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THE DIMENSIONALITY OF THE MATING ENVIRONMENT PREDICTS MALE  
COMBAT AND SEXUAL COERCION IN TURTLES

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## ABSTRACT

Predicting which mechanisms of sexual selection will be in effect in a given species is a topic of ongoing research. It has previously been suggested that terrestrial species have a higher degree of male combat than aquatic species. The hypothesis tested in this thesis is that the dimensionality of the mating environment will influence the evolution of both male combat and sexual coercion. Specifically, male combat and sexual coercion should be more likely to evolve in two-dimensional mating environments, in which females are easier to monopolize and constrain, than in three-dimensional environments where males are easier to evade by both same-sex competitors and females. In a large sample of turtle species with a diversity of mating dimensionalities, we tested the hypothesis that dimensionality predicts the degree of male combat and sexual coercion that will occur in a given species. As predicted, we found that male combat, sexual coercion, large male size, and male weapons are more likely to occur in species in which males compete for mates two-dimensionally than in species in which males compete for mates three-dimensionally. These data support the dimensionality hypothesis and contribute to a greater understanding of the forms that sexual selection will take in a given species.

**TABLE OF CONTENTS**

LIST OF FIGURES.....	iii
LIST OF TABLES .....	iv
ACKNOWLEDGEMENTS .....	v
THE DIMENSIONALITY OF THE MATING ENVIRONMENT PREDICTS MALE COMBAT AND SEXUAL COERCION IN TURTLES .....	1
METHODS .....	12
RESULTS .....	17
DISCUSSION.....	23
REFERENCES .....	26
Appendix. Degree of sexual size dimorphism, dimensionality, habitat, and mechanisms of sexual selection in turtles.....	28

**LIST OF FIGURES**

Figure 1-1. Plot showing mean PC1 values.....	18
Figure 2-1. Plot showing mean weapon presence.....	19
Figure 3-1. Plot showing mean sexual coercion.....	22

**LIST OF TABLES**

Table 1-1. Component loadings of first two varimax-rotated components of PCA.....	16
Table 2-1. Results controlling for habitat with semi-aquatic and terrestrial as one group.....	20
Table 3-1. Results controlling for habitat with semi-aquatic and aquatic as one group.....	21

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## **THE DIMENSIONALITY OF THE MATING ENVIRONMENT PREDICTS MALE COMBAT AND SEXUAL COERCION IN TURTLES**

### **Sexual Selection**

Sexual selection was first proposed to explain why males and females of the same species are often so physically different, and why there are traits that are often seen in males of a species, such as bright colors and exaggerated courtship antics, that seem harmful to survival. Sexual selection refers to the expression of traits that is influenced by differences in reproductive success, caused by competition over mates (Darwin, 1858; 1871; Andersson, 1994). The literature on sexual selection has come to account for the advantages that certain individuals have over others of the same sex and species in exclusive relation to mating. This form of selection is often expressed by costly secondary sexual characteristics that are opposed by natural selection, yet are so beneficial to mating success that they are maintained in the population. Therefore, sexual selection plays an important role in determining what selective pressures are present behind sex differences in size, shape, coloration, and behavior.

Darwin (1858) wrote that sexual selection depends on one sex's struggle for possession of the other sex. Unlike natural selection, failure results not in the death of the individual, but in the individual having fewer or no mates as compared to same-sex rivals. Sexual selection leads to competition, in which an individual makes mates less available to others of the same sex (Andersson 1994).

*The limited sex competes more intensely for mates than the limiting sex.*

The intensity of sexual selection is affected by the operational sex ratio, the ratio of receptive females to potential mating males at any one time. Unequal operational sex ratios are expected to lead to more intense sexual selection. Due to the intense male-male competition that

a skewed operational sex ratio creates, there will generally be a high variance in male reproductive success (Emlen, 1976).

The intensity of sexual selection is also related to male and female potential reproductive rates. The sex that can achieve higher reproductive rates should compete more intensely for mates than the sex with the lower reproductive rate, as a sex difference in reproductive rates will skew the operational sex ratio such that there will be more of the faster-reproducing sex available to mate. Although males have a higher reproductive rate in the vast majority of species, in those where females have a higher reproductive potential more intense competition for mates is often seen among females. This is the case in species of birds where males spend time caring for young, and in some fish where the female's primary contributions are her eggs (Clutton-Brock & Vincent, 1991).

The sex that invests the most in producing offspring becomes a limiting resource over which the other sex will compete, an idea known as Bateman's Principle. This is because when one sex becomes a limiting factor, which in most species is the female, reproductive success of males is much more variable than that of females. Most female animals are limited in fertility by their egg production, and rearing of young in mammals, while males are generally only limited in the number of successful copulations with different females that they can achieve (Bateman, 1948; Trivers, 1972). Males can produce more gametes than females, and therefore compete to mate with as many and as fecund females as possible. As the limited sex, males benefit most from frequent copulation.

Parental investment is defined by Trivers (1972) as "any investment by the parent in an individual offspring that increases the offspring's chance of survival (and hence reproductive success) at the cost of the parent's ability to invest in other offspring." In the majority of species, the main contribution by the male to offspring are the sex cells. Therefore, females generally invest more in offspring, as well as investing more in fewer, larger, higher quality gametes, which



makes them more careful in their choice of partners (Andersson, 1994). Females have more to lose by mating with a male of low genetic quality. These factors contribute to females being the “choosy” sex, those that exhibit choice in their sexual partners, unlike males of most species who are observed to copulate indiscriminately. Female variability in mating success is not regarded as being influenced by the ability to attract mates, in contrast with male mating success which is extremely limited by the ability to be chosen by a female.

*Sexual selection occurs through several distinct mechanisms.*

Conspicuous secondary sexual characteristics such as bright colors, vocal display, or other features in males that are opposed by natural selection and favored by sexual selection may be explained as products of mate choice that evolved through selection by the limiting sex (Darwin, 1871). An important idea in the theory of mate choice is the Fisherian runaway selection model, which hypothesizes that the selection for a certain trait begins with that trait having a selective advantage that establishes it in the species. Female preference for males with that trait becomes genetically associated with it, so that females bear sons with the selected, advantageous trait, and daughters with the preference for the trait. Eventually, the trait becomes maintained by sexual selection, and continues to be expressed at a higher frequency until survival disadvantages balance selective advantages (Fisher, 1930; Andersson, 1994). Courtship involving ornamentation and signals are possible indicators of good genes, genetic fitness that is demonstrated by male secondary sexual characteristics (Williams, 1975; Hamilton & Zuk, 1982). Ornamentation and courtship display are possible advertisements of high parental care abilities (Andersson, 1994), indicators that a courting male is a member of the female’s species (Fisher, 1930; Wallace, 1889), or selected for because of pre-existing biases toward sensory stimuli, which are exploited by the courting male. Female responses that have been selected for in other

contexts may be exploited by the male in his bid for a mating opportunity (West-Eberhard, 1984; Ryan, 1990).

Contest competition is another important form of intrasexual selection, in which males compete with rival males for mates. Male contest competition selects for large size and weapons that are used by males in combat, and which act as conspicuous signals or psychological weapons via threat (Andersson, 1994; Fisher, 1930). Male weapons evolve through sexual selection in contests by the limited sex over the limiting sex.

Scramble competition is a form of intrasexual competition in which mating success is highest for those males who are able to reach the female first. This form of sexual selection is favored in largely dispersed groups, or in species that have large home ranges. Rapid locomotion and improved sensory abilities are favored (Andersson, 1994).

Females benefit from being selective in their choice of mates; it is often beneficial for them to wait for a partner with good genes or investment potential. Males, on the other hand, tend to benefit from copulating more frequently. These important differences create sexual conflict between the sexes. Due to this conflict, males are seen to force copulation in some species (Andersson, 1994), a tactic that may increase reproductive success in males; forcing females to copulate may result in less energy expenditure by the male than engaging in the elaborate courtship that is often necessary in female choice (Smuts & Smuts, 1993).

*Mechanisms of sexual selection vary in their relative importance across species.*

As has been noted, differential reproductive success is an important factor that influences severity of male competition over mates. Therefore, competition is perhaps most severe between polygamous animals, in which there is the most differential reproductive success, and contests are seen to be more peaceful among more monogamous birds, in which female choice is observed to be based on display and antics of the males rather than intrasexual contest competition (Emlen &

Oring, 1977; Andersson, 1994). Different species, and even populations of the same species, display differing intensities of sexual selection. One explanation for this diversity of intensity relates to the habitat constraints which impose limits on the degree to which sexual selection can operate. These constraints of habitat allow a portion of the population, generally males, to control access to potential mates. This can take the form of direct physical defense of potential mates, or indirect defense of resources necessary for potential mates. Harems are seen to develop when females are clustered and relatively immobile, allowing one male to guard a group of many females at one time, monopolizing sexual access to them (Emlen, 1976). Greater ability to monopolize resources or mates allows for the development of more intense forms of sexual selection; the intensity of male-male competition is influenced by the distribution of fecund females in time and space (Trivers, 1972; Emlen & Oring, 1977).

An important example of the intensity in sexual selection that comes from the ability to monopolize mates or resources is the development of male weapons, which are seen to be selected for by contest competition. Weapons evolve when males are able to defend *spatially-restricted critical resources*. In most studied species, weapons are used to defend critical resources that translate into mating opportunities. Across studied species in which weapons are present, resources were limited by time or space, making them defensible. It is therefore predicted that weapons will be seen when critical resources are confined in a way that makes them defensible and able to be monopolized by a small number of males. Greater intensity of sexual selection is seen in very confined spaces, where defense is easiest. This is the case in species that use burrows for nesting. In arthropods, the female uses burrows for laying eggs, and the spatial constraint of the burrow allows for male defense of the female, as well as defense of the resource itself. Males of these burrow-guarding arthropod species are observed to have enlarged weapons. Weapons are characteristically diverse in shape and location, variable in size,

highly sexually dimorphic, not enlarged in males until the end of development, and are utilized in intraspecific male combat (Emlen, 2008).

In an examination of dung beetles, Emlen & Philips (2006) found that tunneling species generally have enlarged horns, unlike their above-ground, dung rolling counterparts. Horn sizes in dung beetles can be extreme, and the contests in which they use them are often intense. Males are observed to use their horns to block tunnel entrances and to pry rivals from burrows. Findings suggest that the confined spaces in which contests occur in tunneling species is an important prerequisite for the evolution of weapons in dung beetles. So important are these contests in confined spaces that the benefits of enlarged weapons seem to outweigh the inherent costs of their development and production.

Territorial behavior by males is also dependent on environmental constraints. In order to develop territoriality, defensibility depends on the ability of an animal to monitor the boundaries of its range. If a range is too large, then the male will not be able to defend it from rival males. Mobility of the male is also important; if his mobility in relation to his range is too low, then he will not be able to effectively patrol and guard his territory. Therefore, evolution of territoriality depends on the ability of males to defend resources that are important to females, as well as the economic defensibility of resources based on their level of constraint in relation to range size and male mobility (Emlen, 1976; Mitani & Rodman, 1978).

The spatial dispersion pattern of resources or mates is a factor on which control of access by the limited sex depends. Female aggregation allows males to defend groups, leading to resource-defense polygyny. When access to females cannot be controlled through resources, male-male contests may take place for direct access to females. However, high population density and increased intensity of competition can mean that successful defense becomes energetically unfeasible, with too many females for one male to guard (Emlen & Oring, 1977).

In a study of polygyny in pinnipeds, Bertram (1940) discussed the significance of terrestrial mating to the maintenance of organized polygyny, suggesting that when aquatic mating occurred, males would be unable to effectively maintain their harems. The high level of mobility in the water, paired with the unfeasibility of maintaining a territory in the water due to its lack of physical boundaries and three-dimensional environment, bars the establishment of territories in which females can aggregate (Bartholomew, 1970). In situations where copulation occurs under the ice, dominant males are able to exclude subordinate males by controlling breathing holes. Because of the ability to defend this limiting resource, some polygyny can be seen to develop, despite the aquatic environment in which the seals copulate. Intensity of contest competition is seen to be greater in terrestrially-mating pinnipeds, where males may develop characteristics such as aggression and large body size.

Sexual coercion is seen to be more intense in polygynous mating systems, where there is the highest variance in male reproductive success; sexual coercion may be the only way that some males can successfully copulate. In species in which males coerce females to copulate by force or threat of force, the male must be large or strong enough in relation to the female for attempts at forced copulation to be successful. The mechanism of forced copulation may favor large body size in males (Andersson, 1994). In the majority of animals, females are larger than males, possibly due to the fecundity advantages of large size. However, in species where forced copulation is a documented mechanism of sexual selection, males are often larger, in some cases to extreme degrees. In turtles, males are larger than females in most of the species in which forced copulation is documented (Berry & Shine, 1980; Andersson, 1994). In northern elephant seals, where polygyny creates a great degree of variance in male reproductive success, males often violently force copulation on females. Ninety-five percent of copulations occur on land after aggressive male-male interactions over a female, and females that try to escape mating attempts are often bitten and pinned down until copulation is successful (Le Boeuf & Mesnick,

1991). Males can be 1.5-10 times larger than females, making northern elephant seals one of the most sexually dimorphic mammals (Le Boeuf et al, 2000; Deutsch et al, 1994).

### **Dimensionality of the Mating Environment**

It has previously been hypothesized that the mating environment plays a key role in the success of contests in which males exclude same-sex competitors from potential mates. Clearly, environmental constraints are extremely important in the evolution and success of contest competition and sexual coercion, which both rely on the ability of the male to limit movements of rivals or potential mates. The current hypothesis examines the ecological variable of dimensionality on the occurrence of contest competition and sexual coercion. The dimensionality hypothesis proposes that the environment has helped shape the traits that are considered to be the products of sexual selection, including large body size of males, weapons, or bright colors (Puts, 2010; Sjare & Stirling 1995). The environment that the male must be able to guard can either be one- or two-dimensional, where exclusion of same-sex competitors or preventing the escape of a potential mate is possible and physical strength and weapons lead to greater reproductive success, or three-dimensional, where the number of possible routes for competitors is too many and female movement cannot be limited. Here, males must rely on a tactic such as sperm competition or female choice to a greater degree than male-male contests or sexual coercion.

Berry and Shine (1980) examined data on mating environment, sexual size dimorphism, and mating behavior in a large sample of turtles from a variety of families. A relationship between large males, fighting, and territoriality was found. In terrestrial and bottom-walking species, males were observed to be larger than females, with a higher prevalence of male-male combat and forced insemination. In semi-aquatic and aquatic species, forced insemination and combat were observed at a lesser degree, with a higher importance placed on female choice.

While Berry and Shine examined mechanisms of sexual selection in relation to terrestrial versus

aquatic habitat, the current hypothesis proposes that the constraint imposed by a two-dimensional mating environment, rather than a terrestrial vs. an aquatic habitat *per se*, allows more intense contests and sexual coercion to evolve.

In contrast to the environment in which a species lives, dimensionality of the mating environment refers to where competition for mates takes place specifically, and can be one-dimensional, two-dimensional, or three-dimensional. One-dimensional mating environments include tunnels, burrows, and crevices, where defending males are able to defend the only path to the female by blocking any in-routes than could be taken by competitors. Agonistic behavior and weapons are common in these one-dimensionally mating species, such as dung beetles that fight intensely over mates and develop enlarged weapons. One-dimensional mating environments offer the greatest level of environmental constraint needed for contest competition to develop, and indeed this is supported by evidence suggesting that dung beetle weapons are more prevalent for one-dimensionally mating species than two-dimensionally mating species (see above; Emlen & Philips, 2006).

Two-dimensional mating environments involve competition occurring on land or another surface which constrains below, yet allows movement on all sides. Contest competition and sexual coercion are important mechanisms of sexual selection in two-dimensionally mating species. The constraint that is imposed by two-dimensional environments makes both contest competition and sexual coercion by males more feasible than for those that compete in three-dimensional environments, as observed in studies of taxa containing species that mate in two-dimensional or three-dimensional environments. Arthropods that compete on land or floors of bodies of water show more extreme forms of contest competition than arthropod species that compete for mates in the air (Puts, 2010).

In pinnipeds, there are species that mate in two-dimensional environments as well as species that mate in three-dimensional environments. In terrestrial territories, males are seen to

defend groups of gregarious females because of their ability to defend these areas (Stirling, 1975; Stirling, 1983). In pinniped species in which mating takes place primarily on land, males exhibit resource or female-defense mating systems and a high degree of sexual coercion (Le Boeuf & Mesnick, 1991, see above). Findings by Stirling (1975) suggest that aquatically breeding seals lack organized polygyny because of the difficulty imposed by a three-dimensional territory, as well as the high mobility of aquatic seals. Phocid seals mate aquatically and show a reduced level of polygyny, due to the difficulty of defending females in a 3D aquatic environment. Due to this difficulty of defense, female choice (Sjare & Stirling, 1995) and scramble competition (Andersson, 1994) are seen to be much more prevalent than contests or sexual coercion.

Fish that compete for mates in unbounded bodies of water show a greater degree of sperm competition (Fuller, 1998) and female choice (Noble, 1938), whereas species that mate near a guarded or shallow territory compete via contests (Turner, 1993; Quinn, Hendry, & Buck, 2001). In sockeye salmon, which are aquatic but compete for mates in water that is too shallow to be considered three-dimensional, males are large and have specialized hooked jaws which they use in contest competition over mates (Quinn, Adkison, & Ward, 1996).

The relative absence of contest competition and sexual coercion is seen in very different environments: air, where birds rely on female choice and ornamentation, and water, where fish for example rely to a greater degree on sperm and scramble competition. The thing that is shared by these two species is their three-dimensional mating environment. The dimensionality hypothesis predicts that some of the variation in the evolution of sexual selection mechanisms can be explained by the ability of males to exclude rivals for mates in two-dimensional mating environments, and the relative inability of males to exclude competitors via contests in three-dimensional mating environments, where males must defend from above and sometimes beneath as well as from all sides.



## **Current Study**

This thesis examines the occurrence of contest competition related to the dimensionality of the mating environment in Order *Testudines*. There are approximately 300 extant species of turtles, with families inhabiting terrestrial, semi-aquatic, aquatic, and pelagic environments. Furthermore, dimensionality of the mating environment can be two-dimensional or three-dimensional. Turtles exhibit a range of mating behaviors, including male-male combat, female choice, male ornamentation, forced copulation, and sperm competition. Both male- and female-biased sexual size dimorphism are observed. This variety of environment and behavior makes turtles an ideal taxon in which to examine the occurrence of contest competition in relation to dimensionality.

Research on what mechanisms of sexual selection will be in effect in a given species is ongoing, and our understanding of this topic is far from complete. The current paper tests the dimensionality hypothesis on a large sample of species in 12 families of Order *Testudines*, with the aim of relating the role of the dimensionality of the mating environment on the evolution of contest competition and sexual coercion. We predict that dimensionality will serve as a more accurate indicator of mechanisms of sexual selection than habitat. We predict that two-dimensional mating environments will more strongly favor mechanisms of sexual selection that allow males to exclude competitors from mates, and to keep females from getting away during forced copulation. Thus, we predict that two-dimensional versus three-dimensional mating environments will favor select for greater contest competition, sexual coercion, male weapon presence, and relatively larger males than females.

## METHODS

### Species Data

Data were collected by reviewing published literature. Subspecies were not counted as separate data points. The most complete data were compiled for each species when subspecies information was available. Sexual size dimorphism was determined by recording male and female average size. Average size was recorded as the average carapace length reported in the literature. Size was recorded for straight carapace length (SCL or CL) in millimeters. As absolute sizes were not available for all species, we also reported the larger sex in each species. In some species average size was unavailable, in which case maximum reported SCL was recorded.

Dimensionality refers to the environment in which all activities related to mating competition take place, including courtship, display, aggression, combat, and copulation. Turtles mate in two-dimensional and three-dimensional environments. Two-dimensional mating is classified as mating competition that takes place on a surface, with movement constrained by dry land or the floor of a body of water, as in species of turtles that walk on the bottom of a stream, pond, or lake. Three-dimensional mating takes place in all other aquatic mating species, in which mating competition takes place in the water, without notable contact with the bottom. In many instances, mating has not been described to the extent that dimensionality can be absolutely determined from the literature. Therefore, it was necessary in many cases to infer dimensionality from environment. In terrestrial species, the dimensionality is always 2, because tortoises do not enter the water or compete in burrows. Similarly, sea turtles always have dimensionalities of 3, due to their environment being fully aquatic. Semi-aquatic turtles can compete on land, some in

water, and others on both. In these species dimensionality was determined by the environment in which the species was observed to spend most of its active time.

Habitat/living environment refers to the habitat in which the individuals of a species live. Turtles are considered terrestrial if they spend all of their time on land and never enter the water. Semi-aquatic turtles are reported to spend considerable amounts of time in the water and on land. Turtles are considered aquatic if the majority of their time is spent in an ocean, stream, lake, pond, or marsh, without time spent on land. Species that spend time on land only for the purpose of basking, traveling from one body of water to another, or nesting are considered aquatic species. In some cases, specific information regarding the environment or dimensionality was not located in published literature. In these cases, environment and dimensionality were determined by the characteristics of congeneric species, so long as species within that genus exhibit a clear tendency to inhabit similar environments.

### **Mechanisms of sexual selection**

Female mate choice was reported in species where it was observed that some form of courtship act by the male is followed by a response from the female leading to copulation, or where the rejection or escape of the female was able to effectively halt copulation.

Contest competition was reported in species where aggression or threat of aggression and fighting are observed between males of that species. Territorial behavior by males falls under contest competition, where territorial behavior is an expression of competition for space and the spatial distribution of resources (including females). The defense of home ranges or resources is also classified as contest competition.

Copulatory interruption occurs during the act of mating, when a male that is not part of the copulating pair attempts to dislodge the mating male and stop copulation, presumably in order to himself gain access to the female. Therefore, copulatory mate guarding occurs along with

copulatory interruption, when the mating male attempts to maintain his position. This comes in the form of grasping the female and/or fighting the interrupting male, including physical attempts to keep him away.

Scramble competition is noted in species where males use their speed and agility to be the first to gain access to a female for the purpose of copulation. The ability of the male to be the first to reach the female is key in mating success, and physical aggression between males is not seen as part of scramble competition (Andersson, 1994).

Sexual coercion was reported in cases where a female's negative response to an approaching male does not fully determine whether copulation takes place. Coercion is reported where, after approach by the male, the female attempts to stop copulation from occurring by removing herself from the situation, but mating still happens because of the strength or speed of the male. This physical force is observed in the form of biting into submission, circling by the male so that there is no route by which to escape, chasing when the male is faster than the female, and grasping the female so that escape is impossible. It should be noted that all of these behaviors can also be part of courtship in which sexual coercion is not present. Coercion was determined when the male was physically able to keep a female from moving away, or when the bites given by the male forced the female into submission, in contrast with bites occurring during courtship and mating where there is no evidence of the female being unable to escape if she attempts to do so. The presence of coercion thus depends on the female's role in the success of copulation, and whether an action taken by the female is observed to make copulation impossible.

It was determined that male weapons were present in a given species if a weapon is used by the male during contest competition. A weapon was decided to occur if it was sexually dimorphic, seen more prominently in males and used during combat associated with direct access to a female, or to resources associated with access to a female. The male weapon that was observed to meet these criteria in turtles is a projection of the gular scute region of the plastron,

which is located on the anteroventral portion of the shell. The gular scute can project outward in one or two prongs. The gular scute projection was considered to be a weapon when it was reported in the literature as being used by in male-male combat or by males in coercive copulation attempts with females.

## **Treatment of Data**

### *Principal Components Analysis*

To reduce alpha inflation, and because combining data across correlated variables should provide more accurate measures than any variable alone, we conducted a principal components analysis (PCA) using varimax-rotation on variables assessing the presence of different mechanisms of sexual selection. Components with eigenvalues  $>1$  were extracted and saved as variables. Based on the rotated component matrix, variables that loaded heavily onto PC1, henceforth called Coercion/Contests, were sexual coercion (.906) and contest competition/male combat (.768). The variables that loaded heavily onto PC2, henceforth called Guarding/Scrambles, were copulatory mate guarding/interruption (.877) and scramble competition (.806). Female mate choice did not load heavily onto either component.

**Table 1.** Component loadings of first two varimax-rotated components of PCA (with eigenvalues and percentage of the total variance explained).

	Component	
	PC1 EV=2.0, 40.6%	PC2 EV=1.1, 22.4%
Female Choice	.366	.110
Contest Competition (Male Combat)	<b>.768</b>	.343
Copulatory Mate Guarding/Interruption	.055	<b>.877</b>
Scramble Competition	.218	<b>.806</b>
Sexual Coercion	<b>.906</b>	-.082

### *Statistical Analysis*

We statistically controlled for phylogeny using a consensus phylogeny for all species represented in our sample (Guillon et al, 2012). We assessed correlated evolution among our variables with phylogenetic generalized least squares (PGLS) in R (caper package). PGLS offers a flexible model of trait evolution that departs from strict Brownian motion by allowing the  $\lambda$  scaling parameter to vary as a measure of the strength of the phylogenetic signal. This measure of the phylogenetic signal ( $\lambda$ ) ranges from 0 to 1, with high values indicating a strong signal (Munkmuller, 2012).

## RESULTS

### Dimensionality

We examined whether the dimensionality of the mating environment predicted sexual size dimorphism, the presence of male weapons, and mechanisms of sexual selection. Dimensionality (coded as 0=2D, 1=3D) negatively predicted sexual size dimorphism ( $\lambda$  estimated at .91 [95% CI lower bound=.77];  $t=-2.75$ ,  $p=.007$ ; model  $F[2,110]=7.56$ ,  $p<.001$ ,  $R^2=.06$ ), weapon presence ( $\lambda$  estimated at 0.00;  $t=-4.97$ ,  $p<.001$ ; model  $F[2,123]=24.73$ ,  $p<.001$ ,  $R^2=.17$ ; Fig.1), and Coercion/Contests ( $\lambda$  estimated at 0.00 ;  $t=-7.74$ ,  $p<.001$ ; model  $F[2,122]=59.95$ ,  $p<.001$ ,  $R^2=.33$ ; Fig.2). Dimensionality was unrelated to Guarding/Scrambles ( $\lambda$  estimated at 0.00;  $t=.79$ ,  $p=.431$ ; model  $F[2,122]=.62$ ,  $p=.538$ ,  $R^2=.01$ ). As predicted, species in which males compete for mates in two-dimensional environments had relatively larger males that were more likely to have weapons and to engage in contest competition and sexual coercion than did species where males compete in three-dimensional environments. Dimensionality was not found to be significantly correlated with scramble competition and copulatory mate guarding.

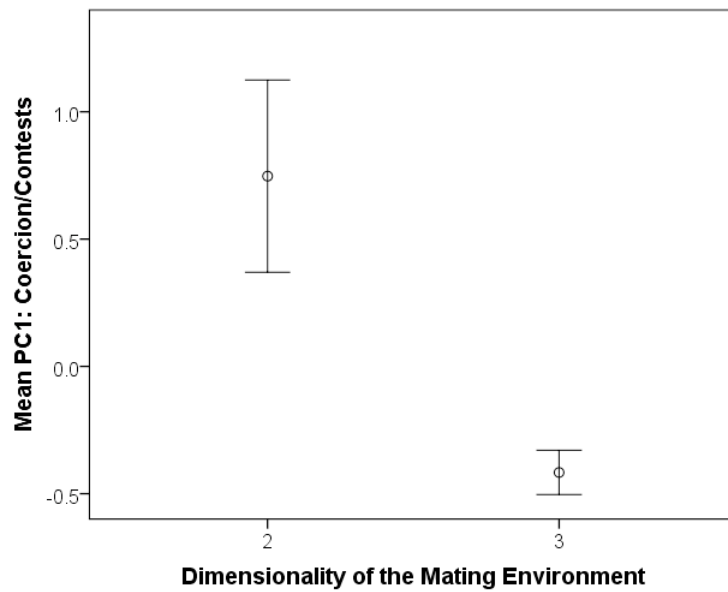


Fig.1. Species in which males compete for mates in a 2-dimensional mating environment have higher mean values for PC1 (“Coercion/Contests”) than do species in which males compete for mates in a 3-dimensional mating environment. (Error bars represent 95% confidence intervals.)



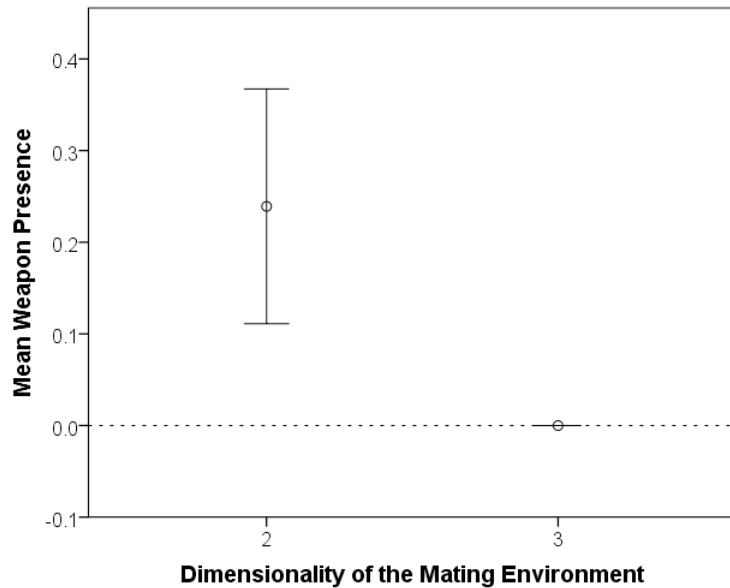


Fig.2. Species in which males compete for mates in a 2-dimensional mating environment are more likely to possess weapons than are species in which males compete for mates in a 3-dimensional mating environment. (Error bars represent 95% confidence intervals.)

### **Dimensionality and Habitat**

In order to test the hypothesis that relatively large males and male contests evolve in terrestrial habitats due to the sensory advantages of competing on land (Berry & Shine, 1981), we ran a second set of analyses, this time including both dimensionality and habitat (0=terrestrial and semi-aquatic, 1=aquatic) as predictors.

**Table 2.** Results controlling for habitat with semi-aquatic and terrestrial as one group.

	Dimensionality		Habitat	
	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>
Sexual Size Dimorphism ( $\lambda=.90$ ; $F[3,109]=3.81$ , $p=.012$ )	-2.44	.016	-.32	.749
Weapon Presence ( $\lambda=0.00$ ; $F[2,122]=13.29$ , $p<.001$ )	-2.30	.023	-1.30	.195
Coercion/Contests ( $\lambda=0.00$ ; $F[3,121]=29.98$ , $p<.001$ )	-4.67	<.001	-.58	.563
Guarding/Scrambles ( $\lambda=0.00$ ; $F[3,121]=.37$ , $p=.774$ )	.26	.798	.35	.725

After controlling for habitat, dimensionality was a significant negative predictor of sexual size dimorphism, weapon presence, and coercion/contests, but habitat was not. Dimensionality and habitat were not significant predictors of guarding/scrambles (Table 2). As predicted, species in which males compete for mates in three-dimensional environments have relatively smaller males than females, are less likely to have weapons, and contest competition and sexual coercion are less likely to be seen than in species where mating competition occurs in two-dimensional environments. Neither dimensionality nor habitat significantly predicted the occurrence of Guarding/Scrambles.

**Table 3.** Results controlling for habitat with semi-aquatic and aquatic as one group.

	Dimensionality		Habitat	
	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>
Sexual Size Dimorphism ( $\lambda=.91$ ; $F[3,109]=3.80$ , $p=.012$ )	-2.19	.03	-.32	.746
Weapon Presence ( $\lambda=0.00$ ; $F[2,122]=24.39$ , $p<.001$ )	0.00	1	-4.49	<.001
Coercion/Contests ( $\lambda=0.00$ ; $F[3,121]=29.83$ , $p<.001$ )	-5.13	<.001	.36	.717
Guarding/Scrambles ( $\lambda=0.00$ ; $F[3,121]=.31$ , $p=.817$ )	.56	.58	-.08	.938

We reran the above analyses, this time grouping habitat into 0=terrestrial and 1=semi-aquatic and aquatic (Table 3). After controlling for habitat and alternatively grouping semi-aquatic species with aquatic species, dimensionality significantly predicted degree of sexual size dimorphism and coercion/contests. Habitat did not predict degree of sexual size dimorphism, but did significantly predict weapon presence, while dimensionality did not. There were weak nonsignificant relationships with Guarding/Scrambles and dimensionality and habitat. We found that males in species that mate three-dimensionally are relatively smaller than females and less likely to exhibit contest competition and sexual coercion than species in which males mate two-dimensionally. We found that species with terrestrial habitats were more likely to have weapons than semi-aquatic and aquatic species. We found that neither dimensionality nor habitat predicted occurrence of scramble competition and copulatory mate guarding.

### Sexual Coercion

Finally, we examined whether sexual coercion was more likely to evolve in 2D mating environments independently of the influence of larger male size. To do so, we included both sexual size dimorphism and dimensionality in a PGLS model to predict sexual coercion. The model was statistically significant ( $\lambda$  estimated at 0.00;  $F[3,108]=18.59$ ,  $p<.001$ ), as was dimensionality ( $t=-5.06$ ,  $p<.001$ ), but not sexual dimorphism ( $t=.82$ ,  $p=.412$ ). As predicted, sexual coercion is more likely to evolve in species where competition takes place in two-dimensional mating environments than in species where males compete for mates in three-dimensional environments (Fig.3).

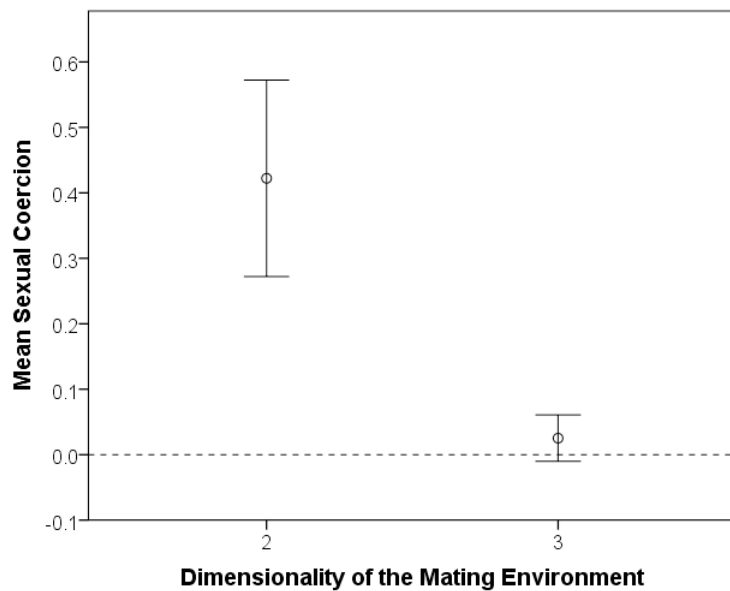


Fig.3. Species in which males compete for mates in a 2-dimensional mating environment are more likely to have been reported to exhibit sexual coercion than are species in which males compete for mates in a 3-dimensional mating environment. (Error bars represent 95% confidence intervals.)

## DISCUSSION

As predicted, we found that dimensionality of the mating environment predicts sexual size dimorphism, male weapon presence, and mechanisms of sexual selection. Species in which males compete for mates in two-dimensional environments are more likely to have relatively larger males than females, male weapons, and a greater likelihood of male-male combat and sexual coercion of females by males than in species where males compete in three-dimensional mating environments.

It has been appreciated since at least (1980) that males tend to be relatively larger and more prone to combat in terrestrial species than in aquatic species of turtles. Berry and Shine (1980) hypothesized that this was because males can see and smell each other on land, and thus combat is more feasible. We tested this alternative to the dimensionality hypothesis by entering both habitat (aquatic, semi-aquatic, or terrestrial) and dimensionality of the mating environment simultaneously into statistical models. In all but one analysis, the dimensionality of the mating environment was a better predictor of the occurrence of mechanisms related to contest competition. We found that grouping semi-aquatic with terrestrial or aquatic did not alter our results, except in the case of male weapons. This is logical, considering the weapons that are used by turtles. The only weapons that were described in the literature as being definitively used by males during contest competition were the sexually dimorphic gular projections seen in male tortoises, species that compete for mates in exclusively two-dimensional environments. Gular projections are used by males during contest competition to ram and flip opponents, or during forced copulation to ram a female until she is subdued. These tactics of ramming and flipping would only be effective on land; ramming would lose its force in the water during combat, and

females would have more opportunities for escape while swimming. Flipping a swimming adversary would have little effect.

Furthermore, we found that bottom-walking aquatic species compete for mates via contest competition and are seen to force copulation more often than aquatic species that swim during competition for mates, supporting the idea that dimensionality is a more important predictor in the occurrence of contest competition than is habitat.

These findings in order *Testudines* lend support for the idea that the constraints imposed by two-dimensional environments select for greater degrees of male contest competition and sexual coercion of females than in unbounded three-dimensional aquatic environments. These results are consistent with our prediction that two-dimensional mating environment constraints allow males to evolve mechanisms of excluding competitors in contest competition and restraining females from escape during forced copulation, mechanisms that would not be feasible in unbounded three-dimensional environments.

### **Limitations and Future Research**

Due to the limited phylogenetic research that has previously been conducted on some genera of turtles, a complete and accurate phylogeny was difficult to locate. Therefore, several of the species on the original data set were excluded from analysis.

Sperm competition is a mechanism of sexual selection that is predicted to be more likely to occur in three-dimensional environments, where promiscuity is higher because of the male's inability to effectively keep other males away from his mate. However, at the time of this paper not enough research was available to confidently assess differences in sperm competition in turtles.

Further research on dimensionality and turtles should examine sperm competition. We plan on including this in future research by examining variance in promiscuous behavior in

turtles, or by using data on multiple paternity of clutches, on which there are a good deal of published data. Studying other diverse taxa will clarify how broadly the dimensionality hypothesis applies across species as a predictor of contest competition and sexual coercion.

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## Appendix

**Degree of sexual size dimorphism, dimensionality, habitat, and mechanisms of sexual selection in turtles.**

Genus	Species	SSD	A	B	C	D	E	F	G	H	Reference
<i>Carettochelys</i>	<i>insculpta</i>	0.814016173	3	3	0	0	0	0	0	0	1,2,3
<i>Acanthochelys</i>	<i>macrocephala</i>	0.831632653	3	3	1	0	0	0	0	0	2,4
<i>Chelodina</i>	<i>longicollis</i>	0.86	3	3	1	0	0	0	0	0	2,5
<i>Chelodina</i>	<i>rugosa</i>	0.890973036	3	3	0	0	0	0	0	0	1,2
<i>Chelus</i>	<i>fimbriatus</i>	0.716662401	2	3	0	0	0	0	0	0	1,2
<i>Elseya</i>	<i>dentata</i>	0.820269778	3	3	0	0	0	0	0	0	1,2
<i>Elseya</i>	<i>latisternum</i>	0.759817003	3	3	1	0	0	0	0	0	2,5
<i>Emydura</i>	<i>macquarii</i>	0.882211538	3	3	1	0	0	0	0	0	1,2,5
<i>Emydura</i>	<i>subglobosa</i>	0.79258878	3	3	1	0	0	0	0	0	2,6
<i>Platemys</i>	<i>platycephala</i>	1.086325967	2	2	1	1	0	0	0	0	1,2
<i>Mesoclemmys</i>	<i>hogeii</i>	1.409482759	3	2	0	0	0	0	0	0	1,2
<i>Rheodytes</i>	<i>leukops</i>	0.984	3	2	0	0	0	0	0	0	1,2,7
<i>Caretta</i>	<i>caretta</i>	1.001401617	3	3	1	1	1	1	0	0	2,8,9,10,11
<i>Chelonia</i>	<i>mydas</i>	0.922102202	3	3	1	1	1	1	0	0	2,12,13,14,15,16,17
<i>Eretmochelys</i>	<i>imbricata</i>	0.963898917	3	3	1	0	0	0	0	0	2
<i>Lepidochelys</i>	<i>kempii</i>	1.034188034	3	3	1	0	0	0	0	0	2
<i>Lepidochelys</i>	<i>olivacea</i>	0.9489301	3	3	1	0	0	0	0	0	2,18
<i>Natator</i>	<i>depressa</i>		3	3	1	0	0	0	0	0	19
<i>Chelydra</i>	<i>serpentina</i>	1.076271186	2	2	0	1	0	0	1	0	2,17,117
<i>Macrochelys</i>	<i>temmincki</i>	1.202820513	2	3	1	1	0	0	1	0	2,17,24,25,26
<i>Dermochelys</i>	<i>coriacea</i>		3	3	1	0	0	0	0	0	27,28,29
<i>Emys</i>	<i>marmorata</i>	1.028169014	3	2	1	0	0	0	0	0	2,17,30,116
<i>Chrysemys</i>	<i>picta</i>	0.79378882	3	3	1	0	0	0	0	0	1,2,17,23
<i>Clemmys</i>	<i>guttata</i>	0.996244131	2	2	0	1	0	0	1	0	2,23,31,32,33
<i>Deirochelys</i>	<i>reticularia</i>	0.696168376	3	3	1	0	0	0	0	0	1,2



<i>Batagur</i>	<i>baska</i>	0.897540984	2	3	0	0	0	0	0	0	0	2
<i>Batagur</i>	<i>borneoensis</i>	0.739130435	3	3	1	0	0	0	0	0	0	2,58,59
<i>Cuora</i>	<i>flavomarginata</i>	0.95036888	2	1	0	0	0	0	0	0	0	2,60
<i>Heosemys</i>	<i>annandalii</i>	1.132142857	3	3	0	0	0	0	0	0	0	1,2
<i>Heosemys</i>	<i>depressa</i>	0.987341772	2	1	0	0	0	0	0	0	0	1,2
<i>Kachuga</i>	<i>dhongoka</i>	0.431818182	3	3	0	0	0	0	0	0	0	1,2
<i>Kachuga</i>	<i>kachuga</i>	0.54	3	3	1	0	0	0	0	0	0	1,2
<i>Malayemys</i>	<i>macrocephala</i>	0.788694482	3	3	0	0	0	0	0	0	0	2,61,62
<i>Mauremys</i>	<i>annamensis</i>	0.882783883	3	3	0	0	0	0	0	0	0	1,2
<i>Mauremys</i>	<i>caspica</i>	0.741935484	3	3	1	1	0	0	0	0	0	2,23,63
<i>Mauremys</i>	<i>japonica</i>	0.707711443	3	3	0	0	0	0	0	0	0	1,2
<i>Mauremys</i>	<i>leprosa</i>	0.819095477	3	3	1	0	0	0	0	0	0	2,63
<i>Mauremys</i>	<i>mutica</i>	1.023907104	3	3	0	0	0	0	0	0	0	1,2
<i>Mauremys</i>	<i>reevesii</i>	0.795180723	3	3	0	0	0	0	0	0	0	2,64
<i>Mauremys</i>	<i>rivulata</i>	0.784	3	3	0	1	0	0	0	0	0	2
<i>Mauremys</i>	<i>sinensis</i>	0.791295228	3	3	0	0	0	0	0	0	0	2,65
<i>Melanochelys</i>	<i>trijuga</i>	0.676681614	3	2	0	0	0	0	0	0	0	1,2
<i>Pangshura</i>	<i>tecta</i>	0.85471297	3	3	1	0	0	0	0	0	0	1,2
<i>Pangshura</i>	<i>tentoria</i>	0.699953553	3	3	0	0	0	0	0	0	0	1,2
<i>Rhinoclemmys</i>	<i>areolata</i>		3	3	1	0	0	0	0	0	0	66
<i>Rhinoclemmys</i>	<i>diademata</i>	0.812807882	3	2	0	0	0	0	0	0	0	1,2
<i>Rhinoclemmys</i>	<i>nasuta</i>	0.745383324	3	3	0	0	0	0	0	0	0	1,2
<i>Rhinoclemmys</i>	<i>punctularia</i>	1.100374065	2	3	1	0	0	0	0	0	0	2
<i>Rhinoclemys</i>	<i>funerea</i>		3	3	1	0	0	0	0	0	0	1,67
<i>Sacalia</i>	<i>quadriocellata</i>		3	3	1	0	0	0	0	0	0	2,68
<i>Vijayachelys</i>	<i>silvatica</i>	0.985457656	2	1	1	0	0	0	0	0	0	1,2
<i>Kinosternon</i>	<i>baurii</i>	0.72593235	2	2	0	1	0	0	1	0	0	1,17,69,70
<i>Kinosternon</i>	<i>flavescens</i>	1.180924287	2	2	0	0	0	0	1	0	0	2,69,71
<i>Sternotherus</i>	<i>odoratus</i>	0.986651835	2	3	1	0	0	0	0	0	0	2,71,72



<i>Malacochersus</i>	<i>tornieri</i>	0.965039578	2	1	1	1	0	0	1	0	2,23,81
<i>Manouria</i>	<i>emys</i>	0.795454545	2	2	1	0	0	0	1	0	1,2,102
<i>Psammobates</i>	<i>oculifer</i>		2	1	1	0	0	0	0	0	2,81
<i>Pyxis</i>	<i>arachnoides</i>	0.950819672	2	1	0	0	0	0	0	0	1,2
<i>Testudo</i>	<i>graeca</i>	0.864881315	2	1	1	0	0	0	1	0	2,81,91,102,103
<i>Testudo</i>	<i>hermanni</i>	0.883428571	2	1	1	1	0	0	0	1	2,83,104,105,114
<i>Testudo</i>	<i>horsfieldii</i>	0.788075178	2	1	0	1	0	0	1	0	2,106,107
<i>Testudo</i>	<i>kleinmanni</i>	0.830985915	2	1	1	0	0	0	0	0	2,81,109
<i>Testudo</i>	<i>marginata</i>	0.979732469	2	1	1	1	0	0	1	0	2,110
<i>Apalone</i>	<i>ferox</i>	0.549313358	3	3	0	0	0	0	0	0	1,2
<i>Chitra</i>	<i>chitra</i>	0.947945205	3	3	0	0	0	0	0	0	2
<i>Chitra</i>	<i>indica</i>	0.926403256	3	3	0	0	0	0	0	0	1,2
<i>Dogania</i>	<i>subplana</i>	1.181395349	3	3	0	0	0	0	0	0	1,2
<i>Lissemys</i>	<i>punctata</i>	1.011622031	3	3	1	0	0	0	0	0	2,111
<i>Pelodiscus</i>	<i>sinensis</i>	1.103703704	3	3	0	0	0	0	1	0	1,2
<i>Apalone</i>	<i>mutica</i>	0.700850873	3	3	1	0	0	0	0	0	1,2,112,113
<i>Apalone</i>	<i>spinifera</i>	0.59223301	3	3	1	0	0	0	0	0	1,2,23

- A. Dimensionality. 2=Two-dimensional, 3=Three-dimensional  
 B. Habitat. 1=Terrestrial, 2=Semi-aquatic, 3=Aquatic  
 C. Female Choice. 1=Present, 0=Absent or No Data  
 D. Contest Competition. 1=Present, 0=Absent or No Data  
 E. Copulatory Mate Guarding/Interruption. 1=Present, 0=Absent or No Data  
 F. Scramble Competition. 1=Present, 0=Absent or No Data  
 G. Sexual Coercion. 1=Present, 0=Absent or No Data  
 H. Male Weapon Presence. 1=Present, 0=Absent or No Data

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# ACADEMIC VITAE

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### Education

Pennsylvania State University, State College, Pennsylvania  
*Schreyer Honors College Paterno Fellows Program* *Class of 2013*  
*Bachelor of Arts in Anthropology with minors in Italian and Linguistics*  
• Dean's List award *Fall 2009-Present*  
Honors Thesis: "The Dimensionality of the Mating Environment Predicts Male Combat and Sexual Coercion in Turtles" under the supervision of Dr. David Puts.  
*Diploma expected December 2013*

### Study Abroad

The Alliance for Global Education, Fergusson College, Pune, India *June-July 2013*  
*Contemporary India Summer Abroad Program*  
• Studied Contemporary India  
• Completed Internship working in a Pune slum through Deep Griha Society

### Research Experience

The Brain, Language, and Literacy Lab, Pennsylvania State University  
*Research Assistant* *July 2012-November 2012*  
• Coded electronic participant responses using Microsoft Excel

Center for Language Science, Pennsylvania State University  
*Research Assistant* *January 2012-May 2012*  
• Ran human subjects for a bilingualism and language processing study  
• Prepared and ran subjects on computer questionnaires  
• Coded participant responses from completed questionnaires

Puts Lab, Pennsylvania State University Department of Anthropology  
*Research Assistant* *September 2010-Present*  
Thesis Research: Thesis research focuses on how the dimensionality of the mating environment (two-dimensional or three-dimensional) predicts the occurrence of contest competition and sexual coercion in turtles.

#### Additional Research Experience

- Run human subjects in behavioral studies
- Record body and voice measurements
- Take 2D and 3D photos

- Run participants on computer based questionnaires

### **Additional Experience**

#### The Pennsylvania State University Hindi Program

*Student Tutor*

*Fall 2011*

- Tutored Hindi 001 students in grammar, vocabulary, and conversation skills

#### India Pavilion, State College, Pennsylvania

*Server*

*August 2009-May 2013*

- Worked with other servers in a variety of tasks during restaurant hours
- Performed new server training during startup of restaurant in Cleveland, Ohio

*June 12<sup>th</sup>-June 15<sup>th</sup>, 2012*

### **Volunteer Activities**

#### American Red Cross, Pennsylvania State University Student Chapter

*Volunteer*

*January 2013-November 2013*

- Performed 55 hours of service
- Performed greeter, canteen, and walker duties in campus Red Cross blood drives

### **Additional Activities**

#### Hindi Sabha, Pennsylvania State University

*Member*

*September 2010-May 2011*

- Attended meetings and assisted in member recruitment and financing

#### Amnesty International, Pennsylvania State University Chapter

*Member*

*September 2010-May 2011*

- Attended weekly meetings
- Participated in petition writing
- Participated in design and creation of signs for awareness events

### **Skills**

- Intermediate knowledge of Hindi
- Advanced knowledge of Italian