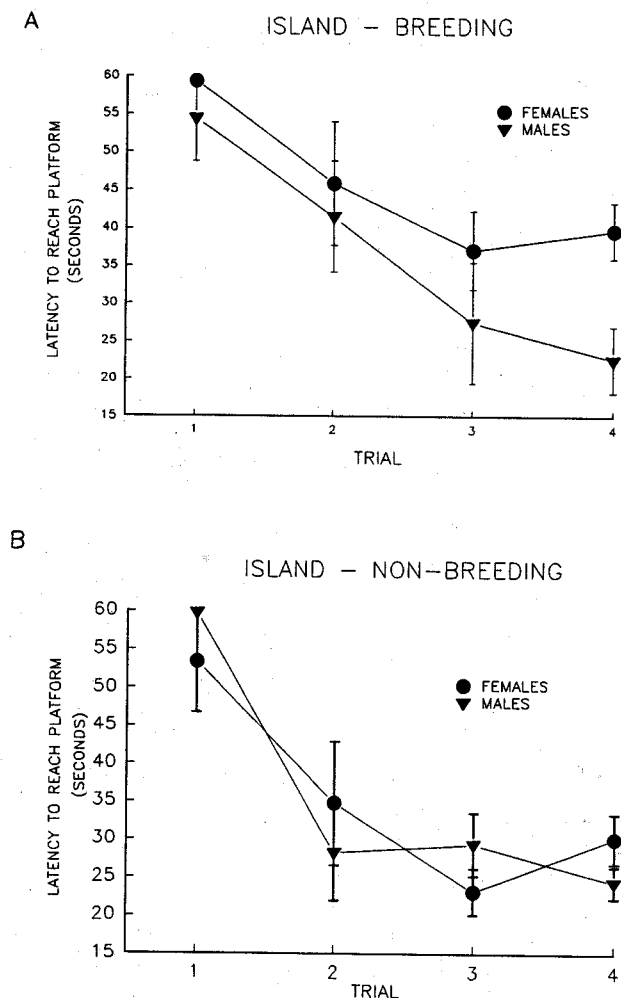


Fig. 3. A represents the group mean latencies to reach the hidden platform across four trials during the first block only for the island population of deer mice during the breeding season ($n = 8$ for males; $n = 8$ for females). B represents the group mean latencies to reach the hidden platform across four trials during the first block only for the island population of deer mice during the non-breeding season ($n = 8$ for males; $n = 8$ for females). Different groups of animals were run in the different seasons. Error bars represent the standard error of the mean.

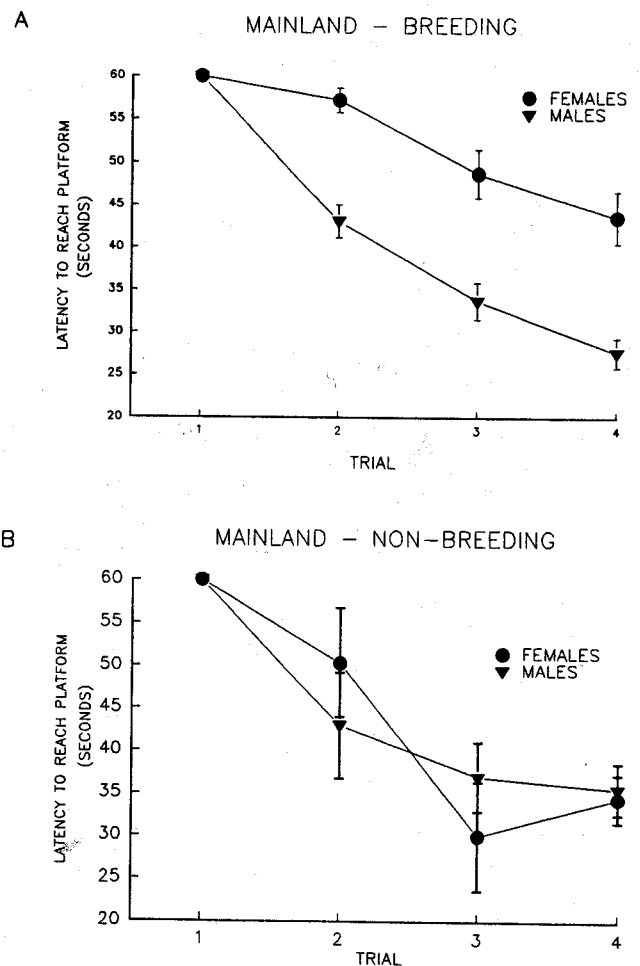


Fig. 4. A represents the group mean latencies to reach the hidden platform across four trials during the first block only for the mainland population of deer mice during the breeding season ($n = 8$ for males; $n = 8$ for females). B represents the group mean latencies to reach the hidden platform across four trials during the first block only for the mainland population of deer mice during the non-breeding season ($n = 8$ for males; $n = 8$ for females). Different groups of animals were run in the different seasons. Error bars represent the standard error of the mean.

retention than did females regardless of season (simple main effect of sex: $P < 0.001$ for non-breeding season, $P < 0.001$ for breeding season). The group mean performances during the Retention Phase are illustrated in Fig. 5 for the island population and in Fig. 6 for the mainland population for both probe tests.

Swimming ability task

Latency. The repeated-measures ANOVA on latency to reach visible platform yielded a significant population by block interaction ($F_{1,20} = 7.18$, $P = 0.014$) and a significant main effect of block ($F_{1,20} = 11.97$, $P = 0.002$). There were no other significant main effects or interactions. Post-hoc testing revealed that there was a significant simple main effect of population

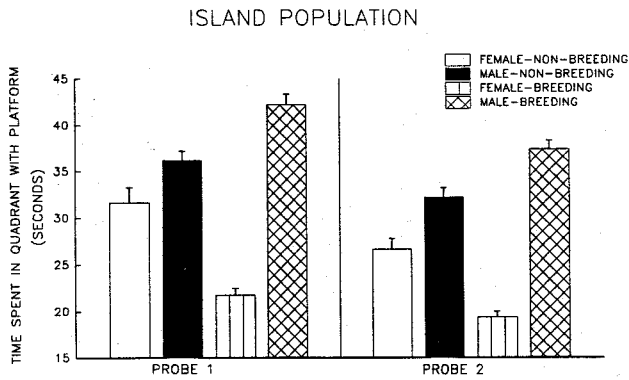


Fig. 5. Group mean time spent in the quadrant that had previously held the platform for the island population of deer mice during breeding ($n = 8$ for males; $n = 8$ for females) and non-breeding ($n = 8$ for males; $n = 8$ for females) seasons. Error bars represent the standard error of the mean.

only during Block 1 ($F_{1,22} = 21.81$, $P = 0.002$), with the island deer mice performing this task significantly faster than the mainland deer mice. There were no significant main effects or interactions during Block 2. Fig. 7 illustrates the group mean performance in the simple swim-to-platform task.

Swim speed. A repeated-measures ANOVA on swim speed did not yield any significant main effects of sex ($P = 0.484$) or population ($P = 0.940$) or an interaction of sex by population ($P = 0.616$).

4. Discussion

This study provides the first demonstration of spatial learning in the Morris water-maze in deer mice. There were three main findings of the present investigation.

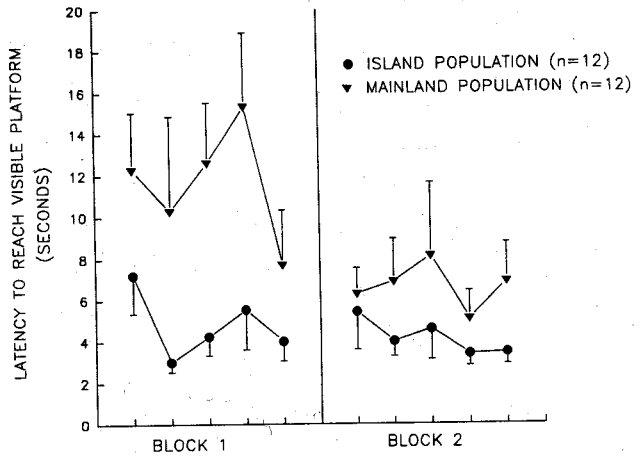


Fig. 7. Group mean latencies to reach the visible platform in the Swimming Ability Test. The experiment was conducted during the breeding season only with both mainland ($n = 6$ for males; $n = 6$ for females) and island ($n = 6$ for males; $n = 6$ for females) population of deer mice. Error bars represent the standard error of the mean.

- 1 Sex differences in the spatial learning of adult deer mice were dependent on the breeding season. 'Breeding' (long-day) adult male deer mice from two different populations displayed significantly faster acquisition and retention of the water-maze task than did 'breeding' (long-day) adult females. There were no appreciable sex differences favoring adult males in spatial acquisition during the non-breeding season in either population.
- 2 The spatial performance of 'non-breeding' (short-day) females was significantly better than that of the 'breeding' (long-day) females, while the spatial performance of 'breeding' (long-day) males was significantly better than that of 'non-breeding' (short-day) males in both populations.

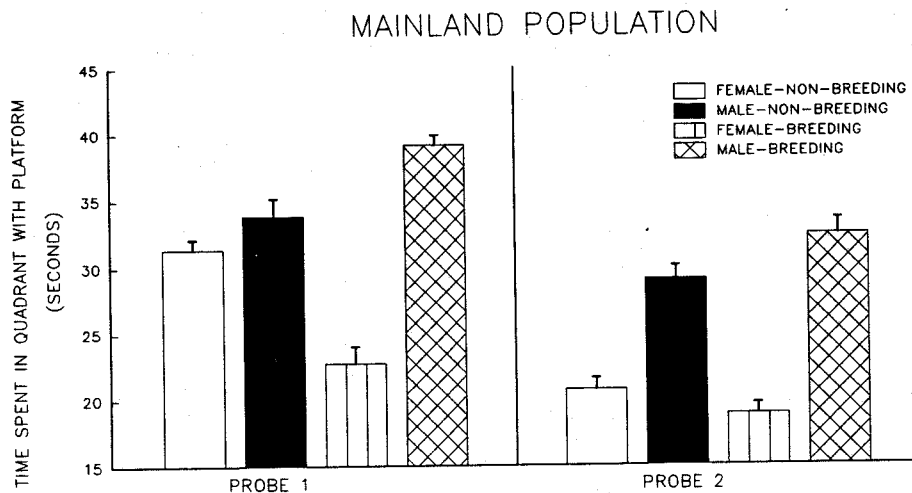


Fig. 6. Group mean time spent in the quadrant that had previously held the platform for the mainland population of deer mice during breeding ($n = 8$ for males; $n = 8$ for females) and non-breeding ($n = 8$ for males; $n = 8$ for females) seasons. Error bars represent the standard error of the mean.

3. There were population (subspecies) differences in spatial performance, with the mainland derived population of deer mice acquiring the spatial learning task more slowly than did the island population.

The present study demonstrates that sexually dimorphic spatial learning varies across the seasons in deer mice. It can be argued that since activity levels also vary across the season in deer mice (as evidenced by changes in home-range size of males, but not for females, during the breeding season [23,31,36,38,42]), that seasonal differences in activity may, in part, account for seasonal fluctuations in spatial performance. However, there were no significant seasonal or sex differences in spatial learning performance during the first trial of the first block in the water-maze test, indicating that baseline performance was not dependent on the season. Moreover, since there is greater activity in males relative to females during the breeding season [42] one might also expect sex differences in swim speed. However, during the breeding season there were no sex differences in latency to reach the visible platform in the Swimming Ability Test, nor were there sex differences in swim speed. Thus, the variation in spatial performance seen across the season does not appear to simply reflect increased motor activity during the breeding season.

The seasonal changes in sexually dimorphic spatial learning of the deer mice was in part related to the seasonal variation in female spatial performance. In both populations 'non-breeding' (short-day) females acquired the spatial learning task faster than did 'breeding' (long-day) females. This difference in spatial performance across the season may be related to the natural seasonal fluctuations in 'female' gonadal hormones. During the non-breeding season (associated with better spatial task acquisition) female deer mice are acyclic, whereas during the breeding season deer mice are normally cycling [11,32]. Thus, greater circulating levels of gonadal hormones [4,32,37,44] and perhaps hypothalamic hormones [3,4,37,44] are related to the poorer spatial performance during the breeding season. Interestingly, Hampson [17] found that spatial performance on a number of tasks varied across the menstrual cycle in humans. The midluteal phase (high estrogen) was associated with poorer spatial task performance, while the menstrual phase (low estrogen) was associated with significantly better spatial performance both within and across subjects. Although to date no studies have examined the influence of the estrous cycle on the spatial learning of rodents [33,34], there are recent data indicating that the number of dendritic spines and synapses in the apical dendrites of CA1 pyramidal cells in the hippocampus vary over the estrous cycle in the rat [16,43] and estradiol appears to mediate these changes in synapse density. The integrity of the hippocampus is necessary for better perfor-

mance in water maze task [26]. Whether or not fluctuations in estrous cycle characteristics and performance can be extrapolated or related to seasonal fluctuations in reproductive (breeding) conditions, such as occurs in deer mice, remains to be determined. In this regard it should also be noted that although no hormonal assays were conducted in the present study, vaginal smear data indicated that all animals were non-cyclic during the non-breeding season and cyclic during the breeding season.

In contrast to females, male spatial task acquisition was improved during the breeding season relative to the non-breeding season. In photoperiodically sensitive male deer mice testosterone levels are significantly higher during the breeding season [9]. Although no hormonal assays were conducted in the present study, all 'non-breeding' (short-day) males had abdominal testes while all 'breeding' (long-day) males had descended scrotal testes. These testes positions are generally associated with reproductive quiescence (lower testosterone) and reproductive facilitation (higher testosterone) respectively [4,37]. There are also some recent data from humans suggesting that seasonal fluctuations in testosterone levels may be associated with a change in spatial ability in males [22].

Results from a variety of studies have indicated that testosterone, and its metabolite estradiol, appear to mediate spatial learning performance both organizationally and possibly activationally [17,18,22,41]. However, past animal literature has primarily focussed on the organizational effects of hormones and mainly discounted any activation effects in males or in females [41]. Interestingly, there is a well-established *seasonally related* activation effect of testosterone on bird song production in the canary [10]. The results of the present study showing that spatial acquisition varies across the season in deer mice further support an activation role for sex hormones in the sexually dimorphic acquisition of spatial tasks. There is also some support from the present study for a stronger activation role of hormones in females than in males, since female performance displayed a greater variation across the seasons than did male performance. In the present study there was, however, no significant effect of season on 'long-term' retention of the spatial task (Probe trials), with males consistently displaying better retention of the task than did females regardless of season. This suggests that there maybe an underlying organizational effect of testosterone in deer mice for spatial memory, with perhaps activation factors primarily influencing spatial task acquisition. However, the first probe trial may have also served as an extinction trial and as such, the male superior performance on the second trial may reflect better extinction in females. It should be noted that a variety of other physiological, behavioral and hormonal parameters also vary across the season in

both male and female deer-mice [4–6,12,37,44]. Thus, it is likely that a number of factors may contribute to the change in spatial task acquisition seen across the season and that sex hormone fluctuations are only a single, though likely major, contributing factor.

In the present study there were also significant population differences in spatial task performance. The population differences in performance were probably related to differences in swimming ability, which may in turn be related population differences in ecology. The mainland population displayed both poorer spatial task performance and acquisition of a non-spatial swim task than did the island population. This suggests that the longer latencies manifested in the spatial learning task by the mainland deer mice are related to their poorer ability to swim rather than poorer spatial learning. Since the mainland population is derived from a dry, relatively arid climate and the island population is derived from a marine environment it may not be surprising that members of the island population were better swimmers and acquired the water-maze task more easily than the mainland deer mice. It should be reiterated, however, that both populations displayed similar sex and seasonal differences in spatial performance. This serves to further reinforce the seasonal variations in sexually dimorphic spatial learning, at least in animals that are strong seasonal breeders.

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References

- [1] Andrews, R.V. and Belknap, R.W., Season affects tolerance of cohabitation by deer mice, *Physiol. Behav.*, 53 (1993) 617–620.
- [2] Boonstra, R. and Boag, P.T., Spring declines in *Microtus pennsylvanicus* and the role of steroid hormones, *J. Anim. Ecol.*, 61 (1992) 339–352.
- [3] Bridges, R.S. and Goldman, B.D., Diurnal rhythms in gonadotropins and progesterone in lactating and photoperiod induced acyclic hamsters, *Biol. Reprod.*, 13 (1975) 617–622.
- [4] Bronson, F.H., *Mammalian Reproductive Biology*, The University of Chicago Press, Chicago, 1989.
- [5] Bronson, F.H., Seasonal regulation of reproduction in mammals. In E.Knobel and J. Neill et al. (Eds.), *The Physiology of Reproduction*, Raven Press, New York, 1988, pp. 1831–1871.
- [6] Bronson, F.H. and Perrigo, G., Seasonal regulation of reproduction in muriod rodents, *Amer.Zool.*, 27 (1987) 929–940.
- [7] Dark, J., Zucker, I. and Wade, G.N., Photoperiodic regulation of body mass, food intake and reproduction in meadow voles, *Am. J. Physiol.*, 245 (1983) R334–R338.
- [8] Desjardins, C., Bronson, F.H. and Blank, J.L., Genetic selection for reproductive photoresponsiveness in deer mice, *Nature*, 322 (1986) 172–173.
- [9] Desjardins, C. and Lopez, M.J., Environmental cues evoke differential responses in pituitary-testicular function in deer mice, *Endocrinology*, 112 (1983) 1398–1406.
- [10] DeVoogd, T.J., Endocrine modulation of the development and adult function of the avian song system, *Psychoneuroendocrinology*, 16 (1991) 41–66.
- [11] Drickamer, L.C., Annual reproduction patterns in populations of two sympatric species of *Peromyscus*, *Behav. Biol.*, 23 (1978) 405–408.
- [12] Galea, L.A.M., Kavaliers, M., Innes, D.L. and Ossenkopp, K.-P., 1. Sex differences in opioid and non-opioid mediated swim-stress induced analgesia in deer mice vary with the breeding season, *Soc. Neurosci. Abstr.*, 19 (1993) 71.12.
- [13] Galea, L.A.M., Ossenkopp, K.-P. and Kavaliers, M., Litter sex-ratios affect adult performance in a spatial task, *Soc. Neurosci. Abstr.*, 18 (1992) 569.9.
- [14] Gaulin, S.J.C. and Fitzgerald, R.W., Sex differences in spatial ability: an evolutionary hypothesis and test, *Am. Nat.*, 127 (1986) 74–88.
- [15] Gouchie, C. and Kimura, D., The relationship between testosterone levels and cognitive ability patterns, *Psychoneuroendocrinology*, 16 (1991) 323–334.
- [16] Gould, E., Wooley C.S., Frankfurt, M. and McEwen, B.S., Naturally occurring fluctuation in dendritic spine density on adult hippocampal pyramidal neurons, *J. Neurosci.*, 10 (1990) 1286–1291.
- [17] Hampson, E., Variations in sex-related cognitive abilities across the menstrual cycle, *Brain Cognit.*, 14 (1990) 26–43.
- [18] Hampson, E. and Kimura, D., Sex differences and hormonal influences on cognitive function in humans. In J.B. Becker, S.M. Breedlove and D. Crews (Eds.), *Behavioral Endocrinology*, MIT Press, Cambridge, MA, 1992, pp. 357–398.
- [19] Innes, D.G.L. and Kavaliers, M., Opiates and deer mouse behaviour: differences between island and mainland populations, *Can. J. Zool.*, 65 (1987) 2504–2512.
- [20] Kavaliers, M., Galea, L.A.M., Hargreaves, E.L., Innes, D.L. and Ossenkopp, K.-P., Spatial learning in deer mice: effects of sex and reproductive status, *Soc. Neurosci. Abstr.*, 18 (1992) 596.6.
- [21] Kavaliers, M. and Innes, D., Stress-induced opioid analgesia and activity in deer mice: sex and population differences, *Brain Res.*, 425 (1987) 49–56.
- [22] Kimura, D. and Toussaint, C., Sex differences in cognitive function vary with season. *Soc. Neurosci. Abstr.*, 17 (1991) 340.13.
- [23] Madison, D.M. and McShea, W.J., Seasonal changes in reproductive tolerance, spacing and social organization in meadow voles: a microtine model, *Am. Zool.*, 27 (1987) 899–908.
- [24] Millar, J.S., Willie, F.B. and Iverson, S.L., Breeding by *Peromyscus* in seasonal environments, *Can.J. Zool.*, 57 (1979) 719–727.
- [25] Morris, R., Developments of a water-maze procedure for studying spatial learning in the rat, *J. Neurosci. Meth.*, 11 (1984) 47–60.
- [26] Morris, R.G.M., Garrud, P., Rawlins, J.N.P. and O'Keefe, J., Place navigation impaired in rats with hippocampal lesions, *Nature* 297 (1982) 681–683.
- [27] Nelson, R.J., Kita, M., Blom, J.M.C. and Rhyne-Grey, J., Photoperiod influences the critical calorie intake necessary to maintain reproduction among male deer mice (*Peromyscus maniculatus*), *Biol. Reprod.*, 46 (1992) 226–232.
- [28] Redfield, J.A., Distribution, abundance, size and genetic variation of *Peromyscus maniculatus*, *Can. J. Zool.*, 54 (1976) 463–474.
- [29] Roof, R.L. and Havens, M.D., Testosterone improves maze performance and induces development of a male hippocampus in females, *Brain Res.*, 572 (1992) 310–313.
- [30] Rowesmitt, C.N., Seasonal variation in activity rhythms of male voles: mediation by gonadal hormones, *Physiol. Behav.* 37 (1986) 797–803.

- [31] Rowsemitt, C.N. and Berger, P.J., Diel plasma testosterone rhythms in male *Microtus montanus*, the montane vole, under long and short photoperiods, *Gen. Comp. Endocrin.* 50 (1983) 354–358.
- [32] Sadlier, R.M.F.S., The ecology of the deer mouse *Peromyscus maniculatus* in a coastal coniferous forest. II. Reproduction, *Can. J. Zool.*, 52 (1974) 119–131.
- [33] Sauve, D., The influence of the estrous cycle on activity and spatial memory in rats, (unpublished) Honours Thesis, Concordia University, Montreal, Quebec, 1989.
- [34] Sauve, D., Mazmannian, D. and Woodside, B., Sex differences and the influence of the estrous cycle on activity and spatial memory, *Canad. Psychol. Abstr.*, 31(2) (1990) 5, p. 360.
- [35] Stetson, M.H., Elliott, J.A. and Menaker, M., Photoperiodic regulation of hamster testis: circadian sensitivity to the effects of light, *Biol. Reprod.*, 13 (1975) 329–339.
- [36] Stickel, L.F., Home range and travels, In J.A. King (Ed.) *Biology of Peromyscus (Rodentia)*, The American Society of Mammalogists, 1968, pp. 373–411.
- [37] Turek, F.W. and Campbell, C.S., Photoperiodic regulation of neuroendocrine-gonadal activity, *Biol. Reprod.*, 20 (1979) 32–50.
- [38] Turner, B.N., Iverson, S.L. and Severson, K.L., Seasonal changes in open-field behavior in wild male meadow voles (*Microtus pennsylvanicus*), *Behav. Neural Biol.*, 39 (1983) 60–77.
- [39] Vanderwolf, C.H., Near-total loss of 'learning' and 'memory' as a result of combined cholinergic and serotonergic blockade in the rat, *Behav. Brain Res.*, 11 (1987) 123–134.
- [40] Williams, C.L., Barnett, A.M. and Meck, W.J., Organizational effects of early gonadal secretions on sexual differentiation in spatial memory, *Behav. Neurosci.*, 104 (1990) 84–97.
- [41] Williams, C.L. and Meck, W.H., The organizational effects of gonadal steroids on sexually dimorphic spatial ability, *Psychoneuroendocrinology*, 16 (1991) 155–176.
- [42] Wolff, J.O., Social behavior, In G.L. Kirkland, Jr. and J.N. Layne (Eds.), *Advances in the Study of Peromyscus (Rodentia)*, Texas Tech University Press, Lubbock, TX, 1989, pp. 271–291.
- [43] Wooley, C.S. and McEwen, B.S., Estradiol mediates fluctuation in hippocampal synapse density during the estrous cycle in the adult rat, *J. Neurosci.* 12 (1992) 2549–2554.
- [44] Zucker, I., Johnston, P.G. and Frost, D., Comparative, Physiological and Biochronometric analyses of rodent seasonal reproductive cycles, *Prog. Reprod. Biol.*, 5 (1978) 102–133.