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MALE SUPERIORITY IN SPATIAL NAVIGATION: ADAPTATION OR SIDE EFFECT?

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ABSTRACT

In the past few decades, sex differences in spatial cognition have often been attributed to adaptation in response to natural selection. A common explanation is that home range size differences between the sexes created different cognitive demands pertinent to wayfinding in each sex and resulted in the evolution of sex differences in spatial navigational ability in both humans and nonhuman mammals. However, the assumption of adaptation as the appropriate mode of explanation was nearly simultaneous with the discovery and subsequent verification of the male superiority effect, even without any substantive evidence establishing a causal role for adaptation. An alternate possibility that the sex difference in cognition is a genetic or hormonal side effect has not been rigorously tested using the comparative method. The present study directly evaluates how well the range hypothesis fits the available data on species differences in spatial ability by use of a phylogenetically based, cross-species, comparative analysis. We find no support for the hypothesis that species differences in home range size dimorphism are positively associated with parallel differences in spatial navigation abilities. The alternative hypothesis that sex differences in spatial cognition result as a hormonal side effect is better supported by the data.

INTRODUCTION

THE MODERN concept of evolution adopted by most scholars is that all organisms on this planet originated from a single common ancestor and subsequently differentiated in response to natural and sexual selection, as well as random genetic processes such as founder effects and genetic drift, within constraints set by physics, biochemistry, and developmental processes. In addition, biologists recognize that many features of organisms evolve in response to selection on other traits, simply because they are genetically correlated. Genetic correlations, often caused by pleiotropic gene action, can cause traits to evolve as “side effects.” One example is male nipples, which most likely occur as a side effect of selection for female reproductive success (Francis 2004). Other traits can result from developmental constraints. For example, the human chin is probably not shaped by natural selection directly, but rather is an inevitable byproduct of the growth fields of the jaws (Gould and Lewontin 1979).

The relative contribution or importance of natural selection as compared with other influences in shaping the evolution of traits has been one of the great debates in evolutionary biology over the past half century (Gould and Lewontin 1979). Proponents of the idea that natural selection plays the dominant role include George C. Williams, Ernst Mayr, and Richard Dawkins. Others, including Stephen Jay Gould, Richard Lewontin, and Elisabeth Lloyd, insist that developmen-

tal constraints, phylogenetic inertia (but see Blomberg and Garland 2002), side effects of selection due to genetic correlations, and other influences not directly related to evolutionary adaptation make equal if not more important contributions to the origin and/or maintenance of certain phenotypic traits (Gould and Lewontin 1979; Lloyd 2005).

How should we evaluate evidence that a trait is an evolutionary adaptation? Williams (1966) described an adaptation as a trait that evolved because it conferred a reproductive and/or survival advantage, resulting in higher fitness (essentially, lifetime reproductive success). Environmental conditions and competition among cohorts favored one trait over another, resulting in the bearer’s genes becoming relatively more common in subsequent generations. Hence, a trait is an adaptation if and only if the trait has a specific function and performing that function explains the higher frequency of the trait in the present population, based on the utility of the function in the past. To call a feature of an organism an adaptation is to comment on its history. Hence, merely demonstrating that a trait now increases fitness does *not* constitute evidence that the trait is an adaptation because the trait could have evolved for other reasons—e.g., as a side effect of selection on another trait. Evidence must be provided that the fitness consequences in the past are what increased the frequency of the trait leading up to the present (Sober and Wilson 2011).

As we will review, solid evidence has established that males display superior performance relative to females on tasks pertinent to wayfinding in humans and in many non-human animals. The superior performance in males has been documented across cultures and across species, and appears to be related to the hormone testosterone. Moreover, the trait appears to confer a fitness advantage, i.e., enhanced navigation ability would appear to be advantageous for hunting when distances traveled are far and you have to remember how to get back home (Silverman et al. 2000; Ecuycer-Dab and Robert 2004b). However, the explanation for the male superiority effect in humans is still a matter of debate. The prevailing adaptation hypothesis states that the superior performance of human males over females on spatial navigation tasks is an evolutionary adaptation related to the specific cognitive demands associated with hunting or navigating a larger home range. The problem with the argument is that a side-effect hypothesis that does not invoke the concept of evolutionary adaptation is equally consistent with all the observations brought to bear thus far. Specifically, testosterone could have caused the differences in spatial cognition as a side effect not functionally related to male development akin to male patterned baldness, differences in the lengths of the ring and index fingers, or in the frequency and severity of acne.

The novel contribution of the current study is that it constitutes a direct test of one of the leading adaptation hypotheses about sex differences in cognition by use of a cross-species comparative analysis. In what follows, we argue that the adaptation hypothesis of interest asserts that the two traits, sexual dimorphism in home range size and spatial navigational ability, are causally related, whereas the nonadaptation hypothesis of interest (spill-over or spandrel) denies that this is so. This difference permits empirical observations to be used to discriminate between the two hypotheses.

SEXUAL DIMORPHISM IN SPATIAL ABILITY

The idea that men are better than women at finding their way around the environment using spatial cues to navigate their path is a

controversial topic that has received a great deal of attention. Meta-analyses have been conducted (Linn and Petersen 1985; Masters and Sanders 1993; Voyer et al. 1995) and new papers appear each year documenting and sometimes attempting to refute the claim (Montello et al. 1999; Silverman et al. 2000; Aleman et al. 2004; Ecuycer-Dab and Robert 2004a; Pacheco-Cobos et al. 2010). Note that, if true, a male advantage in one arena of cognition does not imply superior cognition in other areas. Indeed, it has been found that females outperform males on other tasks, such as object memory location, verbal fluency, and recognition of facial emotional expression (Hampson et al. 2006; Silverman et al. 2007; Andreano and Cahill 2009). Also note that the difference in performance abilities on spatial navigational metrics is moderate in degree and concerns a comparison of average performance of males versus females. Many individual females outperform individual males on a given spatial task. Still, the mean difference between the sexes has been found to be statistically significant in humans and many other animals. Voyer et al.'s (1995) meta-analysis of 286 human studies found a significant male advantage for mental rotation (Cohen's d was 0.56). Similarly, Silverman et al.'s (2007) expansive study of 244,893 subjects from 40 nations found a statistically significant male advantage in three-dimensional mental rotation all 40 countries studied, as well as in all seven ethnic groups studied.

The literature provides no universal method of measuring spatial navigational ability. Voyer et al. (1995) discussed varying measurements in their meta-analysis. In the present review, we will consider measurements that reflect wayfinding ability where "wayfinding" is defined as deliberate locomotion from one location to a second location not visible from the starting point because of obstacles. This operational definition, standard in the literature, encapsulates the task and associated cognition in which males tend to show a performance advantage. Animal studies usually involve maze navigation, a direct and de facto measurement of wayfinding. Most human studies under consideration are not of this sort, but nonetheless a

significant number have directly measured human wayfinding and found a consistent male performance advantage (Galea and Kimura 1993; Astur et al. 1998; Moffat et al. 1998; Silverman et al. 2000). For example, Silverman et al. (2000) had experimenters lead subjects into unfamiliar wooded areas. The subjects were asked to imagine they were tracking an animal and that their task would be to return to their point of origin. At three intervals, the subject was asked to place an arrow on the ground indicating the direction of the origin and their accuracy was measured. At the fourth stop, the subject was required to navigate back to the origin and their competency was gauged. Indirect measures of spatial ability, such as mental rotation tests (i.e., determining which drawing of a three-dimensional object could be rotated versions of the drawing serving as the test stimulus; Shepard and Metzler 1971), were correlated with the actual wayfinding ability measurements supporting their use as an appropriate metric in the comparative analysis (Silverman et al. 2000).

RODENT STUDIES

Sexual dimorphism in rodents with regard to performance on tasks dependent on spatial ability has been documented since at least 1915 (Hubbert 1915). Male advantage in spatial tasks in humans and rodents is among the most robust and well-documented cases of cognitive sexual dimorphism (Linn and Petersen 1985; Gaulin and FitzGerald 1986; Voyer et al. 1995; Jonasson 2005). Most frequently, rodent spatial ability is measured by means of the Morris Water Maze apparatus developed by Richard Morris in 1981 (Morris 1984; Lamberty and Gower 1988; Voyer et al. 1995; Markowska 1999; Frick et al. 2000; Warren and Juraska 2000). The maze is actually not a maze in the traditional sense because it has only external walls, not any lining the necessary pathway. Instead, it consists of a large tub filled with water that has been made opaque, usually by adding nontoxic paint. A hidden platform is placed in one quadrant of the tub, just below the surface of the water. Rodents are placed in the tub from different locations and allowed to find the platform. Over repeated trials,

the animals learn where the platform is relative to distal visual cues around the room. This can be measured as a decrease in the latency to find the platform and/or the path length taken to find it over repeated trials. One advantage of the water maze as opposed to traditional mazes with walls is that the animals do not need to be food deprived or motivated for food to complete the task. Rodents do not like to be in water and therefore are highly motivated to solve the maze, regardless of how hungry they are.

Another maze commonly used to measure spatial learning in rodents is a prototypical maze in the sense that it has walls and the animal must navigate along the correct corridors to find food. The test requires moderate food restriction to motivate the animals to find the food. Specifically, Olton and Samuelson's (1976) radial arm maze (RAM) and modified versions are commonly used to measure rodent spatial learning and memory (Einson 1980; Juraska et al. 1984; Lund and Lephart 2001; LaBuda et al. 2002). In the RAM, between three and 24 arms extend from a central, round arena. Each arm has a food receptacle, which may or may not have food. Rodents are trained on food locations relative to distal cues in the room, and later tested for their ability to revisit the correct locations based on memory of spatial locations. RAM testing includes recording of error rates and the number of trials to criterion as measures of spatial memory and learning performance, respectively.

HUMAN STUDIES

The most common measure of spatial ability in humans is the 3D mental rotation test (Shepard and Metzler 1971; Figure 1). The mental rotation test and variations of it require the subject to determine which drawings of a three-dimensional object could be rotated versions of the drawing serving as the test stimulus. The test is considered relevant to navigation ability because, to orient properly, a navigator needs to identify environmental features regardless of perspective. Silverman et al. (2000) found that performance at mental rotation tests strongly predicted performance at real-world navigation tasks, such as the ability to navigate back to a starting location after

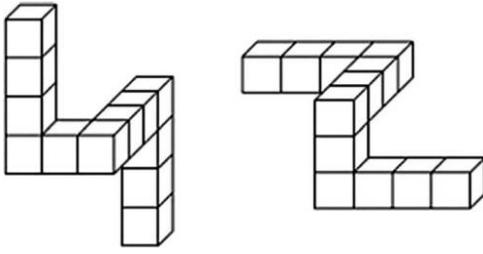


FIGURE 1. MENTAL ROTATION TEST

Subjects must identify whether the object on the right is the same object as the one on the left rotated in three-dimensional space. Men are slightly faster, on average, at solving this task as compared to women, but not more accurate.

moving through the woods. Mental rotation tasks also show the most pronounced sexual dimorphism among measures of navigation. Linn and Petersen (1985) found a strong effect size for sex across 172 studies. Voyer et al.'s (1995) meta-analysis supported Linn and Petersen's (1985) study, also indicating the largest sexual dimorphism effect size for mental rotation tests (Cohen's $d = 0.67$). Other measures that have been used include a virtual water maze (where the subject must navigate to a correct location in a computer simulation), tests of geographical knowledge, and the water-line test (as reviewed in more detail below in the section Cross-Species Comparative Analysis).

ADAPTATION HYPOTHESES FOR MALE SUPERIORITY IN SPATIAL NAVIGATION

The foregoing section demonstrates that males commonly display superior performance on cognitive tasks pertinent to wayfinding as compared to females. Over the last few decades, several authors have proposed adaptation hypotheses to explain this male superiority effect. One common explanation focuses on the greater need among males to range more or farther for the purposes of locating females (Gaulin and Fitzgerald 1986) or, in the case of humans, hunting (Ecuyer-Dab and Robert 2004a,b). The argument is that having to navigate a larger range would impose a greater cognitive demand related to wayfinding.

Note that simply occupying a larger range

does not in itself imply a greater cognitive demand as it depends on how the animals use the three-dimensional space. For example, some animals might range aimlessly in a desert while others might remember multiple locations where they cached food or found shelter. Hence, home range size is an index or a proxy for what is likely a greater demand related to finding your way around a three-dimensional landscape. The reason for using home range size in the comparative analysis, as opposed to developing a variable that specifically measures how the animals use the space, is that data on sex differences in home range size are available in the literature using unbiased sampling methods, whereas information on how the two sexes use space differently is less available and would need to rely on more subjective measures.

The hypothesis that male superiority in spatial navigation is an evolutionary adaptation for larger home range in humans and nonhuman animals is widely cited in the literature. Jones et al. (2003) discussed seven distinct explanations for how sexual dimorphism in spatial ability could have resulted from natural selection, each of which assumes that greater male home range causes the evolution of sexual dimorphism in spatial ability: male dispersal, female fertility and parental care, male foraging, female foraging, male and female range size, male warfare, and female choice. Each of these needs to be considered individually, but here they will be addressed collectively as the "range" hypothesis because the critical explanatory thesis for each is the adaptive significance of larger male home range size. Therefore, all of these adaptation hypotheses predict that males in the species showing sexual dimorphism in spatial ability can be expected to have a larger home range size as compared to females. Ecuyer-Dab and Robert (2004b) found that men in industrial societies range farther than women. The finding was congruent with studies of African hunter-gatherer societies (Hewlett et al. 1982; MacDonald and Hewlett 1999) and with observations that males range more in most nonhuman mammals (Trivers 1974).

An alternative adaptation hypothesis states

that the spatial ability dimorphism in humans evolved specifically along the human lineage because of the Pleistocene division of labor (Silverman et al. 2000, 2007). Offspring-laden females would not be able to hunt effectively, so males would necessarily have been the primary hunters, while females would have foraged in a more restricted local area for edible plants. More specifically, this hypothesis states that selection for male advantage in spatial navigation had more to do with the unique features of hunting versus gathering and the navigational skills required to perform these tasks effectively, and less to do with the differences in home range size. However, a fundamental problem with this “man the hunter, woman the gatherer” hypothesis is that many other species besides humans (see Table 1) also show the same pattern of sexual dimorphism in spatial ability. Proponents of the human division of labor hypothesis have acknowledged this fact (Silverman et al. 2007). For example, Silverman et al., citing many supportive papers conclude: “Studies with wild and laboratory rodents have shown that males consistently outperform females in maze learning tasks . . . Rats also demonstrate the same sex differences in navigational strategy as do humans. When navigating in radial-arm mazes, males are capable of using distal cues such as the shape of the room, suggesting an orientation strategy, while females require landmarks” (Silverman et al. 2007: 263). If the trait is common across species, then it may have been inherited from ancestors shared by all the species rather than having arisen multiple times independently. In other words, it is not clear why selection within the human lineage is necessary to explain the male superiority effect, as it would appear to be conserved, i.e., inherited from distant ancestors as opposed to derived in the human lineage. As an analogy, consider the fact that humans and most other tetrapods have five fingers on each hand. It would be a mistake to conclude that selection within human lineages was what led to five fingers in humans, even though the ecological significance of having five fingers could be described for all of the species that have them. In both the case of five fingers

and male superiority in spatial navigation, a single event of selection rather than multiple events is a more parsimonious explanation of the data. Although the question arises as to why parsimony is relevant for deciding which hypothesis is more likely to be true (see Sober 2008; Sober and Wilson 2011), we think that if the sexual dimorphism in spatial ability is an adaptation, the better explanation is that it is an ancient adaptation, not a distinctively human one.

In nonhuman mammals, the range hypothesis is typically formulated by saying that the males range more in order to secure access to multiple females. The closely related meadow vole and pine vole species are often cited as evidence for the ranging male adaptation hypothesis (Sawrey et al. 1994). Monogamous pine voles (*Microtus pinetorum*) show low sexual dimorphism in both spatial navigation and home range size (FitzGerald and Madison 1983; Gaulin and FitzGerald 1986), whereas the highly polygamous meadow vole (*M. pennsylvanicus*) shows high dimorphism in navigational ability and moderate home range size dimorphism (Getz 1961; Webster and Brooks 1981; Gaulin and FitzGerald 1986, 1989; Galea and Kimura 1993; Sawrey et al. 1994). The main problem with these analyses is that only two species were compared, which greatly limits logical and statistical inference. For example, degrees of freedom are zero for statistical assessment of a correlation between two species (Garland and Adolph 1994). Any two species are expected to display differences in heritable traits due to random genetic drift, reproductive isolation, and speciation, among others (Garland and Carter 1994). Therefore, at least three species data points are needed to avoid spurious correlations, and preferably many more for adequate statistical power (see Garland and Adolph 1994; Rezende and Diniz-Filho 2012).

The adaptation male range hypothesis has also been questioned on theoretical and experimental grounds. The mere observation that, in certain species of animals, males display larger home ranges and slightly better spatial navigation ability than females is not sufficient to establish the soundness of the

TABLE 1
Summary of sexual dimorphism data for home range size and spatial ability extracted from the literature for comparative analysis

Home range data					
Species	Measure/Method	Male	Female	Dimorphism index	References
Meadow Vole (<i>Microtus pennsylvanicus</i>)	Radiotracking	51.6 m ²	39 m ²	0.32	Webster and Brooks (1981) Table 1, 24 hours, composite all seasons and conditions
	Trapping	565 m ²	464 m ²	0.22	Getz (1961) 13 month average
Prairie Vole (<i>Microtus ochrogaster</i>)	Radiotracking	44.1 m ²	35.2 m ²	0.27 0.25	Ophir et al. (2007) Table 2
Pine vole (<i>Microtus pinetorum</i>)	Radiotracking	44.7 m ²	41.7 m ²	0.07	FitzGerald and Madison (1983) page 185
Deer mouse (<i>Peromyscus maniculatus</i>)	Trapping	2.31 acs	1.39 acs	0.66	Blair (1942) Table 1, adult home range average
Mouse (<i>Mus musculus</i>)	Powder tracking	447.7 m ²	229.9 m ²	0.95	Mikesic and Drickamer (1992) Table 1
	Radiotracking	473 m ²	187.9 m ²	1.52	Mikesic and Drickamer (1992) Table 2
	Trapping	212 m ²	176 m ²	0.20	Zielinski and Vandenberg (1991) Figure 2
Rat (<i>Rattus rattus</i>)	Radiotracking	0.78 ha	0.45 ha	1.20 0.73	Whisson et al. (2007) Figure 1, average 100% minimum convex polygon
Human (<i>Homo sapiens</i>)	Survey and mapping	1277 km ²	929 km ²	0.37	Ecuyer-Dab and Robert (2004b) Table 4, sum of all range measurements
	Survey and mapping	58.3 km	32.4 km	0.80	Hewlett et al. (1982) Table 2, average half-range of Aka adults
	Ethnographic observation	50 km	20 km	1.50	O'Connell and Hawkes (1984) map radius of areas used for foraging (females) and vehicle-assisted hunting (males)
	Survey and mapping	89.7 km	21.7 km	3.13	Gaulin and Hoffman (1988) page 144, average of maximum travel distances reported by adults
	Survey and mapping			0.00	Harpending (1976) page 161, discussion of male, female mobility
Talas Tucu-Tucu (<i>Ctenomys Talarum</i>)	Radiotracking	70.1 m ²	34.91 m ²	1.16 1.01	Cutrer et al. (2006) Figure 1, minimum convex polygon (MCP)
Rhesus monkey (<i>Macaca mulatta</i>)	Field observation			0.00	Lindburg (1969) page 166, rhesus social organization
Horse (<i>Equus Caballas</i>)	Field observation			0.00	Linklater (2000) and Linklater et al. (2000)
Cuttlefish (<i>Sepia officinalis</i>)	Locomotor activity	210.0	105.0	1.00	Jozet-Alves et al. (2008) Figure 2, adults, 15 cm ² , squares crossed

continued

TABLE 1
Continued

Spatial ability data					
Species	Measure/Method	Male	Female	Dimorphism index	References
Meadow Vole (<i>Microtus pennsylvanicus</i>)	Morris water maze	11.5 s	23.25 s	1.02	Galea et al. (1995) Figure 4, final trial latency
	Maze performance	21.6 mean errors	27 mean errors	0.25	Gaulin et al. (1990) Figure 2A, errors
	Morris water maze	17 s	17 s	0.00	Sawry et al. (1994) Figure 5, latency
	Radial arm maze	7.0	15.0	1.14	Gaulin and FitzGerald (1986) Figure 2, median maze performance rank
				0.60	
Prairie Vole (<i>Microtus ochrogaster</i>)	Maze performance	22.2 mean errors	20.8 mean errors	-0.07	Gaulin et al. (1990) Figure 2A, errors
Pine vole (<i>Microtus pinetorum</i>)	Radial arm maze	10.5	11.0	0.05	Gaulin and FitzGerald (1986) Figure 2, median maze performance rank
Deer mouse (<i>Peromyscus maniculatus</i>)	Morris water maze	35.3 s	61.2 s	0.73	Galea et al. (1994) Figures 1 and 2, sum of mean latency of breeding and nonbreeding 6th trial
Mouse (<i>Mus musculus</i>)	Morris water maze	79.2 s	43.75 s	-0.81	Lamberty and Gower (1988) Figure 2A, mean total latency, final trial
	Radial arm maze	30.83 % correct	14.2 % correct	1.17	La Buda et al. (2002) Figure 3, mean percent correct responses, day 5
	Radial arm maze	2.6 rewards	1.5 rewards	0.72	La Buda et al. (2002) Figure 1, mean number of rewards obtained, day 5
	Radial arm maze	1.7 mean errors	4.6 mean errors	1.71	Mishima et al. (1986) Figure 3, number of errors, trial 10, day 2
				0.70	
Rat (<i>Rattus rattus</i>)	Morris water maze	38.7 s	43.8 s	0.13	Markowska (1999) Figure 3, mean of 6 and 12 month ages latency
	Morris water maze	956 cm	1264 cm	0.32	Markowska (1999) Figure 3, mean of 6 and 12 month ages swim distance
	Morris water maze	56.3°	66.5°	0.18	Markowska (1999) Figure 3, mean of 6 and 12 month ages heading angle off platform
	Radial arm maze	61.3 correct choices	60.7 correct choices	0.01	Juraska et al. (1984) Table 1, combined correct choices EC and IC, and replication 1 and 2
	Radial arm maze	53.2 correct choices	53.7 correct choices	-0.01	Juraska et al. (1984) Table 1, correct choices before error, combined EC and IC, and replication 1 and 2
	Radial arm maze	21.3 errors	23.8 errors	0.12	Juraska et al. (1984) Table 1, total errors, combined EC and IC, and replication 1 and 2
	Radial arm maze	7.4 days to acq.	15.4 days to acq.	1.08	Lund and Lephart (2001) Figure 1, oil (control) days to acquisition
					0.44

continued

TABLE 1
Continued

Spatial ability data					
Species	Measure/Method	Male	Female	Dimorphism index	References
Human (<i>Homo sapiens</i>)	Mental rotation test	8.5	5.5	0.55	Ecuyer-Dab and Robert (2004b) Table 3, mean score
	Waterline test	4.1	14.5	2.54	Ecuyer-Dab and Robert (2004b) Table 3, mean score
	Embedded figures	5.5	4.6	0.20	Ecuyer-Dab and Robert (2004b) Table 3, mean score
	Surface development	14.5	11.5	0.26	Ecuyer-Dab and Robert (2004b) Table 3, mean score
	Wayfinding compass placement	120.41°	161.64°	0.34	Silverman et al. (2000) Table 1, sum of deviations from true compass heading
	Mental rotation test	25.1	16.5	0.52	Silverman et al. (2000) Table 3, mean score
	Waterline test	9.9	7.7	0.29	Silverman et al. (2000) Table 3, mean score
	Mental rotation test	56.7	44.8	0.27	Mann et al. (1990) Sum of Tables 1 and 2, mean score
	Virtual Morris water maze	11.3 s	16.9 s	0.50	Astur et al. (1998) Figure 4B, trial 5. Latency in seconds
	Mental rotation test	16.6	11.8	0.41	Montello et al. (1999) Table 2, mean score
	Campus route learning	81.6	113.1	0.39	Montello et al. (1999) Table 3, sum of scores other than route-landmark
	Geo. knowledge Santa Barbara distance			0.00	Montello et al. (1999) Table 5, sum of scores, male and female scores not significantly different, ratio set to 0
	Geo. Knowledge city cardinal locations			0.00	Montello et al. (1999) Table 5, sum of scores, male and female scores not significantly different, ratio set to 0
	Geo. knowledge city ordinal distances			0.00	Montello et al. (1999) Table 5, sum of scores, male and female scores not significantly different, ratio set to 0
	Geo. Knowledge city placements	941.2	1273.1	0.35	Montello et al. (1999) Table 5, sum of scores
	Talas Tucu-Tucu (<i>Ctenomys Talarum</i>)	Longitudinal and radial arm maze			0.44 0.00
Rhesus monkey (<i>Macaca mulatta</i>)	Delayed recognition span test	2.7	2.3	0.19	Lacreuse et al. (2005) Table 1, mean scores of young monkeys

continued

TABLE 1
Continued

Spatial ability data					
Species	Measure/Method	Male	Female	Dimorphism index	References
Horse (<i>Equus Caballas</i>)	Novel 4-stall test apparatus	4.88 errors	6.39 errors	0.31	Murphy et al. (2004) Paragraph 3.2.1, mean errors for all tests
	Novel 4-stall test apparatus	52.90%	25.0%	1.12	Murphy et al. (2004) Paragraph 3.3, percentage of males/females which completed task
	Novel 4-stall test apparatus			0.00	Murphy et al. (2004) Paragraph 3.1, mean time to completion, male and female performance not significantly different
				0.48	
Cuttlefish (<i>Sepia officinalis</i>)	Modified T-maze			0.00	Karson et al. (2003) Experiment 5. Authors report no sex difference in performance (but not data by sex)
	Modified T-maze	6 trials	6 trials	0.00	Jozet-Alves et al. (2008) Mean trials to task acquisition
				0.00	

Note: The dimorphism index was calculated as follows. The equation $[(\bar{X}_g/\bar{X}_f) - 1]$ was used, where \bar{X}_g is the mean for the sex with the greater value and \bar{X}_f is the mean of the sex with the lesser value. Female biases were assigned a negative value. Ratios in bold font represent the values used in the comparative analysis. For species with multiple experiments, the index represents the average of multiple measurements.

hypothesis. Rather, it must be demonstrated that the trait in question impacted the ability to survive or reproduce at some point in the past. However, the available experimental data cast doubt on that idea. Mark Spritzer (Spritzer et al. 2004, 2005) conducted two studies with meadow voles in which he measured the spatial ability and home range size of each male and then observed which males sired the most offspring utilizing paternity tests. Although high-performing males had larger ranges as predicted, neither experiment showed that high-performing meadow vole males sired significantly more offspring than low-performing voles, as predicted by the male range theory. On the other hand, an inevitable limitation of the Spritzer et al. studies (2004, 2005) is that they evaluated fitness of voles in the present. It is entirely possible that a positive relation existed in the past.

An effort must also be made to rule out other factors that could plausibly drive parallel sexual dimorphism in home range size and spatial navigation. In the case of the male range hypothesis, phenotypic plasticity

could explain a correlation between home range size and spatial ability. Perhaps the process of moving around a larger environment trains and thereby enhances cognitive machinery within an organism's lifetime, as might also occur for exercise abilities such as endurance capacity (Garland 1999), which would constitute a type of self-induced adaptive plasticity (Swallow et al. 2005). In addition, an alternative hypothesis that we refer to as testosterone spill-over (explained below) needs to be evaluated.

INTERGENDER HITCHHIKING

As a general rule in quantitative genetics, when a trait is heritable and selection acts on that trait in one sex, the other sex will also exhibit a correlated response to selection. This is because alleles for the trait will be passed on to both male and female offspring. For instance, selection that favors larger body size in one sex is likely also to increase body size in the other sex. As a further example, nipples occur in males not because they serve any fitness advantage in males, but

rather because they serve a clear advantage in females and evolved as a correlated response in males. Nipples are not a major disadvantage for males and do not impose much if any fitness cost for them, but they are a major advantage in females, and therefore male nipples evolved and now persist.

The genetic correlation between the sexes for a given trait will generally be less than one for various reasons, e.g., some alleles have sex-limited effects or their effects depend on the hormonal milieu in which they occur. Therefore, some sexual dimorphism is expected to evolve when selection acts on a trait in only one sex. Beyond this, sexual dimorphisms may be especially pronounced when the fitness consequences of the trait are different for the two sexes. For example, larger body size of males as compared to females may result from antagonistic selection in each sex. In males, larger size could have been beneficial for agonistic encounters with other males, whereas in females, smaller body size could have been beneficial because it required fewer (of the presumably limited) resources needed to bear young instead of building and maintaining a larger body. We are aware of no such published discussions with regard to the male range hypothesis.

If natural selection enhanced spatial navigation in males for hunting or navigating a larger landscape, then it is not clear why enhanced navigation did not also evolve as a correlated response in females via intersex hitchhiking. Enhanced spatial navigation would presumably benefit both sexes. One possible reason is that an individual might be constrained to be either cognitively adapted to ranging or to nesting/foraging, but not to both simultaneously. This would imply that the same brain locus or resources a male uses for navigation is put to some other important function in females, and that an organism cannot do well at both (i.e., a tradeoff exists). As we should expect that navigation ability would generally benefit both sexes (all animals need to successfully traverse terrain without getting lost), the function that such ability displaces in female brains must be identified. The ranging male/foraging female hypothesis implies that the same neuronal

real estate is modified to aid in the respective spatial abilities of the sexes or, failing that, it must be explained why superior way-finding ability would not have evolved as a correlated response in females due to intergender hitchhiking.

NONADAPTATION HYPOTHESES FOR MALE SUPERIORITY IN SPATIAL NAVIGATION TESTOSTERONE SPILL-OVER

In mammals, testosterone is secreted from the developing testes during embryonic development and determines male primary and secondary sex characteristics. The absence of testosterone during development results in female anatomy, physiology, and behaviors. During childhood, testosterone is mostly absent in both sexes (and circulating levels are not different from females), but reappears during male adolescence and continues throughout adulthood to generate and maintain such secondary sexual characteristics as muscles and facial hair. Although the genetically adaptive qualities of the hormone are clear for males (e.g., development of the penis), it also has nonadaptive side effects. Examples of testosterone side effects in humans include acne (Lawrence et al. 1986), male pattern baldness (Choi et al. 2001), and a slightly lower 2D:4D ratio (index finger being slightly shorter than the ring finger after elevated prenatal exposure to testosterone; Galis et al. 2010). These phenotypic traits appear to have either no adaptive significance or negative fitness consequences. If the latter, then perhaps the fitness benefit of testosterone in males (fertility) outweighs any negative aspects of the side effects. We hypothesize that sexual dimorphism in spatial ability in humans and many nonhuman animals could represent a side effect of testosterone. It is possible that the slight male advantage on specific navigation tasks was *never* shaped by natural selection, but rather was a side effect of the chemistry of androgens acting in the brain, akin to male pattern baldness, without any clear fitness consequences.

Consistent with the testosterone spill-over effect, several studies in both humans and nonhuman animals have demonstrated that testosterone itself can enhance spatial navi-

gation either administered acutely to adult females or when applied during prenatal development. For example, Lund and Lephart (2001) have shown that the presence or absence of testosterone during prenatal development in rats can produce male- or female-level spatial ability, respectively, regardless of whether the animals are genetically female (i.e., XX) or male (i.e., XY). The leading hypothesis in rodents is that testosterone gets converted to estradiol in the brain, which causes changes in the neurons and brain circuits involved in spatial navigation, such as numbers of neurons or synapses in the hippocampus (Roof and Havens 1992). For example, Williams and Meck (1991) and Williams et al. (1990) administered estradiol prenatally to female rats at a level similar to what male rats would experience at that stage in development (by conversion of testosterone to estradiol by aromatase) and found that as adults the female rats displayed enhanced spatial navigation comparable to male performance. Kritzer et al. (2001) showed that gonadectomy in adult male rats impairs T-maze acquisition, demonstrating an acute effect of testosterone on spatial navigation performance in rats. In addition, human studies consistently find that female performance on spatial ability tasks improves with acute administration of testosterone (Postma et al. 2000; Aleman et al. 2004). Moreover, endogenous levels of testosterone in female humans correlates with their navigation performance in virtual water maze tests (Driscoll et al. 2005; Burkitt et al. 2007).

Note that the data described above demonstrating that testosterone improves spatial cognition cannot arbitrate between the adaptation hypothesis and testosterone spill-over because the observations are consistent with both hypotheses. Testosterone could be the means by which males are endowed with better spatial abilities due to natural selection "using" this molecule as the proximate mechanism for enhancing spatial ability. Nonetheless, the observation is important because it is required for the testosterone spill-over hypothesis to be correct whereas it is not required for the adaptation hypothesis. If the adaptation hypothesis is correct, then the distribution or abundance of an-

drogen receptors, estrogen receptors, or the enzyme aromatase (which converts testosterone to estrogen in the brain) would also be expected to change in the male brain along with the increased presence of testosterone to facilitate the enhanced navigation. Therefore, simply adding testosterone to a female brain would not necessarily be expected to be sufficient to change behavior because the correlated and necessary features (e.g., receptors, enzymes) might not be present to produce the behavior.

CULTURAL FACTORS

In humans, both male and female spatial navigational abilities may be influenced by socialization and experience. Linn and Petersen (1985) observed that in mental rotation studies, accuracy was very high for subjects of both sexes. Male superiority is usually observed as increased speed, which could reflect greater self-confidence, not accuracy. Linn and Peterson speculated that females may be more cautious in responding to queries. Evidence indicates that females generally take more time per item in test situations. Voyer et al. (1995) also noted that sexual dimorphism in spatial ability diminished significantly when tests were scored for accuracy rather than speed. Counter-evidence directly pertaining to mental rotation tasks is found in Robert and Chevrier (2003). Subjects were asked if they had "checked" their answers, and equal numbers of men and women responded affirmatively. Several cross-cultural comparisons of sexual dimorphism in spatial ability have been conducted. Mann et al. (1990) compared sexual dimorphism in mental rotation performance tests using high school students in the United States and Japan. Both nations showed a similar male performance advantage. Silverman et al. (1996) produced a similar result comparing Japanese and Canadian subjects. Owen and Lynn (1993) reported male advantage in spatial performance among white, black, and Indian South Africans, congruent with studies based in industrial nations. Silverman et al. (2007) found the familiar male spatial ability bias in mental rotation performance across seven ethnic groups and 40 countries, which is perhaps the most expansive such cross-

cultural comparison to date (Murphy et al. 2007). The uniformity of results across cultures, together with the data described above showing that testosterone enhances spatial ability, argues against the idea that culture plays a major role in the observed sexual dimorphism in spatial ability.

PHENOTYPIC PLASTICITY

Phenotypic plasticity refers to physiological and morphological changes that take place within the lifetime of an organism in response to the environment that the organism experiences (Kelly et al. 2012). In the case of sexual dimorphism in spatial ability, it is possible that males range farther than females and thereby train those components in the brain to be slightly more efficient. An example of changes in the morphology of the brain in response to spatial navigational training comes from London taxi drivers. Maguire et al. (2000) found that London taxi drivers had larger hippocampi than controls and that the size of the posterior hippocampus strongly correlated with the duration of the subject's employment as a driver. Note that the cognitive training from driving is not accompanied by any increases in physical activity that would historically be associated with moving through the environment. It is interesting that in nonhuman animals and humans, physical activity alone appears sufficient to enlarge portions of the hippocampus and improve spatial ability even without any navigational demands. For example, a substantial body of evidence in rodents has established that running in place on a running wheel improves spatial navigation. Moreover, the distance traveled on a running wheel is correlated with adult hippocampal neurogenesis and volume of the dentate gyrus of the hippocampus (van Praag et al. 1999; Rhodes et al. 2003; Clark et al. 2009, 2011). In humans, physical activity alone also appears to increase volume of the hippocampus without any navigational training. In a human intervention study, subjects were randomly assigned either to fast-pace walking around a track in a gym or stretch and tone in the interior of the gym and so both groups experienced the same spatial complexity of the

environment. However, only the aerobic exercise group showed increases in volume of the hippocampus from the intervention (Erickson et al. 2011).

On the other hand, there is substantial reason to doubt that phenotypic plasticity alone can be responsible for the sexual dimorphism in spatial ability across species. This is because in many of the animal studies, the animals were kept in cages under uniform conditions and nonetheless the sexual dimorphism in spatial ability was pronounced. Many if not most rodent studies involve cage-reared subjects (Gaulin and FitzGerald 1986, 1989; Lund and Lephart 2001; LaBuda et al. 2002). Sixty-two horse subjects in Murphy et al.'s (2004) equine spatial ability study were raised and kept in the same stables with no significant environmental difference between sexes, but nonetheless showed male superiority in visuospatial ability. Hence, although phenotypic plasticity probably contributes to sexual dimorphism in spatial ability in animals, it is probably not the only contributor. This assessment is supported by the evidence cited in the Testosterone Spill-over section, that testosterone itself acutely enhances spatial ability in females.

SUMMARY

In review of the potential nonadaptation explanations for sexual dimorphism in spatial ability, cultural factors are essentially weak or disputed in the case of humans. Phenotypic plasticity may play a role, but cannot account for large segments of findings in the literature that control for environmental variation or demonstrate direct influences of testosterone. The testosterone spill-over hypothesis remains a plausible nonadaptation hypothesis that could explain sexual dimorphism in spatial ability. Although many studies have endeavored to compare competing adaptation hypotheses for sexual dimorphism in spatial ability, none that we are aware of have attempted to examine how well the adaptation hypotheses fit the data relative to reasonable alternatives that do not invoke the concept of evolutionary adaptation, such as testosterone spill-over. A cross-species comparative analysis using home range size di-

morphism as the independent variable can arbitrate between these hypotheses.

CROSS-SPECIES COMPARATIVE ANALYSIS

The comparative method is an established tool in evolutionary biology for testing adaptation hypotheses against nonadaptation alternatives (Harvey and Pagel 1991; Garland and Adolph 1994; Garland et al. 2005; Sober 2008; Nunn 2011; Rezende and Diniz-Filho 2012). A standard example (e.g., see Alkahtani et al. 2004) would involve collecting data on different species of mammals that live in different climates, varying from desert to rainforest, and measuring the length of their nephrons (cells in the kidney involved in water retention, with longer cells facilitating greater water retention). Ideally, multiple individuals from all the species are born and reared in a common environment with *ad libitum* access to water before measuring nephron length. The common environment rules out the confounding influence of phenotypic plasticity (e.g., nephrons growing within individuals because the animals had been reared in a dry environment); note that this is a plastic response to the environment within a lifetime (i.e., an example of acclimation), rather than an evolutionary change across generations.

If the genetic adaptation hypothesis is correct, then even after species are raised in a common environment, a positive correlation should be observed between length of nephrons (on the y-axis) and dryness in the climate of origin (on the x-axis). The logic is that if nephron length was *not* an adaptation, then it would vary among the species due to processes that vary randomly among species (e.g., genetic drift), but that variation among species would not be systematically related to dryness of the ancestral climate. In the case of spatial navigation, the ecological variable is sexual dimorphism in home range size (analogous to climate differences among species). In the case of nephron length, it is differences in the dryness in the climate that are hypothesized to drive the evolution of nephron length for increasing urine concentration capacity. Likewise, for sexual dimorphism in spatial navigation, it is home range size differences among the sexes that are

hypothesized to drive the evolution of sexual dimorphism in spatial navigation ability. Note that, as always, a positive correlation does not specify the direction of causality. The causal direction could be the other way around—i.e., nephron length differences *cause* animals to live in varying climates, and spatial ability *causes* animals to range further. Therefore, in these analyses, it is assumed that the ecological variable (e.g., climate differences, sexual dimorphism in home range size) temporally preceded the adaptation (e.g., nephron size, sexual dimorphism in spatial ability). In practice, it is often difficult if not impossible to determine the temporal relationship because we lack historical data for extinct species and because the two traits could evolve in close temporal proximity (but see Deaner and Nunn 1999). Moreover, the ecological variable could precede the evolution of the phenotype and still the temporal relationship of the putative adaptation and ecological variable could be reversed. For example, even though it is obvious that climate differences predate the evolution of nephron differences, it is still possible that larger nephrons evolved for some reason unrelated to climate, and then animals with longer nephrons were able to move into drier climates, rather than the other way around.

Hence, for the evolution of male superiority in spatial navigation, there are at least three hypotheses to consider:

(A1) Adaptation: home range size dimorphism causes the ability dimorphism to evolve.

(A2) Reverse direction of causality: the ability dimorphism (preexisting or evolving for whatever reason) causes the home range size dimorphism to evolve.

(A3) Testosterone spill-over: testosterone evolved for reasons having nothing to do with its ontogenetic effect on spatial navigation. The spatial ability dimorphism did not evolve as a response to home range dimorphism.

Note that A2 does not specify the origin of the ability dimorphism. One version of A2 could be that testosterone causes the ability dimorphism ontogenetically, which then causes the home range size dimorphism to

evolve. This has two important implications. The first is that a positive correlation between home range dimorphism and spatial ability dimorphism does not on its own imply adaptation because the direction of causality could be reversed and not due to adaptation. Second, the statement that testosterone ontogenetically causes the ability dimorphism is *neutral* on the question of adaptation. It is simply a claim about proximate causation. Testosterone as the proximate mechanism is consistent with all three hypotheses. However, the testosterone spill-over hypothesis as stated in A3 is explicitly *negative* on the question of adaptation because it states that the spatial ability dimorphism is causally unrelated to home range dimorphism. Hence, A3 is testable against A1 and A2 by evaluating the correlation between home range size dimorphism and spatial ability dimorphism across multiple species. Indeed, previous reports have attempted a similar analysis using two species (Gaulin and FitzGerald 1986) but, as we have argued, it is not possible to estimate a correlation with only two species due to confounding influences of genetic divergence (Garland and Adolph 1994). In this article, we are extending the analysis, by considering as many species as we could find for which data on sex differences in home range size and spatial ability were available from the literature.

In total, data on 11 species were extracted from the literature. If the adaptation hypothesis is true, we would expect a positive correlation between sexual dimorphism in home range size and spatial navigational ability. That is, on average, species that show larger male biases in home range size should also show larger male advantages in spatial ability, species that show no bias in home range size should on average show no difference in spatial ability, and species that display a female bias in home range size should on average show a female advantage in spatial ability. On the other hand, if the nonadaptation hypothesis (A3 above) is correct, then sexual dimorphism in spatial ability should be randomly distributed with respect to sexual dimorphism in home range size (i.e., the correlation between these two variables across species should be near zero).

SOURCE STUDIES

We gathered home range and spatial ability data from 35 studies on 11 animal species: pine voles, meadow voles, prairie voles, deer mice, rats, laboratory mice, talas tuco-tucos, humans, horses, cuttlefish, and rhesus macaques (Table 1). Primary source studies were found by entering keyword searches into JSTOR, EBSCO, PubMed, and Google Scholar search engines. Citations within those studies constituted a second source. Keywords included but were not limited to: spatial ability, spatial cognition, navigation, wayfinding, spatial memory, and visual cognition.

Basic selection criteria included the requirement that a given study had as subjects sexually mature animals, provided data on male and female subjects separately, had an adequate sample size (generally at least 10 per sex), used nonexotic methodologies that are relatively common in the literature without significant controversy, and provided original data. No data could be directly utilized from meta-analyses or reviews because raw data are required to calculate the sexual dimorphism index (see Calculation of Sexual Dimorphism section). This unitless index permits the comparison of disparate metrics and types of experiments.

SEXUAL DIMORPHISM IN HOME RANGE SIZE

Home range size is defined as the area (or volume) an animal traverses in the course of its natural activities, such as feeding, mate seeking, nesting, predator evasion, and so on. Measures may be averages of daily areas covered or the total area an animal covered in the course of a season, year, or lifetime. In nonhuman animals, home range size is measured through various standardized methodologies, including powder tracking to determine footprints and movement paths, repeated trapping of marked individuals, and use of radio collars and global positioning system (GPS) tracking that record specific locations at a given moment as a (Cartesian) data point (Blair 1942; Getz 1961; Webster and Brooks 1981; Zielinski and Vandenberg 1991; Mikesic and Drickamer 1992). The collected Cartesian data points are then used to

construct an estimate of the size of the home range, e.g., as a minimum convex polygon or an ellipse with estimated 95% probability bounds, which encompasses the area in which the coordinate points occur.

The cuttlefish provided a unique challenge to measuring home range for Jozet-Alves et al. (2008). They video recorded each individual in a shallow tank to determine the approximate distance it covered in 15 minutes and used this as a proxy estimate of comparative home range size. Hence, this measure is not directly comparable with the measures for most of the other species in our study, and should be interpreted with caution.

Seasonal variance in home range size, particularly due to the seasonality of mating systems in rodents, posed a definitional challenge. For example, many studies show high sexual dimorphism in the summer for meadow voles (summer is their mating season) and lower or zero sexual dimorphism in all other seasons (Getz 1961; Webster and Brooks 1981). We restricted selection to studies with year-round data as a more complete estimate that can then be fairly compared to other rodents and other animals that do not have a restricted mating season. Note that the large variation among home range estimates for meadow voles in Table 1 is due to the time scale of the measurements. Getz (1961) assayed the space traversed in a year by periodic retrapping, while Webster and Brooks (1981) used distances traversed in a 24-hour period based on frequent radio-telemetry recordings.

Home range data specific to sex was not located for horses and rhesus macaques because they were typically studied in groups. However, it is broadly agreed that both are highly social animals and that males and females remain in close proximity to each other for the vast majority of their lives (Lindburg 1969; Linklater 2000; Linklater et al. 2000). Therefore, we estimated that sexual dimorphism in home range size for horses and rhesus macaques is zero.

In contrast to animal home range studies, no methodological consensus on how to measure human home range size is established in the literature. Further, very few

studies of human home range have been conducted. Ecuyer-Dab and Robert (2004a) used a combination of detailed questionnaires and municipal addresses to measure “as the crow flies” distances subjects traveled to get to residences of family and friends, places of employment, locations of recreation, and vacations. Anthropologists who have studied ranging activity in preindustrial tribal groups have also relied on survey methods and map-based distance estimation (Harpending 1976; Hewlett et al. 1982; Garland 1983; O’Connell and Hawkes 1984; Gaulin and Hoffman 1988).

Culture and modernity further complicate human home range sexual dimorphism estimates. Technology allows great and easy travel not available to premodern humans. Industrialized societies also feature cultural innovations such as greater gender equality with the obvious consequence of diminished disparity in human home range size sexual dimorphism. Since we are concerned with what effect evolutionary forces have had on these behaviors, it may seem advisable to restrict consideration to premodern peoples on whom anthropologists have compiled home range data. However, these cultures, too, have unique histories, ethos, technologies, climate, geography, and other variables, which may impugn the assumption that they are especially representative of prehistoric groups of humans. We have included data from both industrial and preindustrial peoples in an effort to provide as complete a picture of human home range dimorphism as possible.

SEXUAL DIMORPHISM IN SPATIAL ABILITY

The majority of animal studies included in the comparative analysis used maze testing to measure spatial ability. Namely, the Morris water maze (MWM), the radial arm maze (RAM), T-maze designs, and modified versions of each of these. Typical metrics included average number of errors made, average latency to completion, or trials to criterion performance.

Human spatial ability studies included in our analysis chiefly consisted of wayfinding tests, virtual wayfinding, and mental rotation test (MRT) measurements. MRT is by far the

most commonly applied test of human spatial ability. The subject is shown a drawing of a geometric figure as a prompt, and then asked which of a set of figures could be the same object (e.g., Figure 1). The subject must mentally rotate the figure to check for a match. Silverman et al. (2000) found that the MRT predicts performance in wayfinding tasks, making it a useful indicator. Wayfinding and virtual wayfinding are direct measures of navigational ability. In these, the subject must traverse a real or computer-based landscape while navigating from one location to another. In some cases, the subject's ability to indicate compass heading or goal location heading was measured. We excluded some experiments and studies that measured aspects of spatial cognition lacking a clear and substantiated link to navigational ability. Some of these include two-dimensional mazes, figure rotation, paper folding, and hidden figures test (Linn and Petersen 1985). Two-dimensional paper mazes are insufficiently representative of the demands of navigation and performance on two-dimensional mazes was not correlated with wayfinding (Silverman et al. 2000). Skills measured by the paper folding and hidden figures test also have an uncertain relationship to wayfinding. Other measures rely on knowledge and learned skills, such as the map-reading component of Montello et al.'s (1999) study.

In view of the possible confounding influence of culture, we made an effort to find studies comparing different nations. Mann et al. (1990) compared Japanese and American students. Owen and Lynn (1993) compared the three-dimensional spatial ability of students from three distinct South African cultures: Indians, blacks, and whites. Silverman et al. (2007) also found consistent male bias in three-dimensional mental rotation across 40 nations and seven ethnicities. All of these studies found a male advantage in human spatial ability relevant to wayfinding across the cultures studied, consistent with findings from more commonly studied industrial subjects.

CALCULATION OF SEXUAL DIMORPHISM

The "raw" data from each study for males and females were distilled into an index in-

dicating the degree to which one sex was superior to the other in spatial ability or displayed the larger home range size (see Table 1). The equation $[(\bar{X}_g/\bar{X}_l) - 1]$ was used, where \bar{X}_g is the mean for the sex with the greater value and \bar{X}_l is the mean of the sex with the lesser value. If females display an advantage in spatial ability or a larger home range, then the equation is multiplied by -1 to assign a negative value. This is the standard formula for calculating sexual dimorphism in a trait for comparative analysis across species (e.g., see Cox et al. 2003). Using just the ratio of male to female values would not work because the range of possible dimorphism values would be vastly different for the two sexes (i.e., it would be 0 to 1 for one sex and 1 to infinity for the other). Subtracting 1 from the ratio and assigning female advantage negative values and males positive values ensures that the range of possible dimorphism values between the sexes is equal and centered at zero. If there were multiple measurements within a species, then the dimorphism indices were averaged to produce an average dimorphism index for the species (see Table 1). If males and females were not statistically different in the study using the conventional 5% type I error rate, then the index was assigned a value of zero. However, in a separate analysis, the data were also analyzed using the estimated index for these species even if not significant.

CONSIDERATION OF PHYLOGENETIC NONINDEPENDENCE

A potential confound inherent in the analysis of comparative data is phylogenetic nonindependence, also referred to as the relatedness confound. This is due to the fact that closely related species may share many traits due solely to their recent common ancestry. For example, rodents are furry, whiskered quadrupeds almost certainly because of their phylogenetic relatedness and not because each rodent species has independently responded to recent selection acting on those traits. Therefore, individual species do not provide entirely independent pieces of information. Ignoring this possibility can lead to inflated Type I error rates—i.e., rejecting the null hypothesis too often (Garland et al.

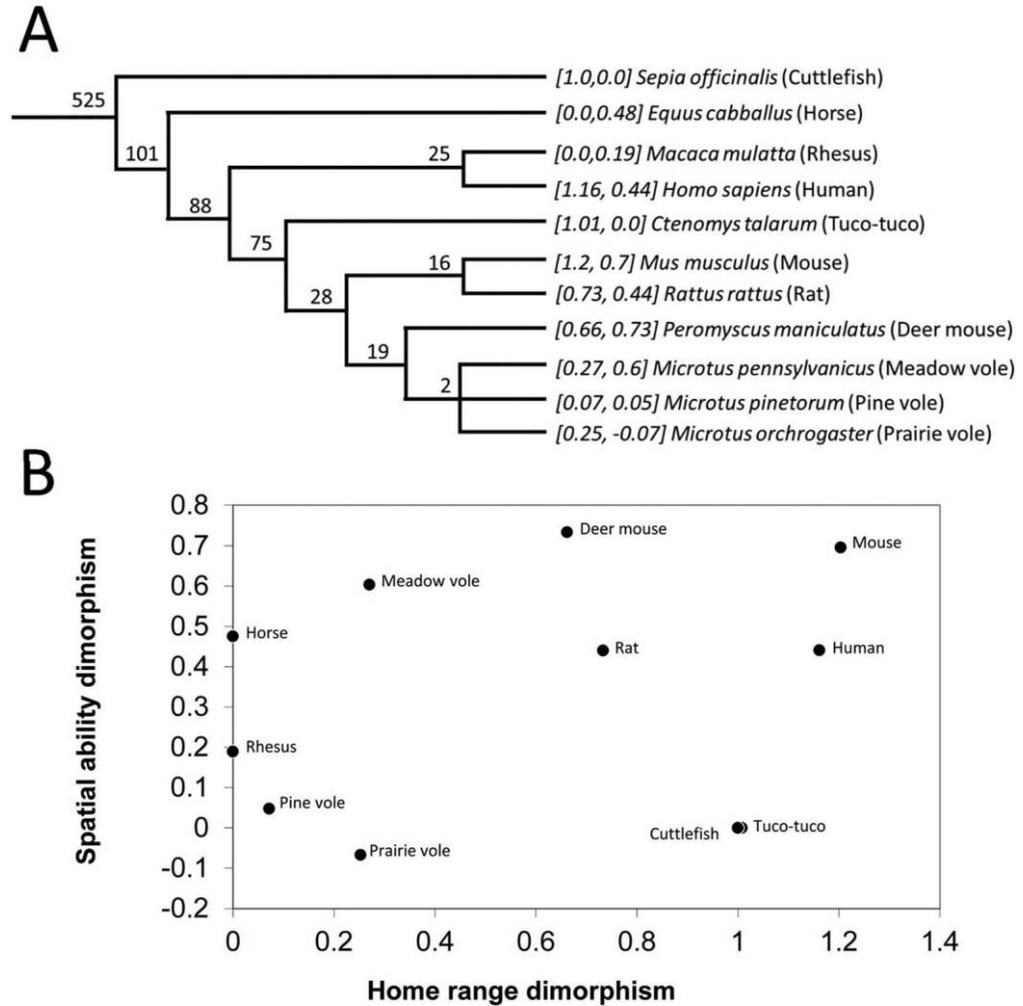


FIGURE 2. COMPARATIVE ANALYSIS OF THE CORRELATION BETWEEN SEXUAL DIMORPHISM IN HOME RANGE SIZE AND SEXUAL DIMORPHISM IN SPATIAL ABILITY ACROSS SPECIES

A) The phylogeny of the species used in the comparative analysis. Estimated divergence times are placed next to the branch lengths. Note that the branch lengths are not drawn to scale. In brackets at the tips of the tree before the species names are the species averages for home range and spatial ability dimorphism, respectively, from Table 1. B) The raw correlation without any transformation to adjust for phylogenetic relatedness.

1993, 2005). Therefore, we performed both conventional ordinary least squares linear regression and phylogenetically informed alternatives to test whether home range size dimorphism was a statistically significant predictor of dimorphism in spatial navigation abilities (for reviews of these methods, see Garland et al. 2005; Lavin et al. 2008; Rezende and Diniz-Filho 2012). Phylogenetic generalized least squares (PGLS) mod-

els were computed using the branch lengths shown in Figure 2A, which represent estimated divergence times, as well as three sets of arbitrary branch lengths suggested by previous workers (Garland et al. 1992; Pagel 1992). In addition, we computed a regression in which the residual dimorphism in spatial navigation abilities is modeled as an Ornstein-Uhlenbeck (OU) process (RegOU), which has been considered a way to model stabilizing se-

TABLE 2

Alternative regression models for predicting dimorphism in spatial navigation abilities from dimorphism in home range size. No model indicates a statistically significant relation

Model	Branch lengths	r ²	F _{1,9}	P	lnML
OLS	Star	0.031	0.29	0.6060	-1.617
PGLS	Time (Figure 2a)	0.114	1.16	0.3093	-13.100
PGLS	Grafen	0.215	2.46	0.1511	-3.456
PGLS	Pagel	0.151	1.60	0.2379	-4.347
PGLS	Constant	0.016	0.15	0.7099	-3.882
RegOU	Time transformed	0.029	0.27	0.6175	-1.663

OLS model is conventional, nonphylogenetic regression.

r² values are not comparable between OLS regression (which assumes a star phylogeny) and phylogenetic regression models. lnML is natural log of the maximum likelihood. Higher values indicate better-indicating models. However, the RegOU model contains one additional parameter as compared with all other models. The estimated OU transformation parameter (d) was 7×10^{-21} , which is statistically indistinguishable from zero. This estimate, which yields a nonhierarchical star phylogeny, in combination with the likelihoods of the models, indicates that the model assuming a star phylogeny (OLS) fits the data better than the PGLS model with estimated divergence time branch lengths (as shown in Figure 2A). The OLS model also has a higher likelihood than any of the three PGLS models that use arbitrary branch lengths.

lection, but also offers a way to compare the fit of conventional nonphylogenetic and phylogenetic statistical models via likelihood ratio tests (Felsenstein 1988; Garland et al. 1993; Blomberg et al. 2003; Lavin et al. 2008).

The phylogenetic tree was constructed from the literature (Hayasaka et al. 1988; Shu et al. 1999; Adkins et al. 2001; Jaarola et al. 2004; Steppan et al. 2004; Murphy et al. 2007). Branch length estimates were culled from recent papers that considered morphological, genetic, and fossil record information. In some cases, we found multiple divergence estimates for a given bifurcation and averaged the values. If a range of time was given, such as "15–25 million years ago," the median value was taken. The three vole species presented a challenge because of their recent radiation and the fact that no broad consensus on the relationships of prairie, pine, and meadow voles is available. Jaarola et al. (2004) analyzed the cytochrome B gene in many *Microtus* rodents, including the three vole species included in our analysis, without resolving a definitive phylogeny (Jaarola et al. 2004). Therefore, we represent the divergence of the three vole species as a polytomy.

RESULTS

Figure 2B shows that the relation between sexual dimorphism in home range size and

spatial navigation abilities is not significantly different from zero (ordinary least squares linear regression $r = 0.17$, two-tailed $P = 0.61$). Table 2 presents the phylogenetic versions of this regression model. Using the branch lengths that represent estimated divergence times (Figure 2A), the relation also is not statistically significant ($P = 0.31$). Applying the Ornstein-Uhlenbeck model of residual trait evolution yields an estimated OU parameter (d) that is indistinguishable from zero, indicating that a star phylogeny fits the data far better than the hierarchical tree shown in Figure 2A. Use of three alternative sets of arbitrary branch lengths (Grafen, Pagel, constant) does not change the conclusion that home range size dimorphism is not a predictor of dimorphism in spatial navigation abilities. Results were similar when the data were analyzed using the estimated indices for all studies, including those where sex differences were not statistically significant. In this analysis, the relationship between home range dimorphism and spatial navigation dimorphism displayed a slightly negative slope, but was also not statistically significant ($r = -0.02$; two-tailed $P = 0.95$, data not shown). The negative trend was caused by the tuco-tuco species, which displayed a large male bias in home range and a slight female bias in spatial navigation that was not statistically significant.

CONCLUSIONS

The multispecies comparative analysis offers no support for the adaptation male range hypothesis. If male superiority in spatial navigation was an evolutionary adaptation for larger home range size in males, then we would expect to see a stronger positive relation between dimorphism values for home range and spatial abilities. However, the slope and the effect size (i.e., R^2) were statistically indistinguishable from zero. Inspection of the graph in Figure 2B shows approximately a 30% male advantage on spatial navigation across species regardless of the range differences between the sexes. This result is consistent with the testosterone spill-over hypothesis because if elevated testosterone causes the dimorphism, then the male bias in spatial ability should be observed in most species and unrelated to home range dimorphism. The only species that did not show a male advantage in spatial navigation were the cuttlefish, tuco-tuco, and prairie vole (see Figure 2B). Note that each of these species was the subject of only one or two studies. Hence, the confidence in these values is weaker than in species where multiple studies were used and measurements were averaged to estimate the dimorphism value. On the other hand, if future studies are conducted in these three species, and the results indicate no sex difference in spatial ability, then an explanation would be warranted for why these species fail to fit into the testosterone spill-over hypothesis.

It is notable that our results and conclusions conflict with a previous report of a positive relationship between home range dimorphism and spatial dimorphism in a two-species comparison of voles (Gaulin and FitzGerald 1986). The two-species comparison is potentially highly confounded by genetic differences unrelated to the traits under consideration, in addition to be essentially anecdotal (Garland and Adolph 1994; Garland and Carter 1994). Therefore, we conclude that the results of the present multispecies comparative analysis trump the two-species analysis. From inspection of Figure 2B, the voles show relatively large divergence in spatial ability, but minimal divergence in home range dimorphism. For example, the meadow vole and

the prairie vole are at opposite ends of the spectrum for sexual dimorphism in spatial ability, but display relatively similar home range dimorphism. Hence, it seems unlikely that home range dimorphism has driven the different evolution of sexual dimorphism in spatial ability in these two species. Finally, we found that the phylogenetic regression models did not fit the data better than the non-phylogenetic one (Table 2). Hence, the raw correlation is an adequate representation of the correlation among these species.

FUTURE DIRECTIONS

The comparative analysis presented here is limited to the 11 species for which we were able to extract both home range data and spatial ability data separately for each sex. Data for more species would allow us to test the generality of the result. Although home range data are relatively easy to find in the literature, relatively few species have been analyzed for sexual dimorphism in spatial navigation ability.

Another problem that we encountered is that many studies in which spatial navigation performance was measured either did not measure both sexes, or did not report the sex differences. This was true for many bird studies, where measuring spatial navigation is typical, but where sex differences are not usually reported (Kamil et al. 1994; Gibson and Kamil 2005; Scheid and Bugnyar 2008). Hence, more studies of sex differences in spatial navigation are needed. Ideally, pairs of species that are closely related but display divergent patterns of sexual dimorphism for home range should be selected to maximize statistical power in the comparative analysis (Garland et al. 2005). Potentially good candidates include cowbirds, of which there are many closely related species with variance in the presence and type of brood parasitism. Cowbirds lay their eggs in the nest of a different species so the host species rather than the cowbirds care for the offspring and incur the costs associated with rearing young. In some cowbird species, both sexes search the environment for hosts, whereas in other species only the female searches to find good hosts, potentially resulting in sexual dimorphism in home range size (Day et al. 2008).

Inspection of Figure 2B shows that for all of the species the males were the sex with the larger home range. It would be extremely useful to add species with the opposite pattern of dimorphism, i.e., females ranging farther than males. If we still observed a male advantage in spatial ability even in species where females range farther, that would add important and compelling evidence against the adaptation hypothesis. On the other hand, if species where females range farther displayed enhanced spatial ability relative to males, this could challenge our conclusion and would support the adaptation hypothesis. Blenniid fish may be a fitting target of research, as females in some species are known to have a much larger home range than males because the males are sedentary caretakers of offspring (Costa et al. 2011).

Beyond the desirability of adding more species to the analysis, the statistically nonsignificant result should be taken as a serious challenge to the adaptation hypothesis that male superiority in spatial navigation evolved as an evolutionary adaptation for larger home range size. This claim about the evolution of sex differences in cognitive performance was not supported by the evidence (Figure 2). The alternative testosterone-spill over hypothesis that predicts that male superiority in spatial ability should be statistically unrelated to home range size dimorphism is better supported by the data. This result is significant because it illustrates the potential importance of “side effects” of selection in shaping animal and human cognitive behavioral traits.

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