THE RELATIONSHIP BETWEEN CHELIPED COLOR AND BODY SIZE IN FEMALE *Callinectes sapidus* AND ITS ROLE IN REPRODUCTIVE BEHAVIOR

A Thesis

by

KIRSTEN LAURENE WILLIAMS

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2003

Major Subject: Zoology

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Approved as to style and content by:

Mary K. Wicksten (Chair of Committee)	Lawrence R. Griffing (Member)
Jane M. Packard (Member)	Vincent M. Cassone (Head of Department)

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ABSTRACT

The Relationship between Cheliped Color and Body Size in Female *Callinectes sapidus* and Its Role in Reproductive Behavior. (August 2003)

Kirsten Laurene Williams, B.S., Humboldt State University

Chair of Advisory Committee: Dr. Mary K. Wicksten

Many species use color during courtship displays, with the more colorful individuals often selected as potential mates. Female blue crabs, *Callinectes sapidus*, display prominent red markings on their chelipeds, which is absent in males. I tested the hypothesis that females use this sexual dimorphism as an effective signal to potential mates.

Body size was positively correlated with size of the colorful pattern on the crusher dactyl. Digital imaging techniques were used to examine and quantify a pattern of coloration in the female blue crab. Morphometric measurements were made using digital images of the carapace and chelae of crabs collected along the Gulf of Mexico coast in Galveston, Texas. Color complexity was examined on digital images of the chelae using Adobe® Photoshop® and Image J. Specific wavelengths were selected and their presence within the attribute quantified and evaluated.

To determine whether male blue crabs prefer more colorful females, males were given a choice between females of different female coloration. Males displayed more often and directed more courtship displays towards the more colorful females. I hypothesize that male blue crabs use cheliped coloration as a visual cue for mate selection.

DEDICATION

I dedicate this thesis to my mother, Patricia Ellen Williams, my father, Charles Leon Williams, my brother Bryan Elliot Williams, and my best friend and companion Christopher Lee Ramey. You provided your endless support and love and helped me achieve my dream of becoming a marine biologist. I couldn't have done it without you and I love you all!

ACKNOWLEDGMENTS

I thank my major advisor, Dr. Mary K. Wicksten, for her support and encouragement during my studies at Texas A&M University. I also thank my committee members, Dr. Larry R. Griffing, who provided advice on my methods and access to the digital imaging equipment, and Dr. Jane M. Packard for her helpful suggestions. I thank my research assistants, Jesse Carrasco, Chris Woodruff, Stephanie Johnston, Jami Sutherland, Anne Rigby, Nicola Major, Ron Miller, Chad Silvertooth, and Toni Palma who helped me collect live crabs from Galveston, Texas and who assisted in the research and animal care. I appreciate the efforts of the graduate students in the TAMU Statistics Tutoring Center, who provided statistical advice. My gratitude goes to Tuhin Giri, who endured my endless list of questions and who was always willing to share advice from his own graduate experience. Thanks also to the Department of Biology, Texas A&M University, USA Funds, and the Susan M. Arseven Make-A-Difference Memorial Award who all contributed money to help fund my graduate research.

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INTRODUCTION

The blue crab, *Callinectes sapidus*, lives in the western Atlantic from Massachusetts Bay to the northern part of South America including the Gulf of Mexico. Blue crabs are especially abundant in the bays and mouths of rivers. During the summer, blue crabs are found in relatively shallow water but migrate to greater depths during the winter (Churchill, 1918). The blue crab is a member of the brachyuran family Portunidae. The last pair of legs in *C. sapidus* is modified into paddles for use in swimming (Churchill, 1918). The carapace in blue crabs is smooth on the dorsal surface and has two large spines that extend out on each side of the body (Jachowski, 1974). Blue crabs are heterochelous meaning their chelipeds are differentiated into a major crusher and a minor cutter cheliped based on different dentition patterns. Both chelae have a different function in feeding. The major crusher chela is used in crushing shells of prey, while the minor cutter chela is used to manipulate and tear prey (Govind and Blundon, 1985). These crabs are generalists and scavengers and consume a wide variety of food items. Major food items of juveniles and adults consist of bivalves, fish, other crustaceans, organic debris, vegetation, and benthic infauna (Darnell, 1961). The estimated duration of life of both male and female blue crabs is three years (Churchill, 1918).

Female blue crabs are conspicuously ornamented, displaying prominent red markings on their chelipeds (Figure 1). Male blue crabs, however, lack the red coloration, resulting in a very distinct sexual dimorphism. In 1859, Darwin described a

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This thesis follows the style and format of Journal of Crustacean Biology.

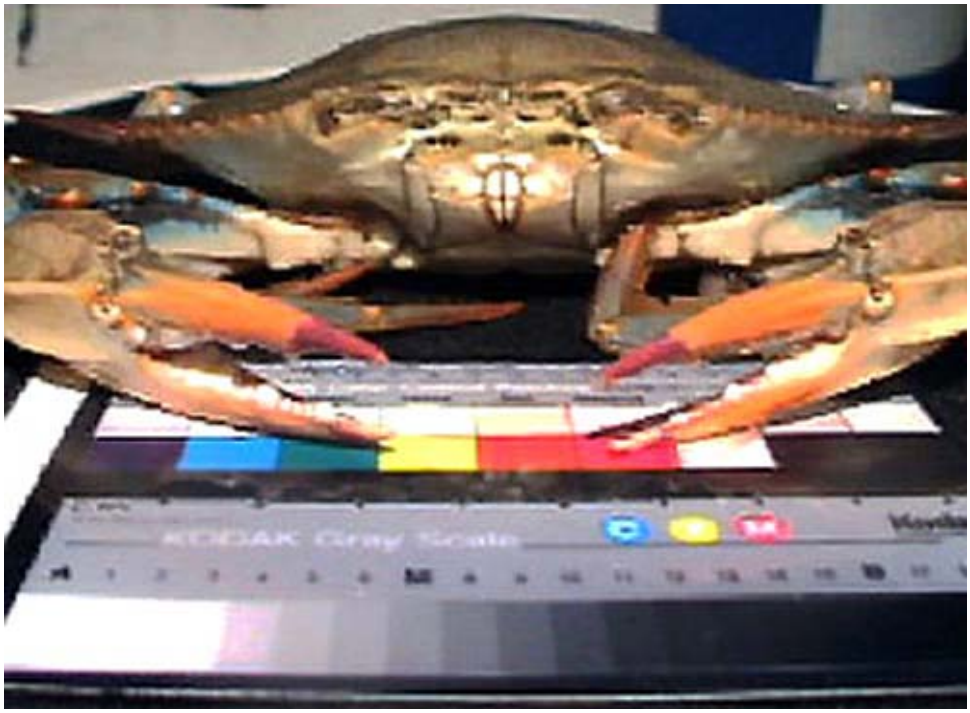


Figure 1. Distinct sexual dimorphism displayed by female blue crabs, *Callinectes sapidus*.

Brazilian crustacean species, *Gelasimus* that displayed a distinct color dimorphism. He described the male as being colored green and white and the females as being uniformly grayish brown (Darwin, 1859). It was thought that the colors of Crustacea were the result of chromatophores and were under control of the nervous system, similar to fishes. It was suggested then, that the males' coloration was in response to excitement of the nervous system during courtship and mate-guarding displays (Cunningham, 1900).

It is not know yet, whether blue crab coloration is a result of chromatophores and is under control of the nervous system, but it is known that the coloration is involved in both courtship and agonistic behavior. During these types of behaviors, blue crabs will utilize cheliped extension and spread, where in females the cheliped coloration will be displayed towards conspecifics (Jachowski, 1974; Jivoff and Hines, 1998). In blue crabs, mating occurs only once for the female, immediately after her final moult, while her carapace is soft (Van Engel, 1958). Pre-pubertal females attract males by releasing a urine-based pheromone (Gleeson, 1980; Teytaud, 1971) and both sexes participate in courtship behaviors such as chelae spread, leg extension, and paddle waving (Jivoff and Hines, 1998). The red color displayed by females may be used as a signal towards potential mates or towards competitors.

A study conducted by Prager *et al.* (1990) found fecundity is significantly related to carapace width in *C. sapidus*. Observations of 135 ovigerous blue crabs showed a positive relationship between the number of eggs carried and the width of the carapace (Prager *et al.*, 1990). A similar study on a euphausiid crustacean, *Nematoscelis difficilis*, found the number of eggs produced was significantly related to the body size (Nemoto *et al.*, 1972). This is also true in four caridean shrimp, *Palaemon northropi, Palaemon*

pandaliformis, Macrobrachium acanthurus, and Macrobrachium olfersii (Anger and Moreira, 1998). Anger and Moreira (1998) discovered a positive linear relationship between female fecundity and total body length. It may be easier for male blue crabs, to evaluate differences in female fertility based on cheliped coloration. The red pigment displayed by female blue crabs may act as a visual cue to carapace size and essentially female fecundity.

In many animal systems, where the sexes are separate, males and females are distinguished by secondary sexual characteristics. In some species, including bluethroats, *Luscinia svecica* (Amundsen *et al.*, 1997), two-spotted gobies, *Gobiusculus flavescens,* (Amundsen and Forsgren, 2001), Coenagrionid damselflies (Sherratt and Forbes, 2001), convict cichlids, *Cichlasoma nigrofasciatum* (Beeching *et al.*, 1998) and threespine sticklebacks, *Gasterosteus aculeatus* (McKinnon *et al.*, 2000), to name a few, the secondary sexual characteristics are defined by differences in coloration. The evolution of these sexual differences in coloration has been intensively studied, but most work has focused on males. Females may also display conspicuous coloration that is not found in males. This 'reversed' sexual dimorphism is often explained with female territoriality and female-female aggression theories (Krebs and Davies, 1993). However, in most taxa, female ornaments are unstudied and the evolutionary reasons for female "beauty" are largely unknown (Amundsen and Forsgren, 2001). There are two main hypotheses today that have been proposed to explain the evolution of female ornaments. Traditionally, female ornaments have been thought of as nonfunctional; merely a genetic response to selection for male ornamentation (Amundsen and Forsgren, 2001). An alternative hypothesis is that female ornaments have developed through sexual selection

based on male mate choice (Burley, 1977; Johnstone *et al.*, 1996; Kokko and Monaghan, 2001; Owens and Thompson, 1994).

The hypothesis that female ornamentation can develop through sexual selection has been studied in a small marine fish, *Gobiusculus flavescens*. Amundsen and Forsgren (2001) found in this species that sexual selection acting directly on females can influence female ornamentation. Female two-spotted gobies develop colorful yellow-orange bellies during breeding. Belly coloration is caused by the pigmented eggs being visible through the skin, but is also caused by orange-red spots on the abdomen. In this study males associated more with and displayed more towards colorful females when confronted with two females of differing coloration. Color can vary from a pale yellow-orange to a bright orange and typically; females carrying more developed eggs (rounder bellies) are more colorful than less round ones. Belly coloration may act as an amplifier of female fecundity in this species, which may explain why male two-spotted gobies are sensitive to the belly coloration (Amundsen and Forsgren, 2001).

Female ornaments may act as quality indicators. There may be a potential relationship with body condition (Johnsen *et al.*, 1996) or reproductive status in *Callinectes sapidus*. In some bird species, males choose those females that possess traits, which potentially communicate genetic quality as well as phenotypic condition. This male preference was observed in bluethroats, *Luscinia svecica*. Males of this species spent more time in front of and showed more sexual displays towards the more colorful females. Results showed that older females were not significantly more colorful than yearlings, but there was a relationship found between female coloration and body mass in this species, and body size may reflect female quality (Amundsen *et al*., 1997; Hansen

et al., 1999).

A study conducted by LeBas and Marshall (2000) evaluated the role of color in signaling and male choice in an agamid lizard. In *Ctenophorus ornatus*, visual displays such as head-bobbing, circumduction and push-ups emphasize the throat and chest areas. It was hypothesized that these areas could play a role in indicating gender, female receptivity or mate quality (LeBas and Marshall, 2000). This study found the area of color associated with the throat and chest areas in female lizards conveys female reproductive state to males. Males showed a stronger preference for those females that displayed the brightest chest patches. There was no evidence the female throat coloration indicated female quality, however, female brightness significantly predicted a female's laying date and thus may be an indicator of female receptivity in this species (LeBas and Marshall, 2000).

Animals that use colors for intraspecific communication can have visual pigments that allow for detection of the color display (Levine *et al.*, 1980). Stomatopod crustaceans have a complex visual system, with a broad spectrum, spanning the range from the ultraviolet to the far red (Cronin and Marshall, 1989a; Cronin and Marshall, 1989b; Cronin *et al.*, 1994; Marshall and Oberwinkler, 1999). Mantis shrimp have the capability to see in true color and use their broad spectral range in communications, such as the ability to detect the colored area of cuticle during threat displays, and prey detection (Caldwell and Dingle, 1975; Chiao *et al.*, 2000; Marshall *et al.*, 1996). A study conducted by Hunt *et al*. (1999) found a similar situation in blue tits. Blue tits, *Parus caeruleus*, are visually sensitive in the ultraviolet (UV) and in the human visible spectrum (Hunt *et al.*, 1999). Reflectance spectrophotometry found that there is obvious

sexual dimorphism in plumage coloration in several areas of the blue tit plumage that reflects maximally in the UV (Hunt *et al.*, 1998). This would suggest that plumage reflectance may act as a visual signal towards mates.

Bruno and Goldsmith (1974) analyzed the visual spectrum in blue crabs and discovered they are capable of seeing the red wavelength. It is highly likely that at least some of the sexual differences between males and females can be perceived by blue crabs. The red pigment displayed by females could be an indicator of female sexual maturity and perhaps fecundity. As female blue crabs near and achieve their terminal moult, their chelipeds reach their maximum size (Hartnoll, 1974). It is possible the amount of red pigmentation on the chelipeds will reach the maximum amount of coverage as well.

Visual displays in sexually dimorphic crustaceans have been extensively studied in the fiddler crab, *Uca*. Male fiddler crabs have one cheliped that is greatly enlarged and can be brightly colored, where this is lacking in females. The enlarged claw is used in courtship displays such as waving or beckoning movements to initiate mating in females (Oliveira and Custodio, 1998). Oliveira and Custodio (1998) found females showed a strong preference for males with larger claws when given a binary choice between two males, one with a large claw and one with a small claw. Although the sexual dimorphism present in *Uca* is opposite of what is found in the blue crab, there may still be some similarities between the two systems. I hypothesize that male blue crabs will show a strong preference for females with more brightly colored claws when given a binary choice between two females, one with a bright claws and one with a dull claws.

This research project will be the first to look at cheliped coloration in blue crabs as a

visual display and consists of two separate, but closely related experiments. The purpose of the first project was to determine whether there is a correlation between female body size and cheliped coloration. Morphometric measurements were made using digital images of the carapace and chelae of female crabs to examine and quantify a pattern of coloration. Hartnoll (1974) discovered the pubertal moult is often associated with an increase in growth rate and cheliped size in crabs. The working hypothesis is that as the female blue crab nears and achieves her terminal moult, her chelipeds, and thus the intensity of red pigmentation she displays, reach their maximum coverage. The second half of this research project examines whether each male blue crab will show a preference when given a choice between a more colorful female and a less colorful female. Each male was given a choice between two females of similar size, but that differed in female coloration. The working hypothesis is that male blue crabs are more stimulated by larger red color patches, which may be an honest indicator of female fecundity or reproductive status.

MATERIALS AND METHODS

CHELIPED COLORATION EXPERIMENT

I collected twenty-two live *Callinectes sapidus* females during early evening to late night, between 1900 and 2300 hours, at low tide along a rocky groin in Galveston, Texas (29° 16´N, 94° 49´W) with dip nets from the months of May to October, 2002 (Figure 2). All animals were transported back to Texas A&M University after collection and held in aquaria (Figure 3). Each aquarium contained 33‰ seawater and was held at constant temperature (~ 65° F) under available light conditions. All tanks were furnished with a sand substrate and large rocks or shells that provided some shelter for the crabs. Power filters on each tank provided filtration and aeration. Specimens were fed frozen shrimp every other day. All crabs were released into their natural environment at the same location as they had been originally collected, after completion of the trials.

A Sony DCR-TRV730 Digital 8 Handycam connected to an iMac computer was mounted on an adjustable Ken-A-Vision tripod and positioned above and in front of the crab to capture digital images (Figure 4A, B). All animals were anaesthetized using a 20 minute immersion in ice water prior to recording. I placed each crab on a black felt background to create contrast. A Kodak color card (KB1802, Calumet Photographic, Inc., Bensenville, Illinois) with a scale bar was located in front of the crab and included in each image (Figure 5). The card was positioned so that it could be seen in both the above view images as well as the frontal view images (Figure 6A, B). I used Adobe® Premier® (version 4.2.1, Adobe Systems Incorporated, San Jose, CA, USA) to capture video clips of the entire body of the female blue crab and of the cheliped coloration. I

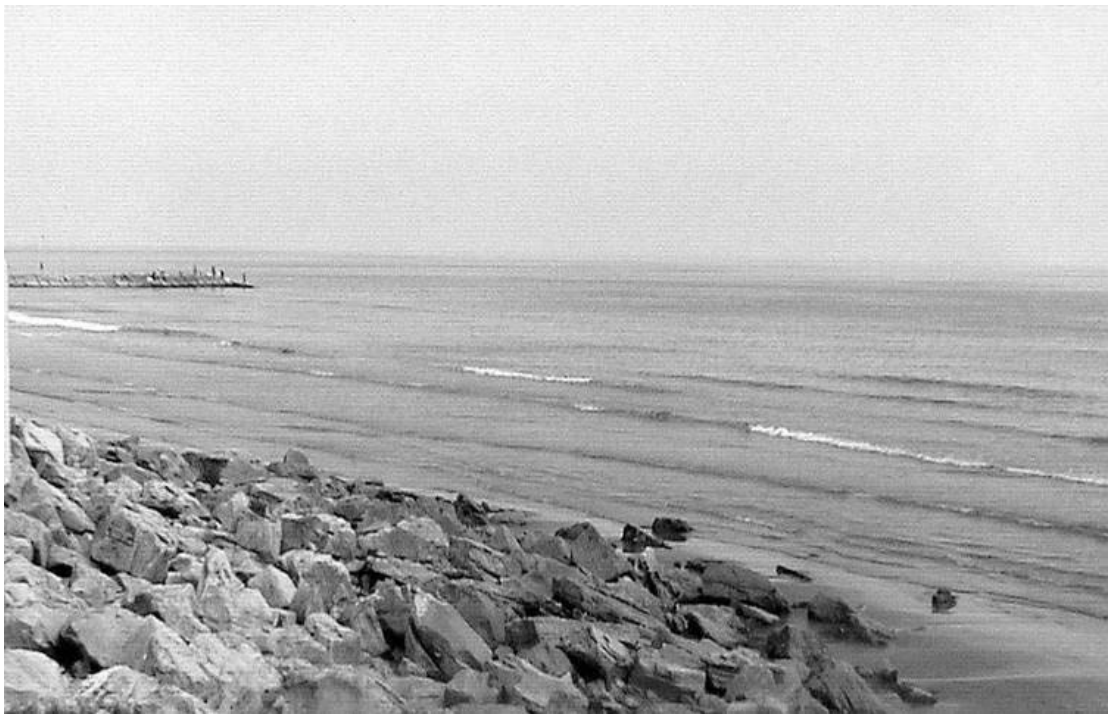


Figure 2. Photograph of rocky groin sample site located in Galveston, Texas (29° 16´N, 94° 49´W).

Figure 3. Aquaria used to house blue crabs during research project.

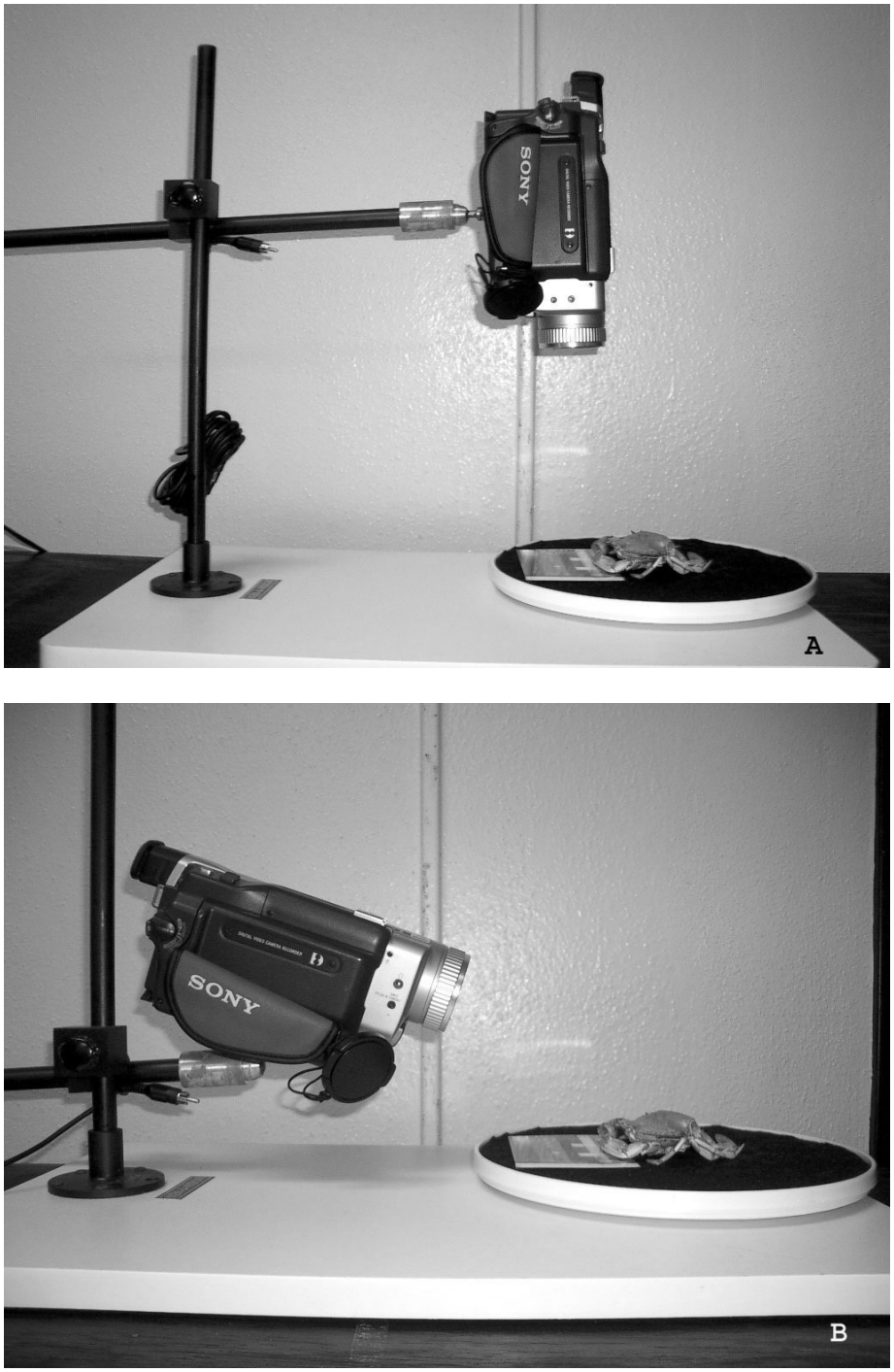


Figure 4. A camera was mounted on an adjustable tripod and positioned above the crab (A) and in front of the crab (B) to capture digital images.

Figure 5. A Kodak color card was included in each image.

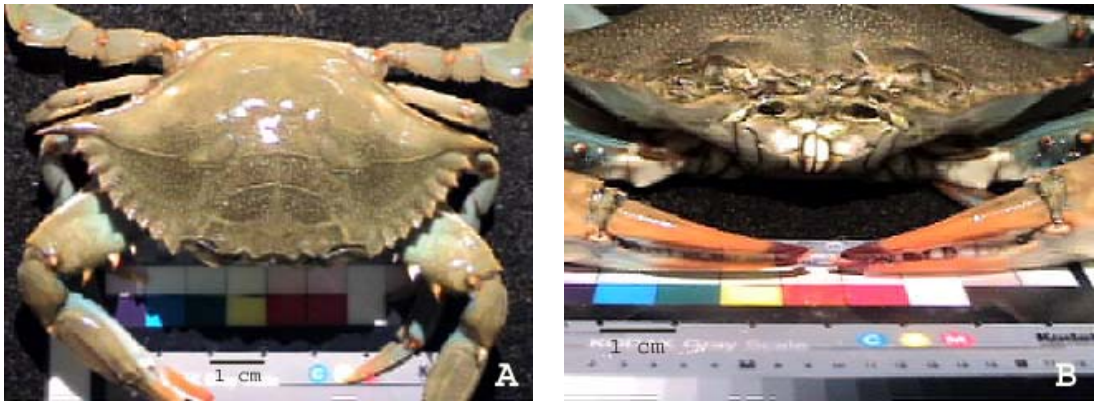


Figure 6. Images of the blue crab carapace (A) and chelae (B).

used the commands File-Capture-Movie to capture the video clips. Five frames were selected from the video clips using the In and Out commands. I exported each frame as an uncompressed filmstrip file and immediately opened each file in Adobe® Photoshop® (versions 4.0.1 and 6.0, Adobe Systems Incorporated, San Jose, CA, USA) to save as a TIFF file. Image J (version 1.27, Research Services Branch, National Institute of Mental Health, Bethesda, Maryland) was used in all image analysis. Carapace width and area, the area and perimeter of color on the upper dactyl, the entire area and perimeter of the upper dactyl, the amount of red/magenta color complex that is present on the chelipeds, and the intensity of the red color on the dactyls were measured from each image.

A combination of interactive color segmentation and automatic color segmentation was used to analyze cheliped coloration. Color segmentation is a process that selects multiple regions of interest based on digital color and range. I used the Magic Wand tool in Photoshop® to select the color of interest from the color card. Pixels in the chelipeds were selected based on this chosen color using the Select Similar command in Photoshop®. The area of color selected from the chelipeds was measured using the Measure tool in Image J.

I used the Measure tool in Image J to calculate carapace width. The scale bar was included to set the standard measurements for each image. Once the scale was standardized, the Measure tool traced from spine to spine and calculated carapace width in centimeters (Figure 7).

In order to measure carapace area and perimeter, I had to first isolate the carapace

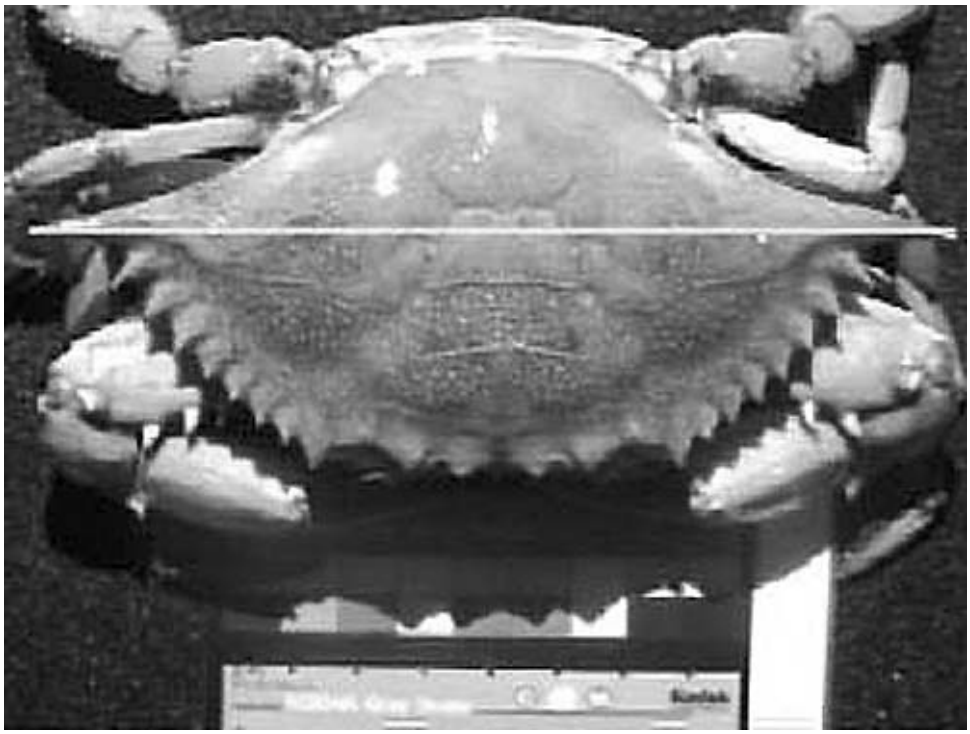


Figure 7. The Measure tool in Image J was used to calculate carapace width.

from the rest of the image using Photoshop®. The carapace was isolated by using the Magic Wand tool in Photoshop® to select pixels in the region of interest. A new image was created with those selected pixels by using the Layer via Copy tool in Photoshop® (Figure 8A). The new image was then opened in Image J for measurement. The ROI Manager tool in Image J outlined the carapace image and measured the area and perimeter. The scale bar was again used to standardize the scale.

The area and perimeter of color on the upper dactyl was measured by using the Magic Wand tool in Photoshop®. I first isolated the color on the upper dactyl and created a new image of those isolated pixels (Figure 8B). The new image was then opened in Image J. The ROI Manager tool in Image J automatically outlined the selected regions and measured the area and perimeter. The total area and perimeter of the upper dactyl was measured in the same process as the area and perimeter of color on the upper dactyl (Figure 8C).

The amount of red/magenta color complex present on the chelipeds was measured by creating a new image that included the color card and the selected region of color on the upper dactyl (Figure 8D). I used the Magic Wand tool in Photoshop® to select the red and magenta squares on the color card. The Select Similar tool in Photoshop®, with a tolerance of 50, was applied to select similar pixels on the upper dactyls. The Layer via Copy tool in Photoshop® was used to create a new image of the selected pixels. This image was opened in Image J and the area and perimeter of the red/magenta color complex was measured. The scale bar was again included to standardize the scale.

The intensity of the red color on the dactyls was analyzed to determine whether there

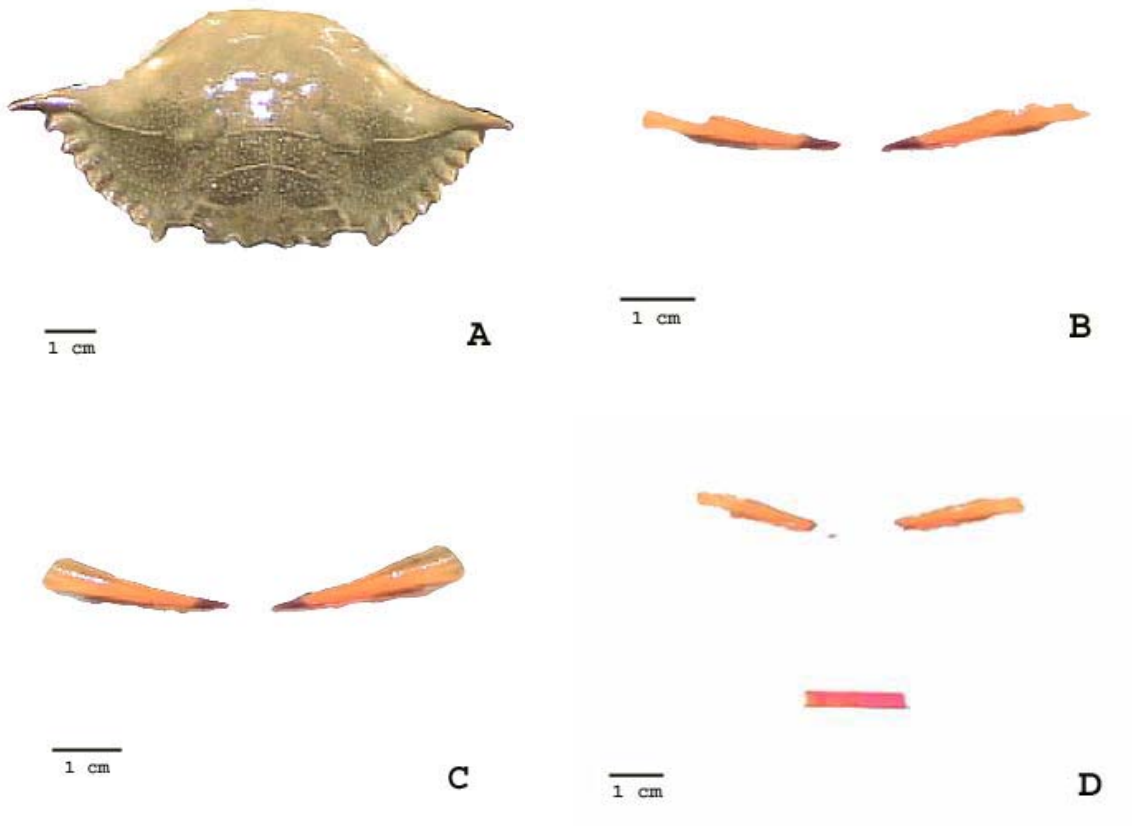


Figure 8. Isolated images of crab carapace (A), area and perimeter of dactyl coloration (B), total area and perimeter of dactyl (C), and area and perimeter of red color complex (D).

was a relationship between intensity of color and body size. The red square on the color card served as a standard for comparison with the red pigment present in the dactyls. I created a new image that contained the area of red coloration on the dactyls and the red square from the color card by using the Magic Wand tool and then the Layer via Copy tool in Photoshop® (Figure 9). Within my new image, the pixels in the dactyls were again selected with the Magic Wand tool. In order to measure only the red color, I isolated the red channel by selecting the Channels tab from the Channel, Layers, and Paths Window and then selected the red option. A histogram of the red intensity was provided by using the toolbar commands Image — Histogram. A mean value, a standard deviation value, and median value were calculated automatically from the red channel histogram. I repeated these steps to measure the red intensity of the red color card square to use as a comparison. The median and standard deviation values are presented in Table 1.

Female moult stage was determined by examining the abdomen of the females. Pre-pubertal females have a triangular abdomen; whereas adult females have a semicircular abdomen (Jivoff, 1997) (Figure 10).

Figure 9. Isolated image showing the area of red coloration on the dactyls and the red square from the color card.

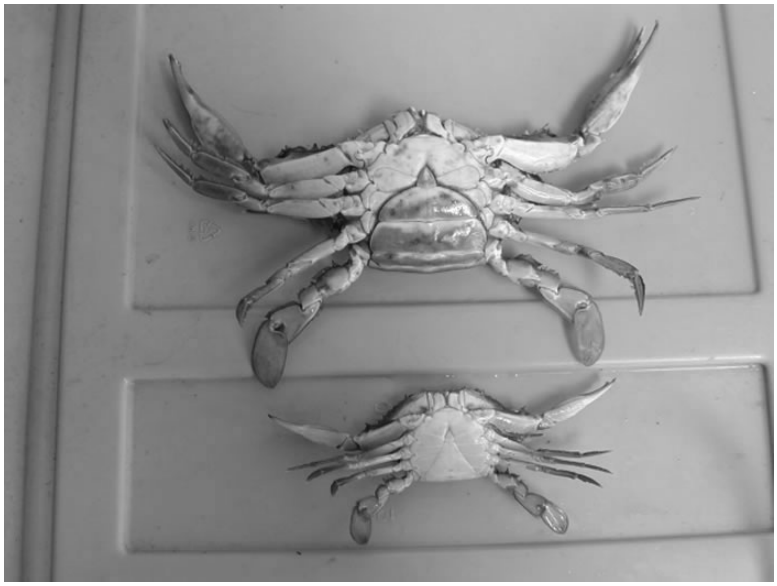


Figure 10. Photograph of a sexually mature and a sexually immature female blue crab.

Table 1. Red intensity and standard deviation values for the red color square and the dactyls (n = 22).

Crab ID	Red intensity of color card	Standard Deviation	Red intensity of dactyls	Standard Deviation
1	255	9.05	211	21.63
2	255	19.94	191	26.12
3	252	14.57	164	36.90
4	255	4.47	165	35.69
5	255	6.09	215	30.39
6	254	13.90	252	18.01
7	255	9.33	233	45.26
8	255	5.40	248	25.63
9	254	16.09	252	16.79
10	255	6.05	242	45.55
11	254	8.71	223	46.36
12	255	4.94	193	43.81
13	255	4.64	234	43.91
14	254	14.92	249	41.36
15	255	4.48	232	35.36
16	255	5.97	224	35.58
17	255	4.78	243	49.22
18	255	6.76	253	14.89
19	255	11.75	251	32.69
20	254	9.66	233	37.10
21	255	6.86	246	34.55
22	253	10.81	250	37.10

DATA ANALYSIS

I used linear regression and least squares analysis to examine the relationship between female size and cheliped coloration. Measurements included carapace area, the width and perimeter of the carapace, the area and perimeter of color on each dactyl, the total area and perimeter of each dactyl, the area and perimeter of the red color complex on each dactyl, the red intensity of the dactyls, and moult stage. Blue crabs are heterochelous (Schenk and Wainwright, 2001) meaning their chelipeds are differentiated into a major crusher and a minor cutter cheliped based on different dentition patterns (Levinton *et al.*, 1995), and thus the cutter and crusher cheliped were analyzed separately for coloration. Since the assumptions of normal residuals and constant variance were not met, a transformation on four of the models was used to determine the correct lambda. A box-cox transformation was used to determine the correct lambda to be used in two of the four transformations. For first and second transformed models, the dependent variables, Perimeter of Color and Area of the Red color Complex on the Crusher Dactyl, were used as exponents to calculate a new lambda for each model. A new Y variable was constructed using the lambda value and was regressed against the variables: area of carapace, perimeter of carapace, width of carapace, area of the crusher dactyl, perimeter of the crusher dactyl, and moult stage. The lambda used to raise the dependent variable, Area of dactyl (cutter), in the third transformation was approximately .80. A new Y variable was calculated and was regressed against the variables: area of carapace, perimeter of carapace, width of carapace, area of color on the cutter dactyl, perimeter of the cutter dactyl, and moult stage. In the fourth transformation, the dependent variable, Perimeter of dactyl (crusher), was raised to an

exponent of 2. A new Y variable was calculated and was regressed against the variables: area of carapace, perimeter of carapace, width of carapace, area of the crusher dactyl, area of color on the crusher dactyl, and moult stage. In the analyses of the relation between body size and color, the latter was considered to be the dependent variable. All independent variables were standardized before statistical analysis.

To determine whether terminal females were larger, more colorful than non-terminal females, I conducted a Mann-Whitney U test. The Mann-Whitney U test is used to compare two independent groups of sampled data. Sexually immature females were given a grouping value of 1.00 and terminal females were given a grouping value of 2.00. A P value of less than 0.05 was considered significant in all statistical tests. All statistical analyses were performed with the SPSS computer package (SPSS Incorporated, 1989-2001).

MATE CHOICE EXPERIMENT

I collected fourteen live *Callinectes sapidus* males and twenty eight females during the afternoon, early evening and/or late night at low tide along a rocky groin and marsh in Galveston, Texas (29° 16´N, 94° 49´W) with dip nets or with seine nets (Figure 2, 11). All animals were transported back to Texas A&M University after collection and held in aquaria. The animals were held and cared for with the same procedures used in the cheliped coloration experiment.

The mate choice experiment was conducted in a 105 –l aquarium. I separated the aquarium into three compartments by glass dividers, thus preventing any water exchange between compartments. This ensured that mate choice was determined visually rather than chemically. The center compartment measured 50 cm × 30 cm × 38 cm. The left and right compartments measured 19 cm × 30 cm × 38 cm and 21 cm × 30 cm × 38 cm, respectively. The bottom of the aquarium was covered with a layer of sand substrate. Complete water changes and cleaning of the testing aquarium was performed after every trial.

Figure 11. Photograph of marsh sample site located in Galveston, Texas (29° 16´N, 94° 49´W).

Carapace width and length, crusher width and length, and cutter width and length were measured for all crabs used in this experiment using digital calipers. All animals were anaesthetized using a 20 minute immersion in ice water prior to measuring to ensure inactivity and to prevent any injury to the crabs as well as to the handler. Females with different patterns of red color used in each trial were matched for size, differing by no more than 8% of all measured variables to eliminate the size aspect from the male's choice. The only obvious difference between females used in each trial was the area of red cheliped coloration displayed.

Each male was placed in the center compartment and one female each (one bright and one dull) of similar size was placed in the compartment to the left and right of the male. Female placement to the left and right was randomized, so the bright female would appear a similar number of times to the left and right of the male. Female coloration was quantified based on human observation. I evaluated each female and assigned each female a value of bright vs. dull based on the area of coloration she displayed. The female that displayed the greatest area of color was assigned the brighter value of the two. After a habituation period of at least 30 minutes for each animal; a pubertal female chemical pheromone was squirted, with a pipette, over the antennal region of the male crab to stimulate mating behavior. Approximately 3 ml of pheromone was used to stimulate the male blue crab. A study by Gleeson (1980) found that pre- and post-pubertal female blue crabs will release a urine-borne pheromone into surrounding water that can stimulate male courtship behavior. Male blue crabs detect the pheromone via chemoreceptors on the outer flagella of their antennules (Gleeson, 1980).

Two black plastic partitions were inserted on the left and right side of the central

compartment to block any visual contact between the male and two females during the habituation period. I lifted both partitions prior to stimulating the male with the female pheromone. I video-recorded the test tank for 1 hour using a Sony DCR-TRV730 Digital 8 Handycam that was mounted on an adjustable Ken-A-Vision tripod and positioned in front of the test tank (Figure 12). All trials were conducted between 0800 and 1900 hours and all animals were returned to their housing tanks after completion of the trial.

I collected pubertal female chemical pheromone from the moult water of three pre-pubertal females. I determined moult stage in the same process as the cheliped coloration experiment. Each female was placed in an aquarium with 10L of water and was held there until she completed her final pubertal moult to sexual maturity. Female blue crabs become sexually mature at the end of her penultimate instar, which is often referred to as the “pubertal moult” (Van Engel, 1958). Approximately, 200ml of moult water was collected from each aquarium and stored in small glass vials. All vials were stored in a -20° C freezer until use in this experiment. The three batches of female urine-based pheromone from the three different crabs were mixed prior to use in this experiment.

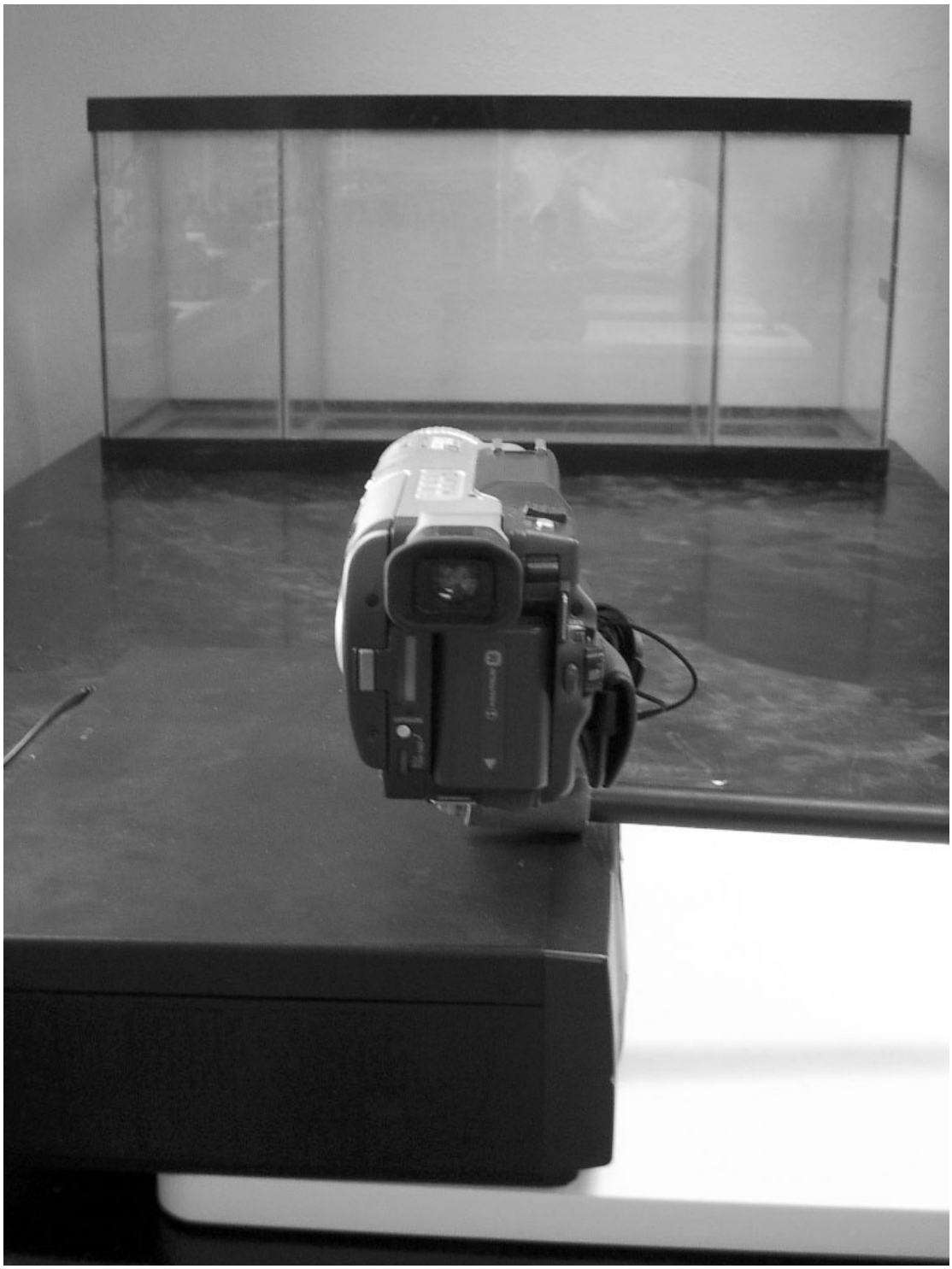


Figure 12. Test tank used in video recording the mate choice trials.

DATA ANALYSIS

The computer program The Observer® (version 2.0, Noldus Information Technology 1989) was used to record data from each video. Scored behaviors included the duration of sexual displays directed towards each of the two females and the number of sexual displays directed towards each female. I defined male association with the females as when the male was oriented towards one female or the other. Male displays were defined as walking legs extended such that the body is elevated to near maximum height above the substrate, chelae extended in the lateral position and swimming appendages rotated anterodorsally and waving from side to side above the carapace (Gleeson, 1980). Any observations that did not include any of the above displays were not included in the statistical analysis. The scored behavioral data was then imported into Microsoft® Excel 2002 (Microsoft Corporation, 1985-2001) to calculate frequencies and durations of each behavior displayed by the male. The SPSS computer package (SPSS Incorporated, 1989-2001) was then used to perform a two-tailed Wilcoxon signed rank test to compare male responses towards bright versus dull females. A P value of less than 0.05 was considered significant.

RESULTS

CHELIPED COLORATION EXPERIMENT

The components of size and color examined in each female blue crab were: carapace area, width and perimeter of carapace, area and perimeter of color on each dactyl, total area and perimeter of each dactyl, area and perimeter of the red color complex on each dactyl, the red intensity of the dactyls, and moult stage. The models selected through the stepwise selection procedure were chosen as the final models for each regression. The area of color on the cutter dactyl has a significant positive relationship to the total area of the dactyl ($p < .001$, $R^2 = .741$) and the area of color on the crusher dactyl has a significant positive relationship to the total perimeter of the crusher dactyl ($p < .001$, $R^2 = .846$) (Figures 13, 14). Perimeter of color on the cutter dactyl is significantly correlated to the total perimeter of the cutter dactyl ($p < .001$, $R^2 = .866$) where the perimeter of color on the crusher dactyl has high correlation to the total perimeter of the crusher dactyl, but not the perimeter of the carapace ($p = .032$ and $.166$ respectively, $R^2 = .863$) (Figures 15, 16). The area of red color complex on the cutter dactyl has a positive relationship to the total perimeter of the cutter dactyl ($p < .001$, $R^2 = .615$) and the area of red color complex on the crusher dactyl has a stronger correlation to the width of the carapace ($p < .001$, $R^2 = .780$) (Figures 17, 18). Total area and perimeter of each dactyl were measured and regressed for each claw against all variables to determine if there is any relationship between dactyl size and body size. The total area of the dactyl is related significantly to the total perimeter of the dactyl for both chelipeds ($p < .001$ for both, $R^2 = .954$ for cutter and $.962$ for crusher) (Figures 19, 20). Total perimeter of the cutter

dactyl is found to correlate highly with the total area of the cutter dactyl, the perimeter of color on the cutter dactyl, and the area of color on the cutter dactyl ($p < .001$, $R^2 = .979$) (Figure 21). The perimeter of the crusher dactyl has a significant positive relationship to the area of the crusher dactyl, the perimeter of color on the crusher dactyl, and the perimeter of the carapace ($p < .001$, $R^2 = .986$) (Figure 22). The red intensity of the dactyls did not have a significant relationship with area of the carapace, perimeter of the carapace or width of the carapace ($p = .771$, .308, and .126 respectively, $R^2 = .168$).

My results from the Mann-Whitney U test found that terminal females are significantly different in all variables except the red intensity value compared to non-terminal females (Table 2). Terminal females had a larger area of carapace, perimeter of carapace and width of carapace compared to non-terminal females ($p < .001$) (Figure 23). The total area and perimeter of each dactyl were significantly larger in terminal females compared to non-terminal females ($p < .001$) (Figure 24). Terminal females had a larger area of color and a larger perimeter of color on each dactyl ($p < .005$) (Figure 25). The area of the red color complex was larger in terminal females on both dactyls compared to non-terminal females ($p < .004$) (Figure 26). There was not a significance difference between the terminal and non-terminal females in the red intensity value ($p = .297$).

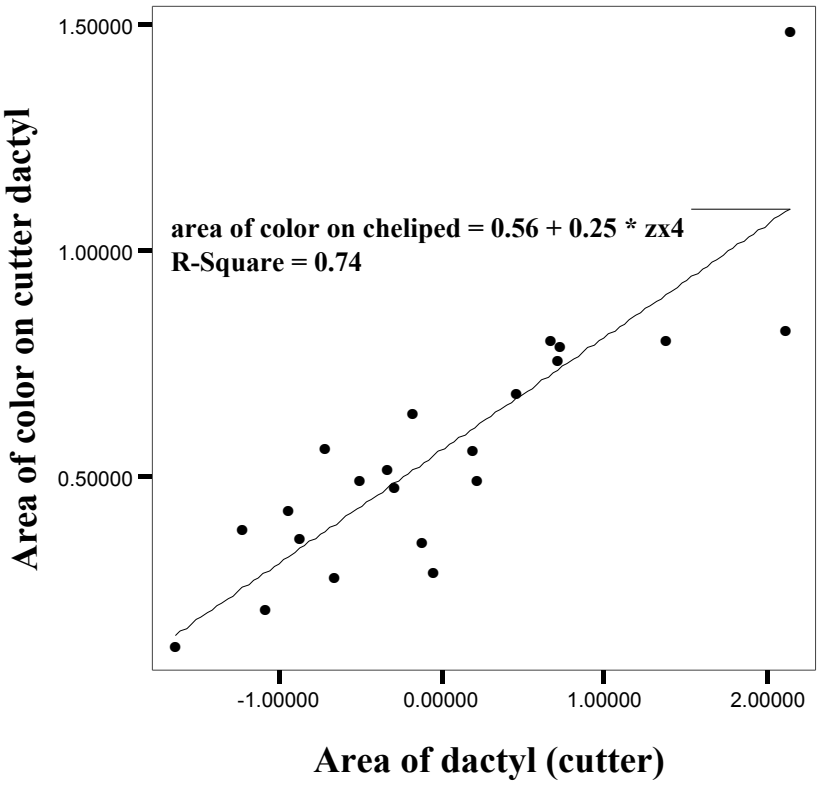


Figure 13. The relationship between area of color on the cutter dactyl and the total area of the cutter dactyl (n = 22).

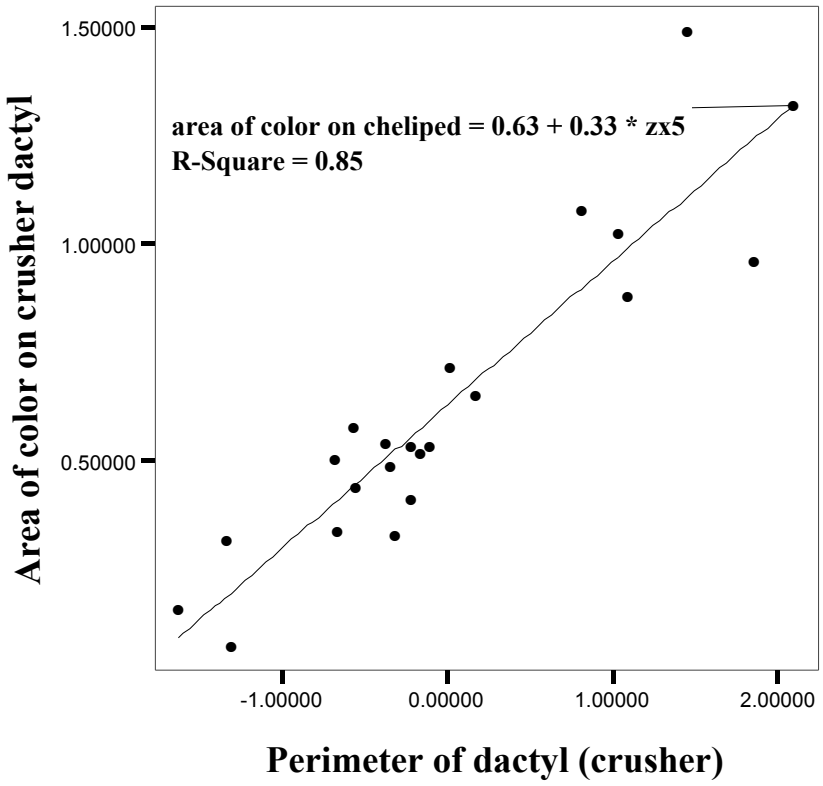


Figure 14. The relationship between area of color on the crusher dactyl and the total perimeter of the crusher dactyl (n = 22).

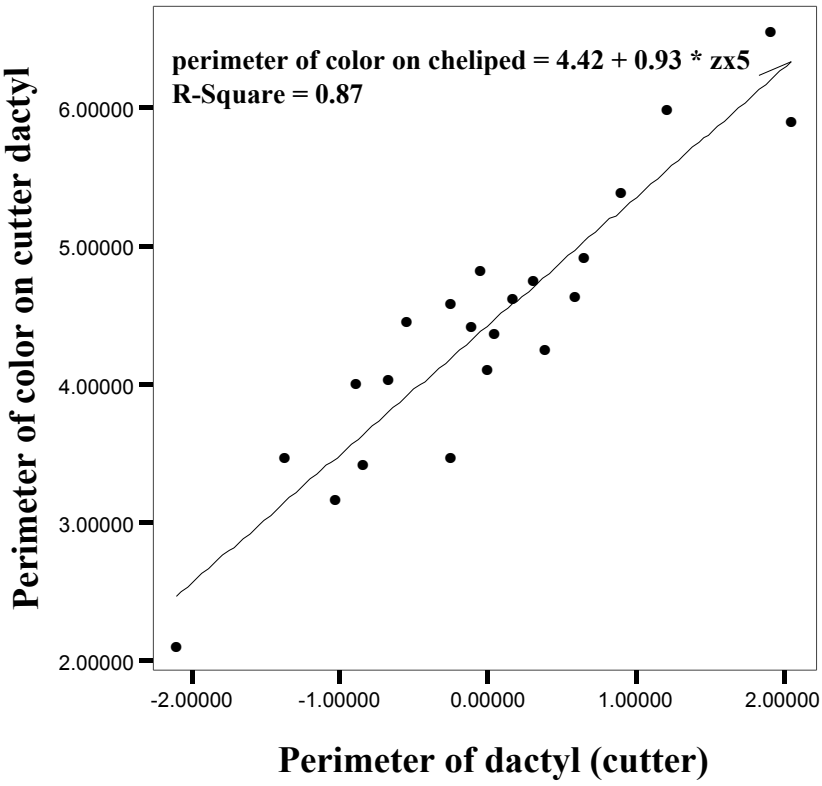


Figure 15. The relationship between perimeter of color on the cutter dactyl and the total perimeter of the cutter dactyl (n = 22).

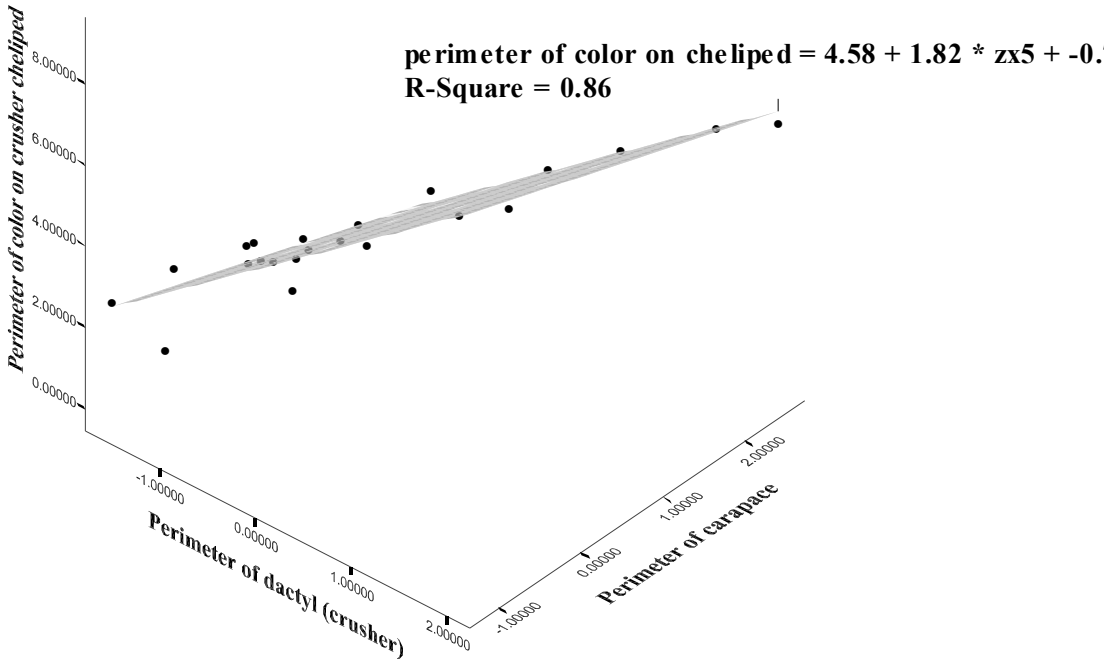


Figure 16. The relationship among the perimeter of color on the crusher cheliped, the total perimeter of the crusher dactyl and the perimeter of the carapace (n = 22).

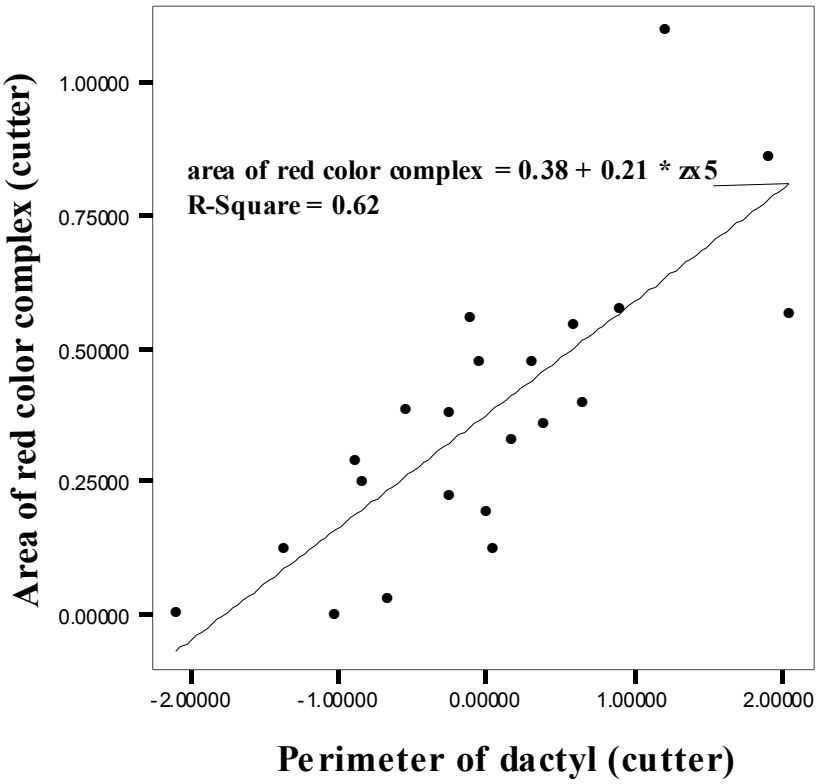


Figure 17. The relationship between area of the red color complex on the cutter dactyl and the total perimeter of the cutter dactyl (n = 22).

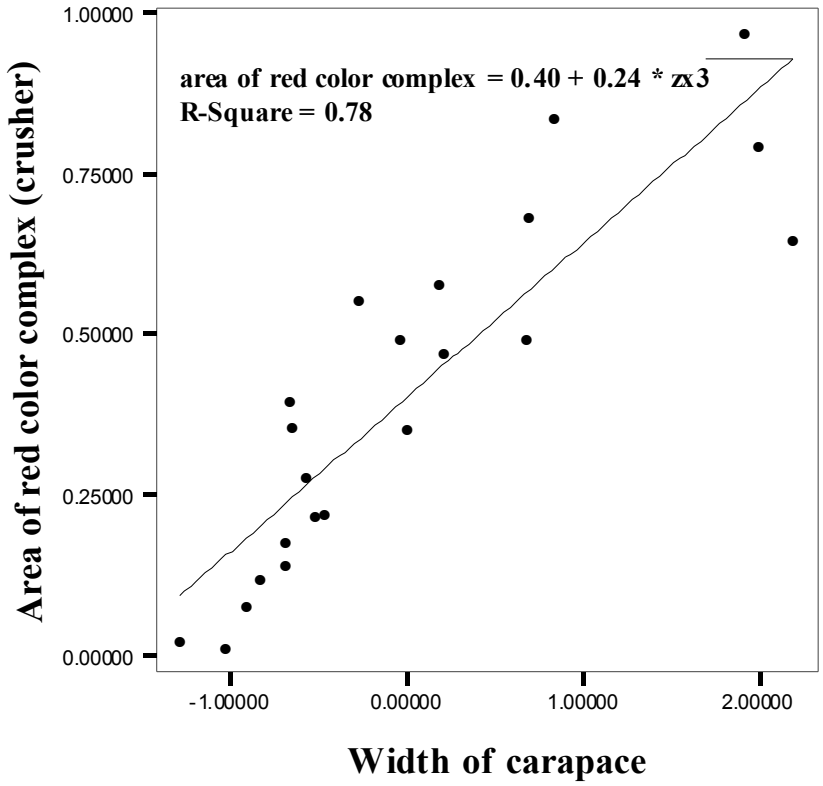


Figure 18. The relationship between area of the red color complex on the crusher dactyl and the width of the carapace (n = 22).

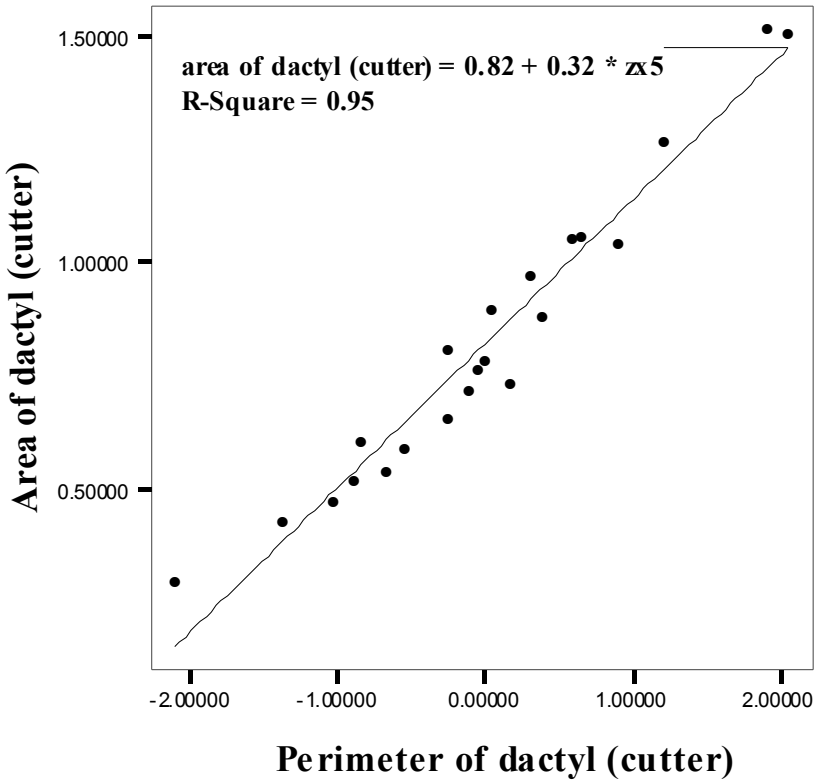


Figure 19. The relationship between area of the cutter dactyl and the perimeter of the cutter dactyl (n = 22).

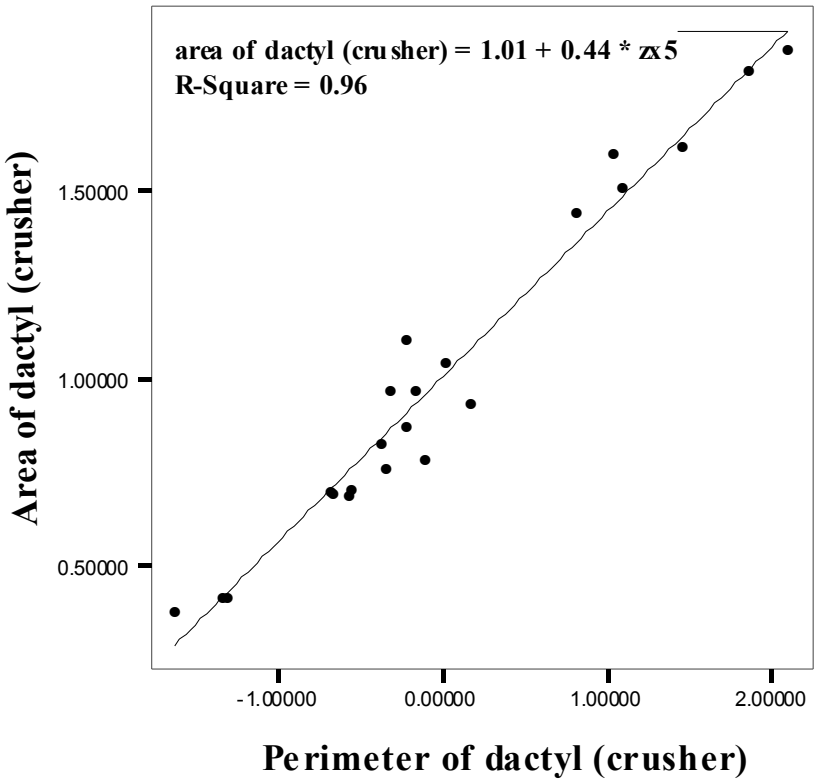


Figure 20. The relationship between total area of the crusher dactyl and the total perimeter of the crusher dactyl (n = 22).

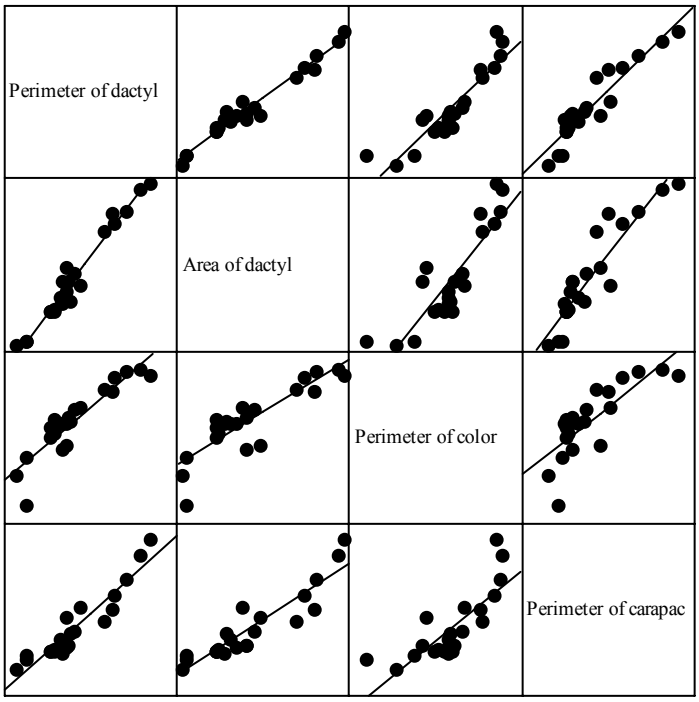


Figure 21. The relationship among perimeter of the crusher dactyl, the area of the crusher dactyl, perimeter of color on the crusher dactyl and perimeter of the carapace (n = 22).

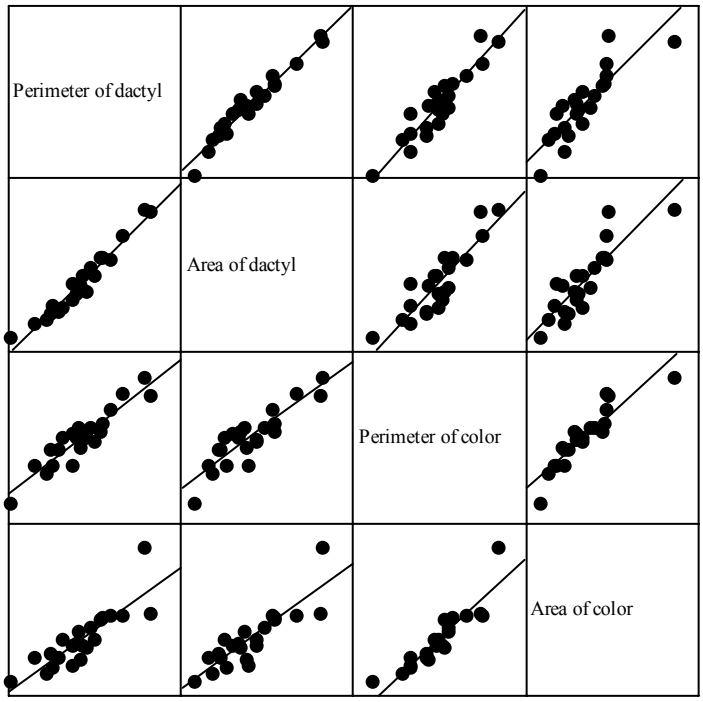


Figure 22. The relationship among perimeter of the dactyl for the cutter dactyl, the area of the cutter dactyl, perimeter of color, and area of color on the cutter dactyl (n = 22).

Table 2. Results from Mann-Whitney U test for comparison of terminal and non-terminal females.

Test Statistics[b]

	area of carapace	perimeter of carapace	width of carapace	area of dactyl (crusher)	perimeter of dactyl (crusher)	area of color on cheliped (crusher)	perimeter of color on cheliped (crusher)	area of red color complex (crusher)	area of color on cheliped (cutter)	perimeter of color on cheliped (cutter)	area of red color complex (cutter)	red intensity value	area of dactyl (cutter)	perimeter of dactyl (cutter)
Mann-Whitney U	3.000	2.000	1.000	11.000	6.000	13.00	16.000	10.000	10.000	9.000	15.000	40.000	9.000	3.000
Wilcoxon W	108.0	107.0	106.0	116.0	111.0	118.0	121.0	115.0	115.0	114.0	120.0	145.0	114.0	108.0
Z	-3.617	-3.686	-3.754	-3.071	-3.413	-2.935	-2.730	-3.140	-3.140	-3.208	-2.798	-1.094	-3.208	-3.617
Asymp. Sig. (2-tailed)	.000	.000	.000	.002	.001	.003	.006	.002	.002	.001	.005	.274	.001	.000
Exact Sig. [2*(1-tailed Sig.)]	.000[a]	.000[a]	.000[a]	.001[a]	.000[a]	.002[a]	.005[a]	.001[a]	.001[a]	.001[a]	.004[a]	.297[a]	.001[a]	.000[a]

a. Not corrected for ties.

b. Grouping Variable: moult stage

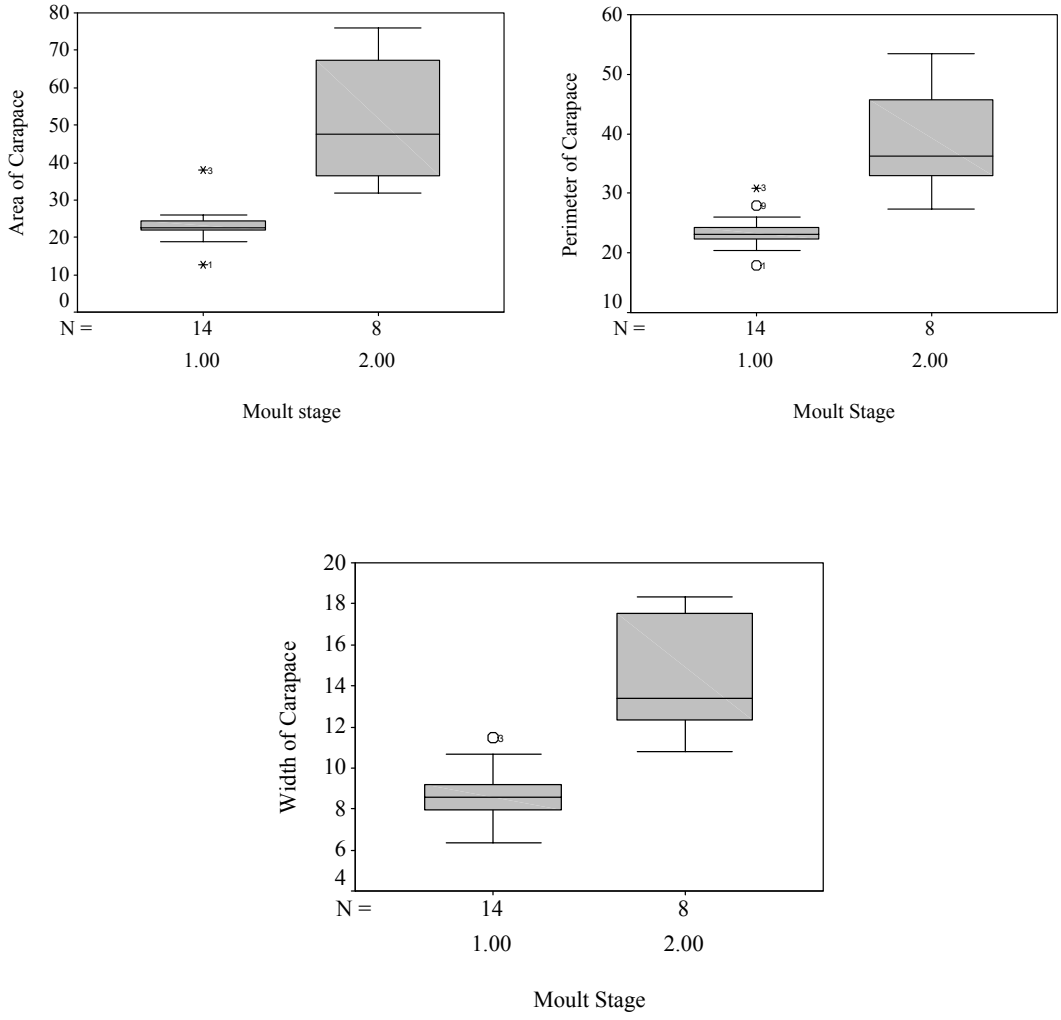


Figure 23. Difference between terminal females and non-terminal females for area of carapace, perimeter of carapace and width of carapace (n = 22).

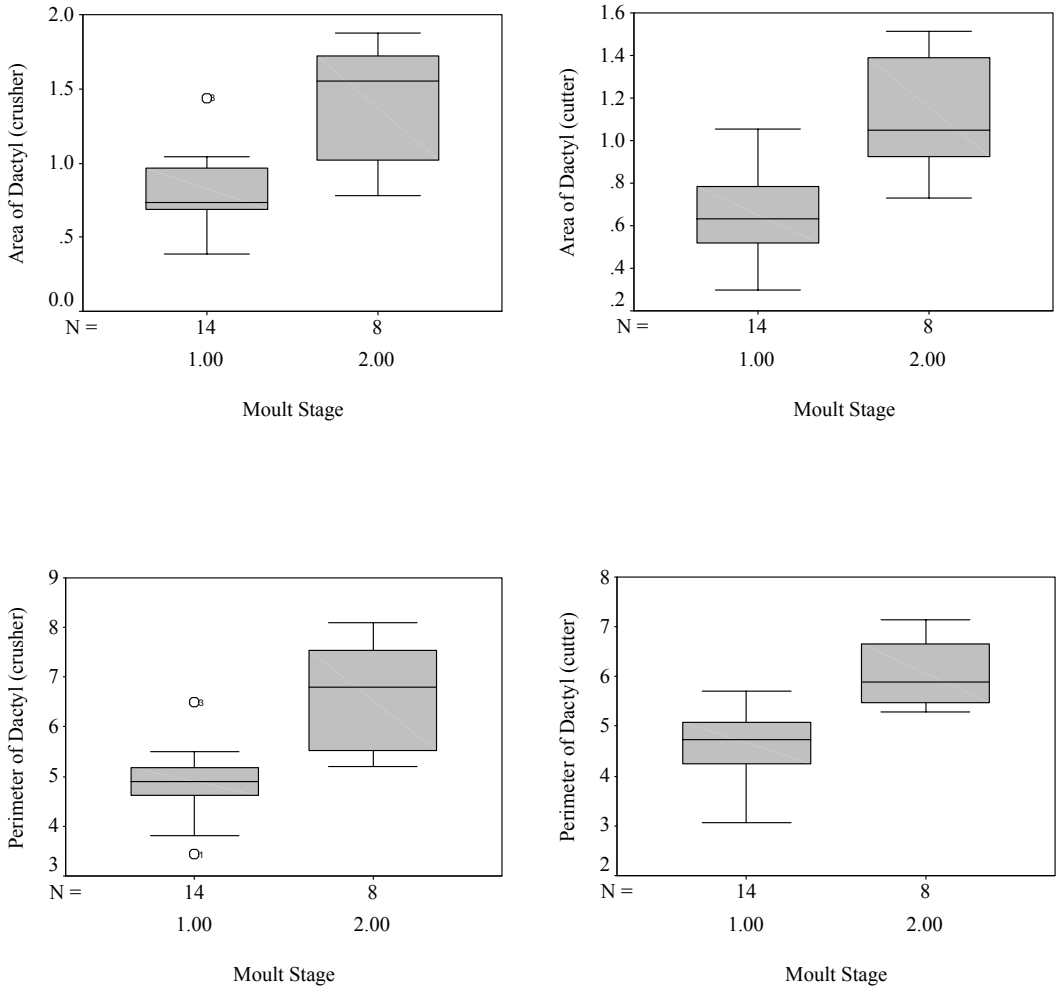


Figure 24. Difference between terminal and non-terminal females for total area and perimeter of each dactyl (n = 22).

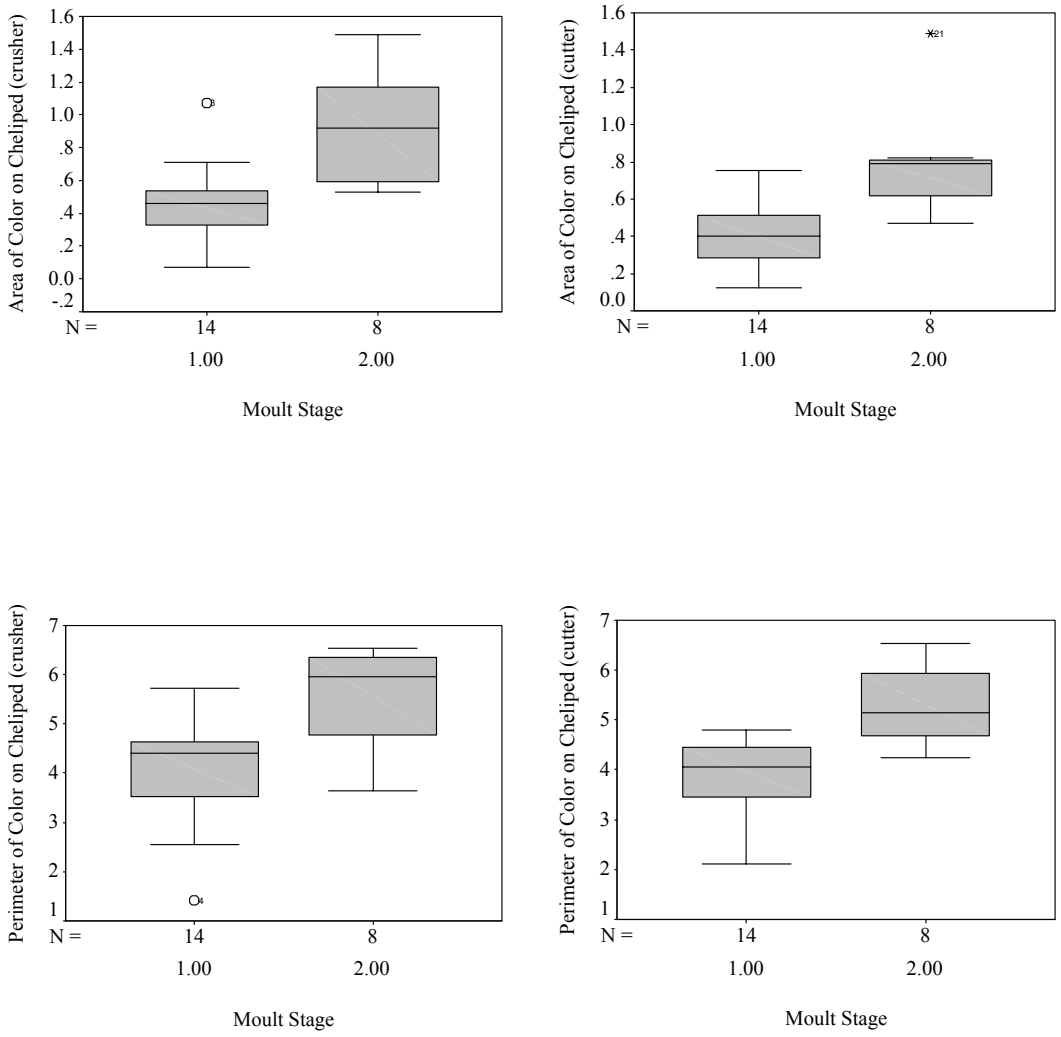
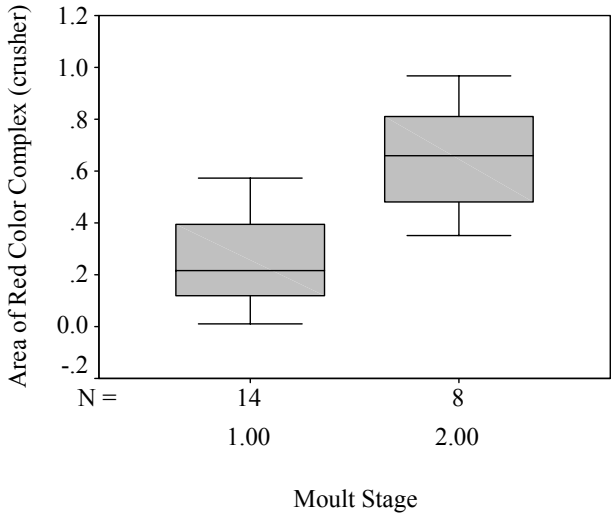


Figure 25. Difference between terminal and non-terminal females for area of color and perimeter of color on each dactyl (n = 22).



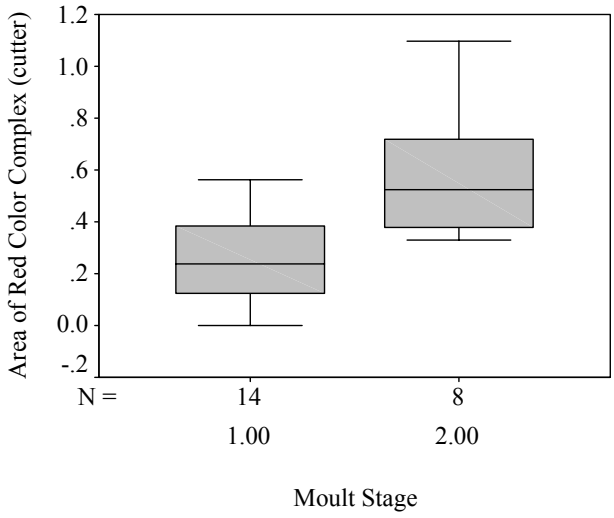


Figure 26. Difference between terminal and non-terminal females for area of the red color complex on each dactyl (n = 22).

MATE CHOICE EXPERIMENT

The males spent significantly more time displaying towards the brighter females compared to dull females (Table 3). Eleven of thirteen males displayed the meral spread behavior towards the brighter females. On average, males spent time directing the meral spread behavior towards the bright females about four times as much as the dull female ($p = .028$) (Figure 27). Twelve of twelve leg extension behaviors were displayed towards the brighter females compared to the dull females. Males spent time displaying the leg extension behavior towards the brighter females about 12 times as much compared to the dull female ($p = .003$) (Figure 28). When the paddle wave behavior was observed, five of six duration displays were directed towards the bright females. Males spent time displaying the paddle wave behavior towards the bright females approximately 200 times as much compared to the dull females ($p = .046$) (Figure 29). Males also displayed more often towards the brighter females compared to the dull females (Table 3). The number of meral spread displays directed towards the brighter females was approximately 1.5 times higher than for the dull females ($p = .019$) (Figure 30). The males displayed the leg extension behavior more than 2 times as often towards the bright females ($p = .040$) (Figure 31). When the paddle wave behavior was witnessed, the males displayed it towards the brighter females more than 27 times as much compared to the dull females ($p = .046$) (Figure 32).

Table 3. Results from Wilcoxon-signed ranks test for duration and counts of display behavior.

Test Statistics[b]

	meral spread dull - meral spread bright	leg extension dull - leg extension bright	paddle wave dull - paddle wave bright	meral spread count dull - meral spread count bright	leg extension count dull - leg extension count bright	paddle wave count dull - paddle wave count bright
Z	-2.197[a]	-2.934[a]	-1.992[a]	-2.345[a]	-2.059[a]	-1.992[a]
Asymp. Sig. (2-tailed)	**.028**	**.003**	**.046**	**.019**	**.040**	**.046**

a. Based on positive ranks.

b. Wilcoxon Signed Ranks Test

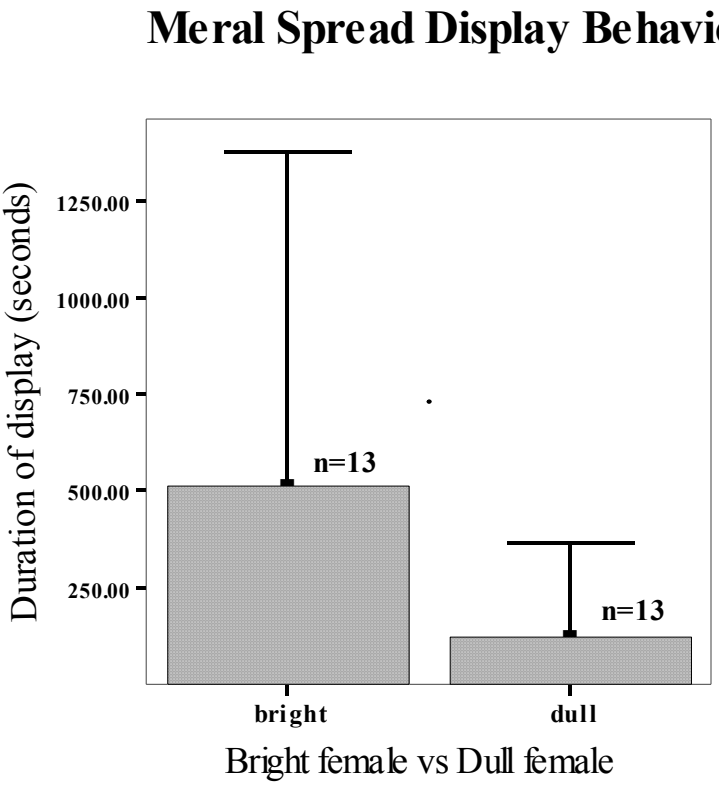


Figure 27. Duration of time spent by each male displaying the meral spread behavior (n = 14).

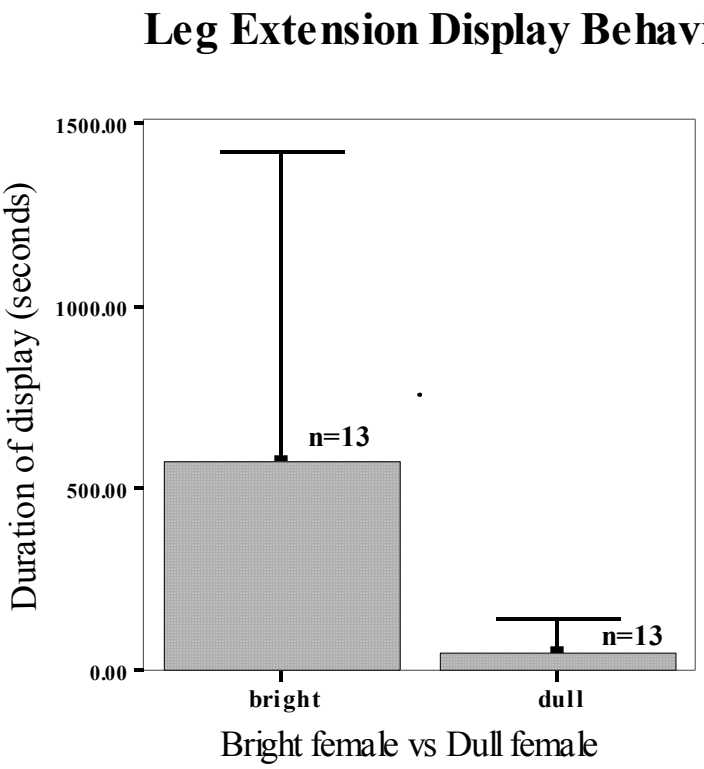


Figure 28. Duration of time spent by each male displaying the leg extension behavior (n = 14).

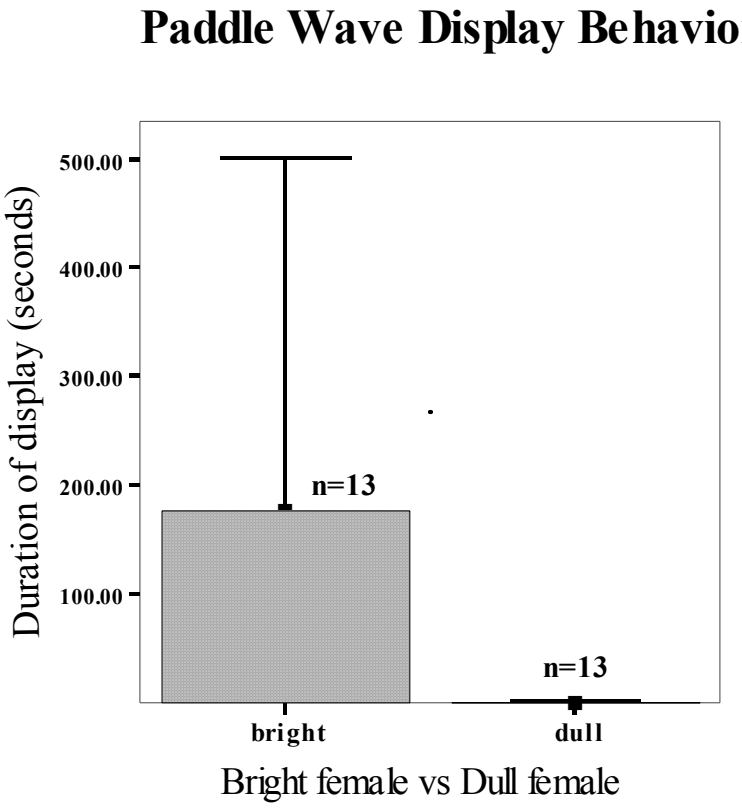


Figure 29. Duration of time spent by each male displaying the paddle wave behavior (n = 14).

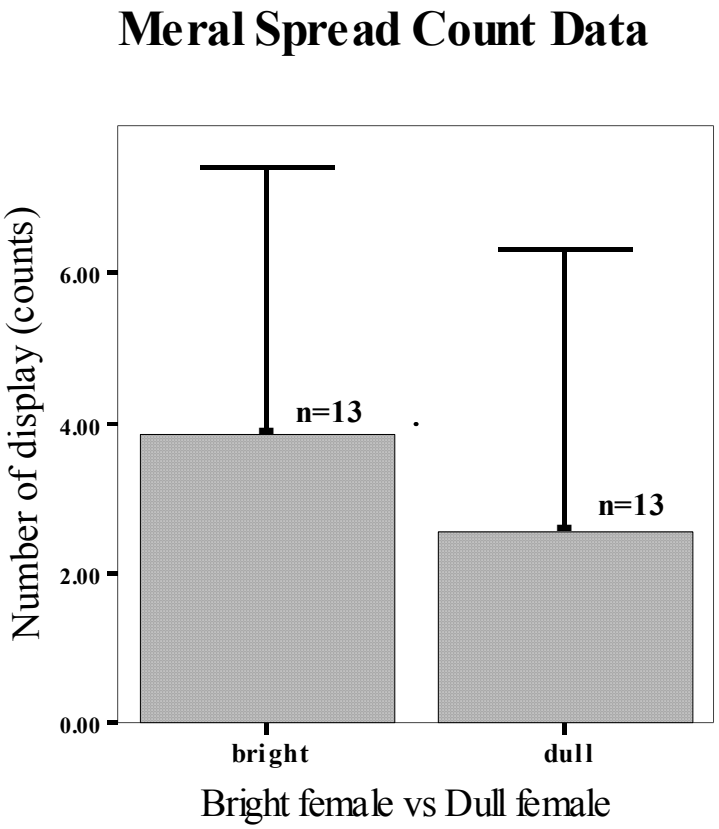


Figure 30. Number of meral spread behaviors displayed by each male (n = 14).

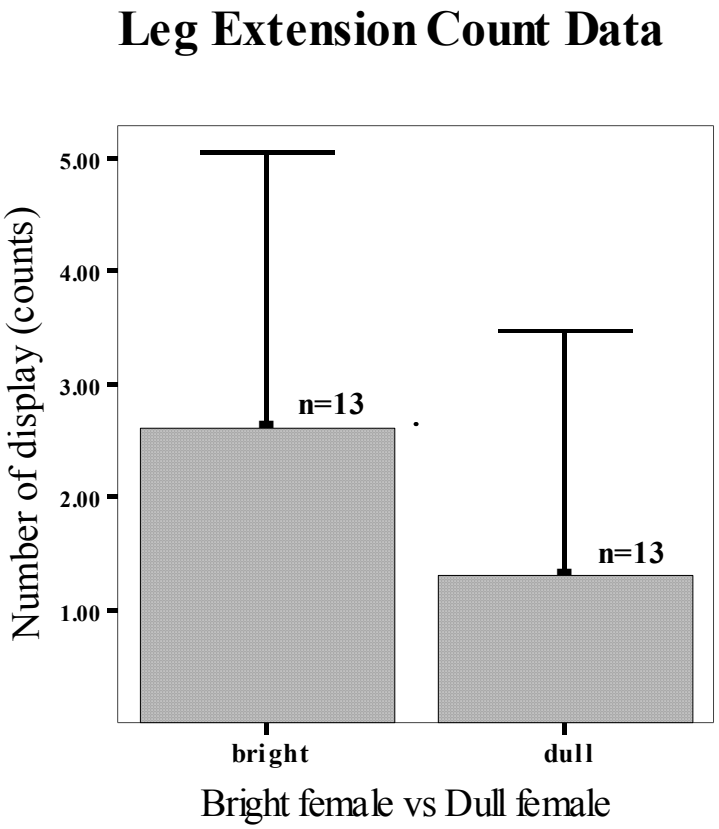


Figure 31. Number of leg extension behavior displayed by each male (n = 14).

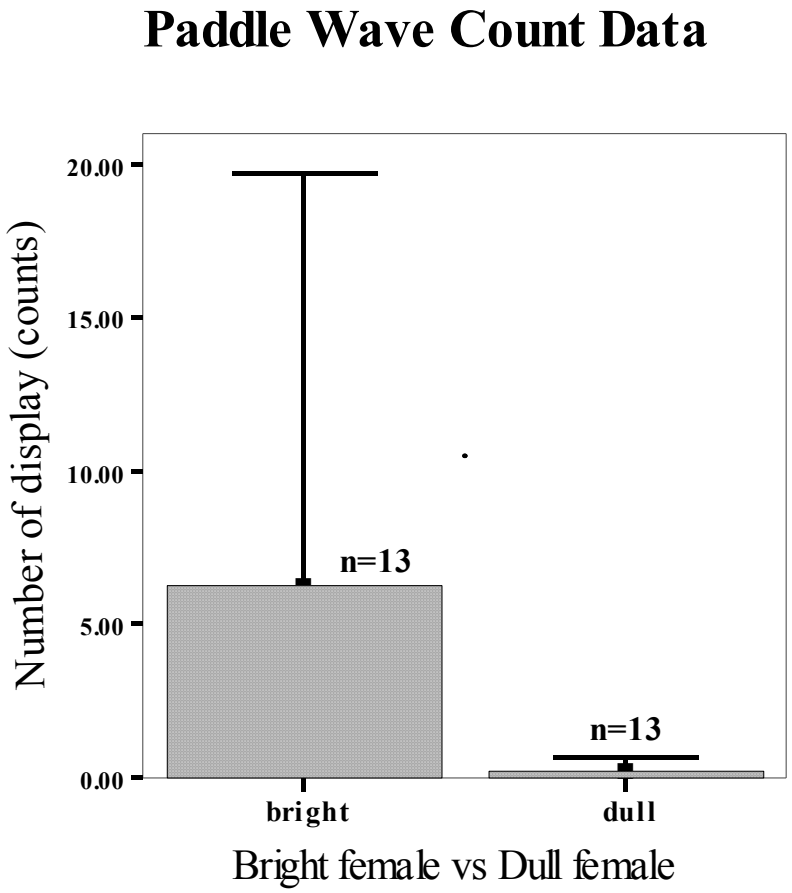


Figure 32. Number of paddle wave behaviors displayed by each male (n = 14).

DISCUSSION AND CONCLUSIONS

My results show there is a significant relationship between crusher dactyl coloration and body size. Female blue crabs that posses a larger crusher cheliped and displayed a greater area of red color on their crusher dactyls had a greater width and perimeter of the carapace. The cutter dactyl was not significantly related to size of the carapace. There is a significant difference in all variables except red intensity values between females that are pre-pubertal and females that have completed their terminal moult. Those females that had completed their terminal moult had a larger body size and displayed a greater area of red color on both dactyls. This may mean that cheliped coloration is an indicator to female reproductive state if there is an increase in the relative intensity of color present on the chelipeds.

In many crustaceans, such as lobsters, shrimp, isopods, and crabs mating occurs soon after the female sheds her exoskeleton while her carapace is soft (Hartnoll, 1969). Female *C. sapidus* never moult again after completing the puberty moult (Carlisle and Knowles, 1959) and thus the female mates only once during her entire life (Gleeson, 1980). Female blue crabs that have not mated at the time of the puberty moult remain sexually receptive for some time after their exoskeletons have hardened (Teytaud, 1971). The cheliped coloration appears brighter to human vision immediately following moulting, especially in terminal females. The increase in brightness may indicate an increase or a decrease in female receptivity. There would be a selective advantage for female blue crabs to signal when they are sexually receptive in that there would be a reduction in the costs of searching for a mate, and may reduce the risk of failing to

become fertilized.

This type of visual signal has been investigated in female Mediterranean chameleons, *Chamaeleo chamaeleon*, where changes in body coloration are in synchrony with reproductive state throughout the reproductive season (Cuadrado, 1998). The color changes and mating behavior of twenty-two female chameleons were monitored during the reproductive season (Cuadrado, 1998). Cuadrado (2000) found that the pattern of yellow spots appear to convey information to mates about receptive vs non-receptive female (Cuadrado, 2000). In three-spined sticklebacks, *Gasterosteus acleatus*, females display a conspicuous mottled or bar-like pattern to signal sexual receptivity. This pattern is as a signal used by females to stimulate courtship in males. When given a choice between two stickleback models, one with the mottled pattern and one without, males directed more courtship displays to the ornamented model (Rowland *et al.*, 1991).

My study also provides evidence that the area of red coloration displayed on female blue crabs' chelipeds is an effective visual signal to potential mates. I found when males are confronted with two female blue crabs differing in red cheliped coloration, males displayed longer with and more often towards the brighter females. The red coloration on the chelipeds may enhance the attractiveness of females by either, drawing the attention of males to the color pattern or perhaps the red coloration enhances the effectiveness of the courtship display (Endler, 1992). Pre-pubertal female *C. sapidus* attract the males with a urine-based pheromone (Gleeson, 1980; Teytaud, 1971) and both sexes participate in courtship displays (Jivoff and Hines, 1998). Courtship displays include chelae extension in the lateral position where the female ornamentation is

presented in front of the body and visible to her potential mate (Gleeson, 1980). Cheliped coloration may act as an honest signal and reflect some aspect of female fecundity in this species.

Examples of male mate choice of female traits are rare in species that are not sex-role reversed (Andersson, 1994). However, it has been found in systems that do have male mate choice that male mating preferences tend to favor female phenotypes that are associated with high female fecundity, such as large body size (Bonduriansky, 2001). The reproductive success of males is increased through successful matings with larger, more fertile females (Ridley and Thompson, 1985; Ward, 1988). In systems where females vary widely in fecundity, males are expected to be choosy (Andersson, 1994) and to court females that have higher fecundity (Sargent *et al.*, 1986) and are more sexually receptive (Sumner *et al.*, 1994). In the tidewater goby, *Eucyclogobius newberryi*, females display the secondary sexual characteristic of black markings on their bodies while gravid (Swenson, 1997).

Males could potentially discriminate between females of varying fecundity based on characteristics that are correlated with quality. Male zebra finches, *Taeniopygia guttata*, spent more time with females that received a high-quality diet than with females that had received the standard diet (Jones *et al.*, 2001). The high-quality supplement increases clutch size, egg size and offspring production in zebra finches (Monaghan *et al.*, 1996; Selman and Houston, 1996). Male zebra finches made their mate choice on the basis of some aspect of the females' present condition, which was directly linked to her fecundity (Jones *et al*., 2001). Bill color becomes more yellow in female zebra finches when fed a protein-enriched diet (Cottam, 1998) and this may be the aspect of a females' condition

that is the basis for male mate choice. Regosin and Pruett-Jones (2001) found that tail length in female scissor-tailed flycatchers, *Tyrannus forficatus*, is a sexually selected trait and is correlated with female quality. Clutch size, an aspect of female fecundity in this species, was correlated with female tail length (Regosin and Pruett-Jones, 2001). In the pipefish, *Nerophis ophidion*, males select for fecund females also on the basis of color. It was found that males prefer to mate with females that had more extensive areas of blue color. Blue color is an honest signal of female quality and mating success in this species (Berglund *et al.*, 1986).

In addition to sexually selected signals serving as mate attractants, they can also serve as status symbols for competitors (Berglund *et al.*, 1996). In a different species of pipefish, *Syngnathus typhle*, it was shown that the female ornamentation serves a dual function for attracting males as well as repelling female competitors. Female-female competition was tested in this species by allowing two females to interact with each other while in the presence of a single male (Berglund and Rosenqvist, 2001). Females displayed their ornaments toward each other more persistently than they did to the male. A more intense ornament display made the dominant female more attractive to the male, who spent more time displaying towards her (Berglund and Rosenqvist, 2001).

Female-female competition has not been investigated in blue crabs; however it is known that the chelipeds are employed in most agonistic acts of blue crabs. The chelipeds can be spread in front of the body during a threat posture, can be used to grab or deter an opponent, or they can be folded in front of the body, which seems to be a submissive posture (Jachowski, 1974). Females are presenting the red coloration on their chelipeds during these types of behaviors and the coloration may be an important visual

signal to competitors.

Johnson (1988) performed experiments on a group of captive pinyon jays to determine which female traits are strongly associated with female-female competition. Female pinyon jays, *Gymnorhinus cyanocephalus*, have been observed competing for food, nesting materials, nest site, and access to males during the breeding season. Female-female dominance interactions were observed and the following variables were measured: weight, wing length, tarsus, maxilla length, bill depth, size of the throat patch, brightness of malar feathers, and brightness of head feathers. The data did not indicate a strong relationship between dominance and any single female trait, but it was found that dominant females usually had brighter malar feathers (Johnson, 1988).

This is the first study to show male mate choice in blue crabs and that male choice is directly related to relative intensity of female cheliped coloration. Results from this project may suggest that the cheliped coloration of female blue crabs has evolved in part as a response to male mate choice. This project focused on the role color plays as a visual signal towards potential mates; however the role of color signaling and bright coloration in female blue crabs requires further investigation.

Examining the blue crab coloration provides an excellent opportunity to test the hypotheses regarding the function and evolution of female ornaments. A good understanding of male ornamentation has been provided through scientific efforts. More attention should be directed at the unstudied ornamentation in female animals (Amundsen and Forsgren, 2001). A clearer understanding of the blue crab sexual dimorphism may create better insight to other invertebrate or vertebrate systems that display a distinct reverse sexual dimorphism. In the broader sense, the study of animal

coloration may help explain the importance of color in comparative physiology as well as in the current theories of evolution.

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