SEXUAL SELECTION AND SEX DIFFERENCES IN SPATIAL COGNITION

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ABSTRACT: It is argued that a reliable and substantive sex difference, favoring males, exists in dynamic forms of spatial cognition, in particular, in the ability to mentally manipulate 3-dimensional representations of information, track movement in 3-dimensional space, navigate, and in terms of an implicit understanding of Euclidean features of physical space. It is proposed that these sex differences arise from the greater elaboration of the neurocognitive systems that have evolved for navigating and tracking movement in the 3-dimensional universe in males than in females. An evolutionary model of these sex differences is specified and examined in terms of the pattern of sex differences in navigational abilities that is evident across mammalian species, as well as in terms of anthropological, hormonal, and developmental patterns.

The thesis of this article is that a substantive sex difference exists, favoring males, in dynamic 3-dimensional spatial abilities and that this sex difference is largely the result of sexual selection and associated proximate biological (e.g., sex hormones) and developmental (e.g., play patterns) mechanisms. The sex difference in 3-dimensional spatial abilities appears to reflect the greater elaboration of the neurocognitive systems that support habitat navigation and representation in males than in females (Gaulin 1992). Sex differences are expected to be the largest for tasks that require the dynamic processing of information in three dimensions, because the neurocognitive systems that support habitat navigation directly mirror the 3-dimensional physical universe and are responsive to movement within physical space (Shepard 1994). Sex differences are expected to be smaller or nonexistent for processing 2-dimensional representations, because the neurocognitive systems that support habitat representation have evolved in a 3-dimensional, not a 2-dimensional universe, as well as for more static forms of spatial cognition (e.g., object...
location; Eals & Silverman 1994). Thus, the position presented herein should not be taken to mean that males have an advantage over females in all forms of spatial cognition (e.g. Caplan, MacPherson, & Tobin 1985; Halpern 1992).

As an organizing framework, the consideration of the sex difference in 3-dimensional spatial cognition will be in terms of goal structures and procedural and conceptual competencies, rather than simply in terms of the mental operations underlying this form of spatial cognition. This is because it appears that many forms of cognition are best understood in terms of goal structures, and conceptual and procedural competencies (Gelman 1990). Consider counting as an example of these competencies: the goal of counting is to determine the number of items in a set. Counting is achieved by means of procedures, such as pointing to or tagging with a word name each item as it is counted. The use of counting procedures, in turn, is constrained by conceptual knowledge. For instance, counting appears to be constrained by an implicit understanding that each item must be tagged once and only once (Gelman & Gallistel 1978). As in counting, a complete understanding of all forms of cognition might require models that accommodate each of these competencies, as well as biological and environmental influences on their development and expression (Hall 1992).

A complete consideration of the sex difference in 3-dimensional spatial cognition also requires a consideration of the pressures that might have differentially affected the evolution of males and females, that is, sexual selection. The first section below briefly describes the principles of sexual selection and how sexual selection might have operated to create a sex difference in 3-dimensional spatial cognition. The second section describes sex differences on relevant spatial tasks, while the third presents a consideration of hormonal and developmental mechanisms in the expression of spatial skills.

SEXUAL SELECTION

Darwin (1859/1872) argued that sexual selection "depends, not on a struggle for existence in relation to other organic beings or external conditions, but on a struggle between the individuals of one sex . . . the result is not death to the unsuccessful competitor, but few or no offspring" (p. 69). If sexual selection has operated in the evolution of a species, then males and females of that species differ, to some extent, in reproductive strategies (i.e., relative amount of time devoted to finding mates or raising offspring). A sex difference in reproductive strategies, in turn, is typically associated with physical and behavioral differences, shaped by sexual selection, between males and females (Daly & Wilson 1983). Trivers (1972) argued differences in male and female level of investment in offspring "governs the operation of sexual selection" (p. 141), and, as such, is the ultimate cause of any associated sex difference in reproductive strategies. The model predicts that the sex that invests the least in
offspring will show less discriminant mating, on average, and more intrasexual competition over access to members of the opposite sex. The higher investing sex, in contrast, is expected to be much more discriminating in terms of choosing sexual partners, with discrimination focusing on a potential partner's physical characteristics or behaviors that might benefit future offspring.

In these species, sexual selection appears to operate largely by means of intramale competition and female choice of mating partners, and is typically associated with polygynous mating systems. For nearly all polygynous mammalian species, males invest less in offspring than females, are physically larger, show more intrasexual competition, and have higher mortality rates than females (Daly & Wilson 1983). At the same time, many of these sexual dimorphisms are not evident in monogamous mammalian species, such as the prairie vole (*Microtus ochrogaster*), where intense intrasexual competition is not evident (Daly & Wilson 1983; Gaulin 1992).

Many human sex differences appear to parallel those found in polygynous mammalian species. In humans, males are larger than females, have higher mortality rates, are more casual in their sexual behavior, and show more intense (e.g., homicide) forms of intrasexual competition (e.g., Daly & Wilson 1983; Frayer & Wolpoff 1985; Gaulin & Boster 1992; Oliver & Hyde 1993; Wilson & Daly 1985). Moreover, although most human societies are functionally monogamous, most non-Western cultures are polygynous, that is, they allow males to have more than one wife, although most males cannot support more than one wife (Murdock 1981). Human males, in fact, show tendencies of both monogamous (e.g., higher levels of paternal investment than most other primates) and polygynous species (Lovejoy 1981). Regardless, the finding of consistent human sex differences in physical size, mortality rates, sexual behavior, and intrasexual competition argue that sexual selection and any associated proximate mechanisms (e.g., sex hormones) need to be seriously considered as a potential source of human sex differences in cognition and social behavior (Buss & Schmitt 1993; Daly & Wilson 1983; Feingold 1992; Gaulin & Boster 1992).

The goal here is to consider how sexual selection might have operated to produce sex differences in 3-dimensional spatial cognition. Gaulin (Gaulin 1992; Gaulin & Fitzgerald 1989) has proposed that in nonhuman polygynous mammals, the often found male advantage in 3-dimensional spatial cognition is directly related to intramale competition and courtship of females. In these species, the home range of males is larger than the home range of females, and, as a result, it overlaps the home range of several females. Thus, males are able to simultaneously court several females. For these species, the sex differences in the size of the home range and in 3-dimensional spatial cognition are only evident during the mating season. Moreover, in monogamous species there appear to be no sex differences in either the size of the home range or on tasks that assess 3-dimensional spatial abilities (Gaulin 1992). The overall pattern appears to be in keeping with the position that the sex difference in 3-dimensional spatial cognition in polygynous mammalian species is
directly related to reproduction and likely shaped by sexual selection (Gaulin & Fitzgerald 1989).

Given that the sexual dimorphisms found in humans parallel those found in other mammalian species where sex differences are evident, it is possible that the same ultimate mechanisms, associated with sexual selection, are the source of some of the sex differences found in humans. In particular, intramale competition appears to be an important mechanism associated with the evolution of sex differences in the size of home ranges and in 3-dimensional spatial abilities in many polygynous mammal species (Gaulin 1992). Thus, intramale competition might be the ultimate source of the human sex difference in 3-dimensional spatial cognition.

Two potential ultimate sources of intramale competition in humans are hunting and small-scale warfare (Alexander 1979; Hill 1982; Symons 1979). In most preliterate societies hunting is almost exclusively a male activity that, when successful, provides a substantial benefit to the group (Ember 1978; Kaplan & Hill 1985; Murdock 1981). More important, in many preliterate societies “a man’s hunting prowess is directly related to the number of wives” (Symons 1979, p. 159) he can support, and, as a result, skilled hunters often have more offspring than their less skilled peers. With more monogamous pairings, skilled hunters appear to have more surviving offspring than less skilled hunters (Kaplan & Hill 1985). The other, and perhaps more likely, possibility is that the sex difference in 3-dimensional spatial cognition is related to more direct male-male competition, in particular, small-scale warfare between kin-based groups (Alexander 1979; Wilson & Daly 1985; Rohner 1976). In such situations, groups of related males often travel relatively long distances to ambush males from other groups or to capture females, which makes foraging far from the home base dangerous for females (e.g., Chagnon 1977). These activities are one important source of male mortality in these societies, but nevertheless are carried out because successful raids directly influence the reproductive success of males. In fact, small-scale warfare appears to be more strongly related to male mortality and individual differences in the number of offspring of males than hunting (Alexander 1979; Chagnon 1977).

These scenarios are speculative, of course. However, they suggest that the human sex difference in 3-dimensional spatial cognition is an evolved consequence of sexual selection. Even if these particular scenarios are dismissed, it still appears that during the course of human evolution males traveled farther from home bases than females. For instance, sexual dimorphisms in the shape of the femur and tibia in early hominids and individuals from hunter-gatherer societies indicate greater mobility and larger ranges in males than in females (Ruff 1987); activity patterns influence the morphology of these and other bones. The greater mobility of males likely created greater selection pressures for navigational skills in males than in females. The crucial question is whether the goal structures, and conceptual and procedural competencies that were likely to be associated with navigation and hunting/fighting show consistent and selective sex differences favoring males. These issues are addressed in the following sections.
SEX DIFFERENCES IN 3-DIMENSIONAL SPATIAL COGNITION

In this section, the conceptual and procedural competencies that are likely to be associated with habitat representation and navigation and hunting/fighting and any associated sex differences are considered in turn. The goal of hunting is obvious; the goal of fighting appears to be to establish dominance (Wilson & Day 1985). It is likely that the goal structures of fundamental, or biologically primary, forms of cognition and any associated behaviors can also be inferred from children's play activities (Geary 1992, 1995). This is because goal structures appear to orient the child's attention to relevant features of the environment and motivate engagement in the types of activities that are likely to build on procedural and conceptual competencies (Gelman 1990). Thus, sex differences in the play patterns of boys and girls, as related to the goals of acquiring 3-dimensional spatial abilities and hunting/fighting skills or for establishing dominance, are discussed below in the section on proximate mechanisms.

CONCEPTUAL COMPETENCIES

It appears that all species have neurocognitive systems that enable navigation in 3-dimensional space (Gallistel 1990; Gould 1986; Shepard 1994). Associated with the functioning of these systems is an implicit understanding of Euclidean, or basic geometric, features of the physical universe (Gallistel 1990). That is, the conceptual competencies that appear to be associated with habitat navigation reflect an implicit understanding of geometric relationships among objects in physical space (Geary in press).

More important, males of polygynous, but not monogamous, mammalian species are more skilled in navigating in natural and laboratory settings than are same-species females, and selectively attend to geometric cues during navigation (Gaulin 1992; Williams, Barnett, & Meck 1990). In these species, females rely on landmark as well as geometric cues during navigation, although they do not appear to be as skilled as males in using geometric information for navigation (Williams et al. 1990). Galea and Kimura (1993) found this same pattern in humans. In their study, male college students learned a route with fewer errors and with fewer trials to criterion than their female peers. The "females remembered more landmarks, both on and off route than males ... males outperformed females in knowledge of the Euclidean properties of the map" (Galea & Kimura 1993, p. 53). Moreover, route learning was significantly correlated with performance on a spatial ability measure, specifically the Mental Rotation Test (MRT; Vandenberg & Kuse 1978), for both males and females, but was unrelated to performance on measures of visual memory. The selective relation between route learning and performance on the MRT, a measure of 3-dimensional spatial abilities, is important because the "cognitive coordinate system within which the (MRT) figures are represented is the standard environmentally defined one" (Just & Carpenter 1985).

In other words, of all of the currently available spatial ability measures, the cognitive systems associated with solving MRT items appear to show the closest
correspondence to the cognitive systems that enable navigation in 3-dimensional space (Geary in press). The relation between route learning and performance on the MRT is particularly important because the largest (close to 1 SD) and most consistent sex difference, favoring males, in spatial abilities is found for performance on the MRT (Linn & Peterson 1985; Masters & Sanders 1993). Males also have an advantage over females on more dynamic measures of spatial cognition, in particular on measures that assess the ability to determine the trajectory of moving objects (Law, Pellegrino, & Hunt 1993). The male advantage in spatial tracking does not diminish over the course of, at least short term, practice (Law et al. 1993), nor does the male advantage on the MRT disappear across cohorts or across cultures (Geary, Chen, & Fan 1994; Masters & Sanders 1993).

In summary, human males show a consistent advantage over females in the ability to mentally manipulate 3-dimensional representations of information, to track and predict the trajectories of moving objects, and to navigate. The proposal here is that performance on these tasks reflects the operation of the neurocognitive systems that have evolved for the representation of and navigation in the 3-dimensional physical universe, and an associated implicit understanding of the Euclidean features of space. The sex difference on these tasks likely represents the greater elaboration of the associated neurocognitive systems in males than in females (Geary in press). The finding that these same differences are found in other mammalian species with physical and behavioral dimorphisms seems to be consistent with the argument that this human sex difference in 3-dimensional spatial cognition is related to sexual selection. It was argued that hunting and/or inter-group warfare might have been ultimate pressures that selected for the relatively well-developed navigational skills in males (Alexander 1979; Symons 1979). If so, then consistent sex differences on the procedural competencies necessary for successful hunting/fighting should also be found.

PROCEDURAL COMPETENCIES

If hunting/fighting skills were shaped by sexual selection, then successful males should not only have had better developed navigational skills than less successful males, they should have also had an advantage on the procedural skills associated with hunting/fighting. Since hunting/fighting was a likely mode of intramale, but not intrafemale, competition, the component cognitive and procedural competencies would have influenced the number of offspring of males but not of females. Hence, over the course of human evolution, a sex difference, favoring males, should have emerged on both the conceptual and procedural dimensions of hunting/fighting.

Throwing accuracy is almost certainly a procedural competency that is associated with hunting, as well as male-male warfare (Chagnon 1977). More important, throwing accuracy is associated with 3-dimensional spatial abilities (Kolakowski & Malina 1974) and males are more accurate at hitting targets than are females (e.g., Jardine & Martin 1983). Furthermore, two of the largest sex differences, favoring males, that have been identified are throwing distance and throwing velocity (Thomas & French 1985). The sex difference on these dimensions is, on average,
between 1.5 and 2 SDs during the preschool and early elementary school years, and is more than 3 SDs by early adolescence. Stated differently, there is very little overlap in the distributions of males and females for throwing distance and velocity, even before large sex differences in participation in sports (Thomas & French 1985). Thus, it appears that there are theoretically important and substantive sex differences on the procedural competencies that were likely to have been associated with hunting or fighting skills. The overall pattern appears to be consistent with the view that during the course of human evolution, hunting and/or fighting was an important aspect of intramale competition and the associated procedural and conceptual competencies were shaped by sexual selection.

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**PROXIMATE MECHANISMS: BIOLOGY AND DEVELOPMENT**

In this section, biological and developmental mechanisms that are likely to be associated with the learning and expression of the conceptual and procedural competencies that are likely to be associated with habitat navigation and hunting/fighting are discussed.

**BIOLOGICAL MECHANISMS**

If sexual selection has operated in the evolution of spatial abilities, that is, created a sex difference in 3-dimensional spatial cognition, then sex hormones are very likely to be important proximate biological mechanisms in the expression of this sex difference. Indeed, "there is now substantial evidence that cognitive patterns may vary with phases of the menstrual cycle in normally cycling women and with seasonal variations in androgens in men" (Kimura & Hampson 1994, p. 57). Performance on tests of 3-dimensional spatial abilities, especially the MRT, is at its lowest when estrogen and progesterone levels are at their highest in normally cycling women (Hampson & Kimura 1988; Silverman & Phillips 1993). For young males, performance on such spatial tests varies with testosterone levels, though not linearly, and peaks in the spring (Kimura & Hampson 1994). Moreover, pre- or perinatal exposure to androgens appears to increase the 3-dimensional spatial abilities of human females and females of other species and influences the development of the underlying neurobiological systems (Diamond, Johnson, & Ehlert 1979; Resnick, Berenbaum, Gottesman, & Bouchard 1986; Williams et al. 1990).

Furthermore, pre- or perinatal exposure to sex hormones appears to result in selective attention to geometric cues during navigation. For instance, in one study it was found that "rats exposed neonatally to gonadal steroids [normal males and (hormonally) treated females] selectively attended to geometric cues when they were presented in compound with other types of cues; landmarks are overshadowed by a coordinate system obtained by the geometry of the room" in which navigation occurred (Williams et al. 1990, p. 95). Castrated males and normal females did not selectively attend to geometric cues, although they did attend to
these cues at times. Moreover, the relationship between hormonal fluctuations and cognitive abilities is confined to measures that typically show sex differences, suggesting that the results are not due to changes in mood or attentiveness, but rather are directly due to the organizational and activational effects of sex hormones.

In all, it appears that pre- and perinatal exposure to androgens results in the elaboration of the neurobiological systems that support habitat navigation and that later hormonal levels directly influence performance on navigational and 3-dimensional spatial tasks, but not performance on other types of tasks, such as vocabulary tests (Diamond et al. 1979; Kimura & Hampson 1994). Given this, it seems reasonable to assume that sex hormones might also influence the development of the conceptual competencies associated with habitat representation and navigation, in particular an implicit understanding of Euclidean features of the physical universe (Geary in press).

DEVELOPMENTAL MECHANISMS

The argument that the development of navigational abilities is influenced by sex hormones does not mean that learning and experience are not involved in the development of 3-dimensional spatial abilities and any associated sex differences. In fact, it is likely that all biologically-primary forms of cognition, such as habitat representation (e.g., cognitive maps), require extensive experience for normal development (Greenough, Black, & Wallace 1987). I have argued elsewhere that children's play is likely to be intimately related to the development of the neurocognitive systems that support primary forms of cognition, by ensuring the pattern of experience that is necessary for the normal development of the underlying neurobiological systems and for the elaboration of basic conceptual and procedural competencies (Geary 1995).

If so, then the play of children should reflect an implicit goal of elaborating on the conceptual competencies and improving the procedural competencies associated with primary forms of cognition. From the present perspective, the question is whether the play activities of children reflect the goal of improving the conceptual and procedural competencies associated with navigation and hunting/fighting, and, if so, whether there are sex differences in these activities.

In unstructured free-play settings, the play ranges of boys are larger than the play ranges of girls in Western as well as preliterate societies (Eaton & Enns 1986; Eibl-Eibesfeldt 1989; Munroe & Munroe 1971). Moreover, in preliterate societies play hunting and play fighting, and the practice of component skills (e.g., throwing), is much more common in boys' play than in girls' play, even in societies where there are no explicitly articulated sex roles (Endicott 1992). In fact, the play activities of boys often appear to reflect the implicit goal of achieving dominance over other boys (Maccoby 1988). These differences appear to emerge from sex differences in interest patterns and a selective attention to and imitation of same-sex adults (Eibl-Eibesfeldt 1989), as well as prenatal exposure to androgens (Berenbaum & Hines 1992; Resnick et al. 1986). Moreover, the play activities of children, especially
boys, in societies where play hunting is not common often appear to have the goal of elaborating the conceptual and procedural competencies associated with navigation and hunting/fighting, as well as reflecting intramale competition.

To illustrate, on the surface hunting, fighting, and baseball appear to be unrelated. However, baseball involves engaging in activities that will likely elaborate on the conceptual knowledge associated with navigation, such as tracking moving objects (i.e., a baseball) in 3-dimensional space, as well as improving the procedural competencies associated with hunting/fighting, such as accurate throwing. In this sense, play fighting and playing baseball reflect similar implicit goals, that is, elaborating on implicit Euclidean knowledge and practicing procedural skills, and is done in a context of intrasexual competition. This is not to say that children, or adults, are explicitly aware of some relationship between baseball and hunting/fighting. Rather, the types of activities that children enjoy will lead to the evolution, culturally speaking, of games and activities that serve the larger goal of acquiring adult-like competencies, at least adult-like competencies that have been selected for by means of natural or sexual selection. For present purposes, it appears that boys are more likely than girls, on average, to seek out and engage in play activities that will likely elaborate on the conceptual competencies associated with navigation and that will enable practice of the procedural skills associated with hunting or male-male fighting (Eibl-Eibesfeldt 1989; Maccoby 1988).

The principles of sexual selection appear to provide a useful theoretical framework for examining sex differences in human cognition and behavior (Geary in press), and appear to provide a useful organizing theme for approaching and understanding the sex difference in 3-dimensional spatial cognition. Nevertheless, this framework does not imply that all human sex differences are solely the result of sexual selection and any associated proximate mechanisms. It is clear that the magnitude and expression of many sex differences vary across cultures and historical periods and therefore their expression is highly sensitive to contextual and cultural factors (Geary in press; Oliver & Hyde 1993; Rohner 1976). Confusions often seem to occur when sex differences are approached using broad categories, such as spatial abilities, verbal abilities, mathematics, or sexual behavior, rather than in terms of the component features of these more general categories (Halpern 1992).

From an evolutionary perspective, males and females are expected to be largely equivalent in their cognitive abilities. For instance, because we live and develop in the same physical universe, males and females must perforce have similar systems for habitat navigation (Shepard 1994). Sexual selection would operate by means of differentially elaborating some of these cognitive systems in males and females. When such elaborations occur they are very likely to be highly specialized modifications of these systems. So, if hunting, for instance, were a source of intramale
competition, and an important feature of sexual selection in humans, then we would anticipate sex differences only on those conceptual and procedural competencies that facilitated hunting or the acquisition of the associated component skills, but not for other forms of spatial cognition. From this perspective, a male advantage in the spatial skills that support habitat navigation are expected, but sex differences in other forms of spatial cognition, such as the memory for object location are not (Eals & Silverman 1994).

Indeed, Silverman and Eals (1992, 1994) have argued “that the critical factor in selection for spatial dimorphism in humans was sexual division of labor between hunting and gathering during hominid evolution. . . . (If) these (spatial skills) have evolved in males in conjunction with hunting, spatial specializations associated with foraging should have, correspondingly, evolved in females” (Silverman & Eals 1992, pp. 534–535). In particular, the demands of foraging might have resulted in a female advantage in the recognition and recall of the location of objects within arrays of objects and “increased peripheral perception and incidental memory for objects and their locations” (Silverman & Eals 1992, p. 535). Across a series of studies it was shown that females do indeed outperform males on tasks that assess memory for objects and memory for the location of those objects (Eals & Silverman 1994; Silverman & Eals 1992). In fact, in one naturalistic study of the memory for object locations, the female advantage was as large (i.e., about 1 SD) as the typical male advantage on the MRT (Silverman & Eals 1992, Study 2).

The contrast in the pattern of sex differences in 3-dimensional spatial cognition and for the memory for object location highlights the specificity of human sex differences and provides a useful framework for examining cultural influences on sex differences as well. For instance, there is considerable cross-cultural and historical variability in the valuation of female chastity (Buss 1989; Oliver & Hyde 1993), suggesting that any sex difference in this area likely reflects culture attitudes and values with regard to male and female sexuality. The sex difference in attitudes towards casual sex (i.e., males are more willing to engage in sexual activity outside of a committed relationship than are females) are much more robust (Buss & Schmitt 1993; Oliver & Hyde 1993), however, and are understandable in terms of sexual selection. Females are more discriminating in their sexual behavior than males in those species where males invest little in the rearing of offspring or where the level of male investment is not always predictable (Trivers 1972). In other words, for those sex differences that follow the principles of sexual selection, show similar patterns across species, and vary with sex hormones, there is reason to believe that the differences between males and females have been shaped by sexual selection. However, any such differences are likely to be highly specific and rarely, if ever, encompass broad categories of behavior (e.g., sexual behavior) or cognition (e.g., spatial abilities).

Finally, the framework presented in this article might be useful for the analysis of sex differences in other cognitive abilities. In particular, the conceptualization of cognitive sex differences in terms of goal structures, and conceptual and procedural competencies, all nested within the theoretical framework of the principles of sexual selection, should enable a rather more complete and satisfactory analysis of any
such differences than is possible with the simple comparison of scores on cognitive tests. Stated differently, within this framework cognitive sex differences are conceptualized as simply one aspect of a much more complex system that includes social or ecological (e.g., navigation) goals, implicit knowledge associated with these goals, and behaviors (i.e., procedures) designed to achieve these goals. Finally, within this framework sex differences in children’s play are seen as providing the foundation for later cognitive sex differences, based on the position that sex differences in children’s play reflect more fundamental differences in the goal structures of males and females and provide the practice needed to flesh out rudimentary conceptual and procedural competencies.

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NOTE

1. Biologically-primary cognitive abilities, such as language, are defined as those forms of cognition that appear to have been directly shaped by natural or sexual selection, whereas biologically-secondary cognitive abilities, such as reading, appear to involve the co-optation of primary systems for purposes other than their original evolution-based function, and primarily emerge in school (Geary 1995).

REFERENCES


