Female Mate Choice And Male-male Competition In The Variegated Pupfish, Cyprinodon Variegatus.

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FEMALE MATE CHOICE AND MALE-MALE COMPETITION IN THE VARIEGATED PUPFISH, CYPRINODON VARIEGATUS.

by

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of Lehigh University

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ABSTRACT

Field observations and laboratory experiments were designed to examine female mate choice and male-male competition in *Cyprinodon variegatus*. Exploitative competition over territories and interference competition in the form of spawning interruptions, were more important than female mate choice in determining male reproductive success in this species. Territory size was found to be highly variable in the field, and was significantly related to the number of eggs fertilized by males. Males that defended larger territories received more eggs from each female with which they spawned, perhaps due to reduced interference competition. Both field and laboratory evidence suggests that male body size is very important in acquiring and defending territories. In the field, the relationship between male body size and territory size was highly significant, and smallest sexually mature males (< 30 mm) were entirely absent from the territorial population. In the lab larger males always defeated smaller males in territory competition in neutral arenas. Larger males were also capable of usurping the territories of smaller prior residents, although not always. The field observations of males and females revealed no evidence of female mate preference for large or brightly colored males, but in highly controlled lab choice tests, females did prefer larger males. Quite possibly the absence of female choice in the field was due to the intense male-male interference competition that effectively overpowered it's expression. In the lab, male-male competition was prevented and thus may have afforded the females the opportunity to choose.

Chapter 1

Theoretical Interest and Background Information

Darwin was perplexed by the gaudy adornments and highly developed weaponry exhibited by males of many species. He theorized that male weapons and ornaments were a consequence of two separate, but not mutually exclusive processes: males competing amongst themselves for access to mating opportunities (weapons) and females selecting some males preferentially (ornaments) (Darwin, 1871). He reasoned that these two processes could cause intense selection for male traits that either were correlated to success in male-male competition (intra-sexual selection), or were attractive to females (inter-sexual selection). Darwin felt that this type of selection, which he called "sexual selection", was potentially intense enough to overshadow the effects of natural selection, leading to males that were less fit to survive in their habitats but still able to consistently sire more offspring.

For the most part, very little was added to our understanding of sexual selection until Fisher (1930) substantiated the validity and importance of Darwin's predictions with his mathematical models, thus breathing new life into this important field of evolution. Bateman (1948), Orians (1969), Trivers (1972), and Emlen and Oring (1977) added additional empirical and theoretical support which attempted to predict under what circumstances sexual selection should be most prevalent. These classic works collectively tied sexual selection to conspicuous processes like parental investment, sex ratios, and the mating system, and a paradigm quickly began to emerge.

It was theorized that males typically invest less in their offspring than do females. Thus, the reproductive success (RS) of males would be most often limited by the number of females with which they mate. Conversely, female RS would be limited by her own fecundity and the quality of her mates. Therefore, it would be expected that males often compete amongst themselves for access to females, while females are "choosy", discriminating against certain "low quality" males. Thus some males should be more successful than others, leading to high male reproductive variation, while females should have lower reproductive variation.

It is now widely agreed that male-male competition and female choice often work synergistically to cause high variation in male RS, and much research has focused on which component of sexual selection is most important in causing this variation. This is typically accomplished by investigating the relationship between certain male secondary sexual characteristics (i.e., those that are important in male-male competition or mate attraction) and male RS. However, it is intrinsically difficult to determine the ultimate cause of male reproductive variation (and hence the probable agent of selection), because male secondary sexual traits can often be simultaneously advantageous in intra-sexual competition and in attracting females (but see Moore, 1990, for an example of how this has been attempted). Further, since male traits are often highly correlated to his resource quality, it is also difficult to determine if females are choosing male qualities or resource qualities or both (e.g., Downhower and Brown, 1980). In fact one recent review of the literature found that more than half of the papers that attribute non-random male RS primarily to female discretionary mating, failed to properly eliminate male-male competition as a causal agent (Andersson, 1994).

In this dissertation I examine female mate choice and male-male competition in a polygynous territorial fish. There is strong evidence that both components of sexual selection have been critical in the evolution of many diverse polygynous fish species. However, much of the research has focused on species that exhibit paternal care. Females of these species are expected to be "choosy" because of the direct impact the male has on the survival of her offspring. For example, large male body size is often beneficial in defending eggs and fry against predators, and may reduce the potential for egg cannibalism. Thus it is not surprising that females of many polygynous territorial fishes with paternal care prefer larger males (Downhower and Brown, 1980; Bisazza and Marconato, 1988). On the other hand, in some species the habitat may be more important to the survivorship of the offspring than male quality. For example, females of a several fish species prefer to spawn in larger nest sites (Lindstrom, 1988; Bisazza, Marconato, Marin, 1989), or in concealed nest sites (Sargent and Gebler, 1980). In these species, male-male competition over these preferred areas is critical in determining male RS. Further, females of some species may first have a preference for habitat type and then may choose between males that are defending sites in these areas (e.g., Thompson, 1986). In any event, in fishes with paternal care, female choice for male traits or habitat traits is common.

Less is known about sexual selection in territorial fishes that have limited parental care, no parental care, or that have maternal care. Males in these species do not bestow any direct benefit to the offspring. Depending on the mating system, females may discriminate on the male's resources, especially as they relate to her safety from predation or the safety of her offspring (Jones, 1981; Warner, 1987; Sato, 1994). On the other hand, for some species with no paternal care, females may mate more-or-less randomly, leaving male-male competition to account for most of the variation in male reproductive success (Warner and Schultz, 1992; Pyron, 1995). Although female choice of male characteristics in species with no paternal care is a matter of debate, it is possible that females may select among males based on secondary sexual traits that signal "good genes". For example, female Pecos pupfish (a species with no direct paternal care) prefer to mate with brightly colored males (Kodric-Brown, 1983).

My research centers on the variegated pupfish, Cyprinodon variegatus, a polygynous territorial species with no direct paternal care (or incidental paternal care). This species is a small euryhaline cyprinodontid fish that is endemic to the Atlantic coastal regions of North and South America, and throughout the West Indies (Hoese and Moore, 1977; Kaill, 1967). The social system is resource-defense polygyny (Hildebrand, 1919; Raney et al., 1953). Females visit male territories on a daily basis throughout the breeding season (Raney et al., 1953). Males court females as they approach or enter the territory. If the female is receptive she deposits eggs, one at a time, and the male fertilizes each one as it is extruded. In addition females may leave eggs with more than one male per day (Draud, pers. obs.) Nothing is known about egg survival rates, but the greatest threat to egg mortality is likely to be intruding fishes, especially conspecific males and females. The eggs are not directly protected or cared for by the male, however they are inadvertently protected as the male patrols and defends the territory borders against all conspecifics and most other animal intruders.

Males of this species are larger than females and exhibit bright blue nuptial coloration during territory defense, courtship, and spawning. It is possible that females choose males based on this nuptial coloration as is the case for the related Pecos pupfish (Kodric-Brown, 1983) or perhaps based on body size. Conversely, perhaps male-male competition is more important than female choice in this species. A laboratory study did suggest that females mated at random in this species (Itzkowitz, 1978).

I combine field observations and laboratory experiments to test hypotheses about female mate choice and male-male competition. The remainder of this dissertation is arranged into three papers and a summary chapter. Each of the three papers has it's own Introduction, Methods, Results, Discussion, Literature Cited, and Figures, and Tables. Each of these papers is intended for submission to a peer-review journal.

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Chapter 2

Sexual selection in pupfish: female choice or male competition?

Introduction

In resource-based, territorial, social systems, males secure matings by defending a resource essential to female reproduction (e.g., Emlen and Oring 1977). As a consequence, strong selection pressure is expected to favor male traits that facilitate acquisition and defense of resources. For example, large body size may be selected by male-male competition because it contributes to victory in direct contests (e.g., Lindstrom 1988; Hoelzer 1990; Warner and Schultz 1992). Color signals may also evolve through intrasexual competition as truthful advertisements of male fighting ability (e.g., Rohwer 1982; Roskoft and Rohwer 1987; Olsson 1994).

However, female mate choice may also play a role in the evolution of male traits (e.g., Andersson 1982). For example, females may prefer to mate with large males because they are better nest defenders (e.g., Downhower and Yost 1977; Downhower and Brown 1980; Bisazza and Marcanato 1988; Hastings 1988b; Cote and Hunte 1989), or because, in some species, larger males are less likely to eat their own eggs (e.g., Downhower and Brown 1980; Sargent 1988). Females also may use male color as honest advertisement of phenotypic vigor and genetic quality (Kodric-Brown 1983; Kodric-Brown and Brown 1984; Warner and Schultz 1992; McKinnon 1995).

It is difficult to determine whether male traits evolved through intra-sexual competition or female choice since the same male traits can be advantageous in both (Moore, 1990). In addition, it is often difficult to determine if females are selecting mates based on male resources, male traits, or both, since male quality is often correlated to resource quality. As a result of these confounded issues, the relative importance of female choice and male-male competition in the evolution of male traits is poorly understood (Andersson, 1994).

In this paper I compare the importance of intra-sexual male competition and female choice on male mating success in *Cyprinodon variegatus*. *C. variegatus* is a small, polygynandrous, sexually dimorphic, territorial pupfish which occurs along the Atlantic and Gulf Coasts and throughout the Caribbean. Males grow larger than females and display intense iridescent blue nuptial coloration when defending territories. Males provide no care to their eggs, except the incidental benefit gained from expelling potential egg predators from their territories. Females come to territories to mate, and likely spawn multiple days within the breeding season. Female choice is clearly possible in this species as 1. females can range widely allowing for comparison of males or resources, 2. the mating season is prolonged, and 3. females can easily reject a male if they wish.

Previous studies have found conflicting evidence for the importance of female choice in this genus. A laboratory study on *C. variegatus* indicated that when resource quality is homogeneous, a male's reproductive success is a function of his competitive ability to establish and defend larger territories (Itzkowitz 1978). This study did not attempt to test female choice of male coloration or body size. However, field and laboratory studies on *C. pecosensis* show that while male-male competition is important, that female choice of resources and nuptial coloration is also important (Kodric-Brown 1983, 1986). Though the two species are very similar phenotypically, their habitats are very different. *C. pecosensis* live in freshwater and have a great deal of heterogeneity in their habitat (Kodric-Brown 1977; 1978; 1983), whereas C. variegatus occur mainly in coastal marshes where the substrate is less variable (Raney et al. 1953; Itzkowitz 1974; Draud pers. obs.). Thus a field study of female choice in *C. variegatus* should help to clarify the issue of female choice in this genus.

Predictions

Male traits:

I predict that females will prefer to mate with larger and brighter males. These two highly conspicuous male traits have been selected by female choice in other territorial social systems (Andersson 1994). Females prefer larger males in several species of territorial fishes. For example, in some species, larger males can withstand longer periods of starvation and are thus less likely to eat their own eggs (e.g., Downhower and Brown 1980; Sargent 1988). In other species, larger males are better nest defenders (e.g., Downhower and Yost 1977; Perrone 1978; Downhower and Brown 1980; Bisazza and Marcanato 1988; Hastings 1988). Females may prefer brightly colored males because the intensity of nuptial coloration can provide information on parasite load or phenotypic vigor (Kodric-Brown and Brown 1984). I test my predictions by asking whether brighter or larger males receive more total eggs, receive more eggs per female, or mate with more females than smaller or less colored males. I also ask whether there is a relationship between the propensity of a female to leave without spawning and the color or size of the male.

Territory size:

Variation in territory size may affect male reproductive success, through female choice, male-male competition, or both. Females may prefer to mate with males defending larger territories because territory size could provide accurate information regarding the phenotypic or genetic quality of the defender. For example, if territory defense is energetically costly in this species (but see Feldmeth 1983), territory size may indicate the male's phenotypic vigor, and thus reflect his ability to provide better protection from egg predators (e.g., Grant and Colgan 1983) and perhaps his ability to withstand starvation and refrain from filial cannibalism (Sargent 1988; Unger and Sargent 1988; Sargent 1989). It has also been suggested that large territory size may indicate genetic quality (e.g., Roithmair 1994). Finally, Kodric-Brown (1983) suggested that increased complexity in microtopography could be advantageous because the female had more secluded oviposition sites, thus decreasing the likelihood of the eggs being eaten by the father or by intruding males in the event of a takeover. Large territories may provide a similar advantage owing to the greater area which may make it less likely that a male will "find" his eggs as he forages.

However, large territory size may provide reproductive benefits to males even if females do not prefer to mate in larger territories. For example, in some species, females appear to settle into male territories at random with respect to other females, males, and resource quality (Severinghaus, Kurtak and Eickwort 1981; Lightbody and Weatherhead 1987, 1988; Goulet and Green 1988; Lindstrom 1988). In these species, males defending larger territories have a higher probability of females "settling" into their territories, and consequently a higher reproductive success. In addition, in some species territories function to isolate males from one another, preventing courtship and spawning interruptions from neighboring males (Van Den Assem 1967). Larger territories may provide more visual isolation, and thus facilitate higher male reproductive success.

In the lab, territory size is an important component of male mating success, but not due to female choice (Itzkowitz 1978). Therefore, I predict that territory size is an important feature in male reproductive success, but that females do not bias their matings based on territory size. I test these predictions by comparing the number of females that spawn, and the number of eggs spawned, with males defending territories of various diameters. I also compare the probability of a female spawning once she has entered a territory, among males defending territories of various diameters.

Methods

Study Location

Data were collected during the summer of 1993. The study sites were located in Cape May County, in southern New Jersey. The marsh in this area is dominated by salt marsh cordgrass (*Spartina alterniflora*) and numerous tidal creeks and pannes exist throughout the area.

Pannes (referred to as potholes and ponds by Talbot and Able, 1984) are isolated pools of salt water, which vary considerably in circumference (from < 1 m2 to > 50,000 m2), depth (from < 2 cm to > 1.5 m), shape, and morphology. They are inundated with salt water only during full moon flood tides, and receive fresh water from time to time from rain storms. Because pannes are isolated from tidal influence through most of the month and because they are relatively shallow areas, the pannes fluctuate widely in temperature, salinity, dissolved oxygen and water level.

Male Observations

Territorial males were observed in six pannes from June 07 through August 19, 1993. Short pieces of 0.5 cm diameter wooden dowel were arranged in three parallel lines in each of the pannes to mark-off a rectangular area into 1 m^2 quadrants. The first row of dowels was placed near the water's edge, so that the rectangle began at the shoreline and extended two meters out into the panne. The length of the rectangle depended on the size of the panne and ranged from 3 to 7 meters. All observations were done on males defending areas within these demarcated areas.

The observer approached the panne slowly and sat near the edge (less than 0.5m from the water). Six small rectangular pieces of white acrylic (60 mm x 20 mm) were tossed into the immediate area in front of the observer so that fish body size could be estimated. These pieces were marked at 1 cm intervals on both sides and attached to very fine monofilament line so that they could be moved and retrieved. The fish were often startled by the approach, but quickly acclimated to the observer and usually returned to their normal activities within several minutes. A male, defending a territory near one, or several, of the plexiglass pieces, was chosen and the observation began when the observer was satisfied that the fish was no longer reacting to his presence. All observations were twenty minutes in duration and were taken on a micro-cassette recorder and later entered into a spread sheet for analysis. The observer counted the number of females entering the male's territory, the number of females that spawned with the male, and the number of eggs fertilized by the male. Interruptions during spawning were also recorded and were categorized as "terminating" and "non-terminating" depending on whether the female quit spawning after the interruption. Border disputes with neighboring territorial males and chases directed at non-territorial conspecifics (male and female) and other species were also recorded. The male's brightest color was estimated. Males were categorized as either "no color", "minimum color", "medium color", or "maximum color". (see table 1 for definitions of the color categories). The male's size was estimated by comparison with the nearest piece of plexiglass, and were categorized as either very small (less than 30 mm), small (between 30 and 40 mm), medium (between 40 and 50 mm), and large (50 mm and over). Because only two "very small" fish ever held territories, and because neither had a female visit them, they were not included in the analyses. Territories seemed to be roughly circular when male interactions were plotted on a grid. I use the term "diameter" to refer to the longest distance between the outer-most points covered by the male during the 20 min observation period. This distance was estimated by noting the movements in relation to the nearest wooden dowels in the area. The outer-most points were typically easy to determine as border disputes between neighboring males were common throughout the breeding season.

Female Observations

A total of thirty-eight females (June = 12; July = 10; August = 16) were observed in the same six pannes where males were observed. A female that was not currently spawning but was swimming through male territories was chosen for observation. I observed each female until she was either out of sight or until 45 minutes had passed, the former being much more common. Data were recorded on a micro-cassette recorder and later transcribed to a spreadsheet for analysis. I recorded data on the number of male territories the female entered during the observation, the approximate sizes and colors of the males defending those territories, and all of her spawning events.

Statistical Methods

Unless specifically noted, all data were compared with ANOVA and Tukey multiple range tests.

Results

Monthly Variation

A total of 111 20-min observations were made of territorial males during 1993 ($n = 36$ for June, $n = 41$ for July, $n = 34$ for August). Differences across month were not seen for the number of females entering ($F(2,111) = 1.13$, $P = 0.66$), the number of females mating ($F(2,68) = 1.16$, $P = 0.64$), the probability of a female spawning ($F(2,95) = 0.16$, $P = 0.85$), total eggs fertilized ($F(2,111) = 1.4$, $P = 0.50$), eggs spawned per female ($F(2,68) = 0.09$, $P = 0.92$), and territory diameter ($F(2,111) = 0.25$, $P = 0.78$). June, July, and August samples were combined for all the remaining analyses.

Male Reproductive Success

Ninety five (86%) of the 111 males had at least one female enter their territory (range = 1-6; mean = 2.31; standard error = 0.13). Sixty eight males (61% of all males observed; 72% of all males visited by females) spawned with at least one female for a total of 91 spawning events. Seventy eight (86%) of these spawning events ended due to interruption by neighboring males. Males fertilized between 0 and 17 eggs in twenty minutes (mean = 3.5; median = 2; standard error = 0.4; coefficient of variation = 118.5), and mated with 0 to 3 females (mean = 1.34; median = 1; standard error = 0.065; coefficient of variation = 40.02).

Body Size

Males observed defending territories ranged in size from around 30 mm to larger than 50 mm. A total of 27 small males (< 40 mm), 46 medium males (40-50 mm), and 38 large males (> 50 mm) were observed defending territories. Large and medium males defended significantly larger territories than small males (F(2,111) = 11.9, P < 0.0001) (Figure 2.1). No significant differences were found among male size categories for the number of females entering a male's territory (F(2,111) = 0.16, P = 0.85) (Figure 2.2), the probability of a female spawning (F(2,94) = 0.16, P = 0.85), the number of females spawning (F(2,68) = 0.86, P = 0.86), the number of eggs fertilized by a male (F(2,111) = 0.33, P = 0.72), or the number of eggs spawned per female (F(2,68) = 1.76, P = 0.36).

Coloration

No fish defending a territory was ever scored as a zero coloration, and thus coloration varied from 1 to 3 (See Table 2.1). Coloration among males of the three body size categories was not significantly different (Chi-Square; n=111, df=4, χ^2=2.72). Territory diameters were also not significantly different for the three color categories (F(2,111) = 2.75, P = 0.14) (Figure 2.3). The number of females entering a males territory (F(2,111) = 0.35, P = 0.71), the number of eggs a male fertilized (F(2,111) = 0.14, P = 0.87), the number of females spawning (F(2,68) = 0.76, P = 0.92), and the number of eggs deposited per female (F(2,68) = 0.45, P = 0.98) were not significantly different among the three coloration categories.

Territory Size

Territories ranged in diameter from 30-60 cm. Overall, the median territory diameter was

50 cm. Males defending territories with diameters of 60 cm fertilized significantly more eggs (F(2,111) = 4.5, P = 0.01), and received significantly more eggs per female (F(2,68) = 8.22, P = 0.0002) than males defending all smaller territories (Figures 2.4 and 2.5). Males defending 60 cm territories had significantly more females enter their territories (F(2,111) = 3.27, P = 0.048) (figure 2.6), and had a reduced probability of having no females visit during the 20-min observation period (Chi-Square; n=111, df=3, χ^2=7.46). The relationship between territory diameter and the number of females with which a male mated was not significant (F(2,68) = 0.31, P = 0.98) (figure 4). The relationship between territory diameter and a the probability of a female spawning (F(2,95) = 1.62, P = 0.38).

Female Observations

A total of 38 females were observed. Eleven of the females (29%) did not spawn during the observation period despite entering multiple territories (range 2-5; mean 2.7). Females rarely approached males and either swam away or dropped motionless to the substrate when males approached rapidly. Females typically swam slowly with their ventral surface near the substrate. Females often sat motionless on the bottom when males were not courting or chasing then. Occasionally the female would appear to locate an oviposition site before the territory owner was aware of her presence. In these cases, the female would nip the substrate, assume a spawning posture, and wait motionless for a male to join her. She usually was joined by a male within 15 seconds, but two females waited for nearly two minutes. In one of these cases the female was joined by a neighboring male, and she deposited two eggs with this male before the territory owner became aware of their presence and drove the intruding male back to his own territory. The female also left the area after this attack.

Twenty-seven females (71%) spawned during the observation period. Eight (30%) of these spawned in the first territory where they were observed and then left without further mating. Nineteen (70%) traveled through multiple territories (range 2-4; mean 2.8) and were courted by multiple males before spawning. Three of these latter nineteen (16%) re-visited one of the males in the series, and only one of these mated with the re-visited male. In that observation, the female visited three males, all of which were of the largest size category and of the brightest coloration category. After visiting the third, this female swam back to the second male and proceeded to spawn with him. After spawning three times, the pair was interrupted by male number three and the female fled the area immediately. The other two females re-visited the first male after leaving the third male's territory. However, these females did not spawn with the first male but rather continued on to a fourth male (previously unvisited) where they did mate. In these two cases the fourth male was not the biggest or brightest male visited in the series. The frequency of re-visits could have been higher than estimated, depending on which males had been visited prior to the observation period. Six of the nineteen fish that visited multiple territories (32%) spawned with more than one male (5 females spawned with 2 males; 1 female spawned with four males). In the 35 spawning events; 8 females visited only one male and twenty seven visited multiple males. Thirty two spawning events (91%) ended due to spawning interruptions by neighboring territorial males. Females that entered multiple territories did not bias their matings to the largest or brightest male(s) (Table 2.2).

Discussion

There is no evidence that females in this study preferred to mate with brightly colored or larger males. First, neither the size of the male nor his coloration was related to the total number of eggs he received, the total number of females spawning with him, or the average number of eggs spawned on his territory per female. Second, the probability of females mating once they had entered a male's territory was not related to the male's color or size. In addition, my observations of females also indicate that they were not discriminating based on size or color. Although females were observed to enter multiple territories (range 1-4) before mating (possibly suggesting active comparison), they did not consistently choose the largest or brightest male in the series of males they visited (table 2.2). These data support the view that females are not choosing males based on their color or their body size.

Body size was important in competition for territory space, as larger males defended larger territories (figure 2.1), but the relationship between coloration and territory size was not significant (figure 2.3). Territory size was not related to the number of females that spawned in them, or to the probability that females would spawn once they had entered a territory. However, males defending the largest territories did fertilize significantly more eggs than males with smaller territories (figure 2.4). Thus, large territories were advantageous to males because females deposited more eggs per visit (figure 2.5).

At least two models (not mutually exclusive) can explain the increased eggs per female in larger territories, one supporting female choice and the other supporting male-male competition. In the 'Female Choice' model, females mate with several males each day, but actively choose to leave more eggs in larger territories. In the 'Male Competition' model, females spawn with all males, but some aspect of male competition limits their reproduction in small territories.

Although females often mated with more than one male per day (6 of 19 females in this study; 32%), it was rare for females to end spawning on their own accord. For example, 87% of the observed spawning events were interrupted by neighboring males, and invariably these interruptions caused the female to cease depositing eggs and to leave the territory. The female's spawning behavior may have contributed to the frequency of these interruptions. Females move forward as they spawn, depositing their eggs several inches from one another. Consequently, a female's path during the spawning sequence often takes her out of the male's territory (Itzkowitz 1974; Draud pers. obs.). Itzkowitz (1974) estimated that pairs were most often interrupted within approximately 7 cm of the territory border. The closer pairs are to the neighboring male, the higher their probability of being detected. Perhaps, larger territories provide more area outside of this "high-risk" zone, so that females mating in larger territories are either more likely to complete their spawning and leave of their own accord, or spawn more eggs before moving into areas that attract a neighboring male's attention. The latter seems more likely, since the probability of spawning interference was not related to territory size. Thus it appears that female pupfish do not actively choose to leave more eggs in large territories, but rather do so as the passive result of reduced male-male interference competition.

Interruptions by neighboring males frequently caused the termination of spawning sequences in another study of *C. variegatus* (Itzkowitz 1974), and in a study of *C. atrorus*, where approximately fifty percent of females failed to complete spawning as a result of interruption (Itzkowitz 1968). Courtship interruptions are also common in sticklebacks (Van Den Assem 1967; Sargent 1982), leading the authors to speculate that larger territories (Van Den Assem 1967) or more concealed nest sites (Sargent 1982) result in lower male interference and higher male RS.

This interference behavior clearly curtails the reproduction of neighbors and therefore potentially leaves more eggs for the disrupter. Trail (1985) showed that territorial neighbors were responsible for terminating about one third of courtship visits and one third of all matings of the lek-breeding cock of the rock (Cotingidae: *Rupicola rupicola*), effectively re-directing the 'mate choice' of the female. Persistent disruptors benefited since they received a significantly disproportionate percentage of the re-directed matings. Similarly, it is not uncommon for pupfish interrupters to subsequently spawn with the female they had just disrupted (Itzkowitz 1974; Draud pers. obs.).

Thus, the evidence in this study suggests that intrasexual male competition is largely responsible for male reproductive success, and suggests that females may be mating randomly. Other evidence also corroborates the 'random mating' model. If females are entering territories independently of the males or their territory borders, the probability of entering a given territory increases with increasing territory size. Consistant with this hypothesis, the total number of females entering a territory was significantly positively related to territory size (figure 2.6), suggesting that females were swimming randomly through the area. Weatherhead and Lightbody (1987, 1988) found a similar pattern in yellow-winged blackbirds, where females settled at random and males with larger territories secured more mating opportunities.

It is interesting that while larger males defended significantly larger territories (figure 2.1), and larger territories had significantly more females entering the territory (figure 2.6), that the relationship between body size and the number of females entering the territory was not significant (figure 2.2). This is most likely due to the weak relationship between territory size and the number of females entering, combined with the fact that only three body size categories were used. Perhaps if the exact body sizes were known, a relationship between body size and the number of females entering would emerge.

Females have ample opportunity to exert a mating preference in *C. variegatus* (*sensu* West-Eberhard et al. 1987). First, females range widely, often covering distances that encompass many male territories, affording them the opportunity to compare males.

Second, there is a prolonged breeding season, making time constraints negligible, and third, females can not be forced to mate by males. However, females can easily be forced to end spawning by male interference. Quite possibly, male-male competition, in the form of spawning interference, overpowers any expression of female mate choice in this species. Since courtship and spawning interruptions were not reported in *C. pecosensis* (Kodric-Brown 1977, 1978, 1983), perhaps this explains why female mate choice is important in this species.

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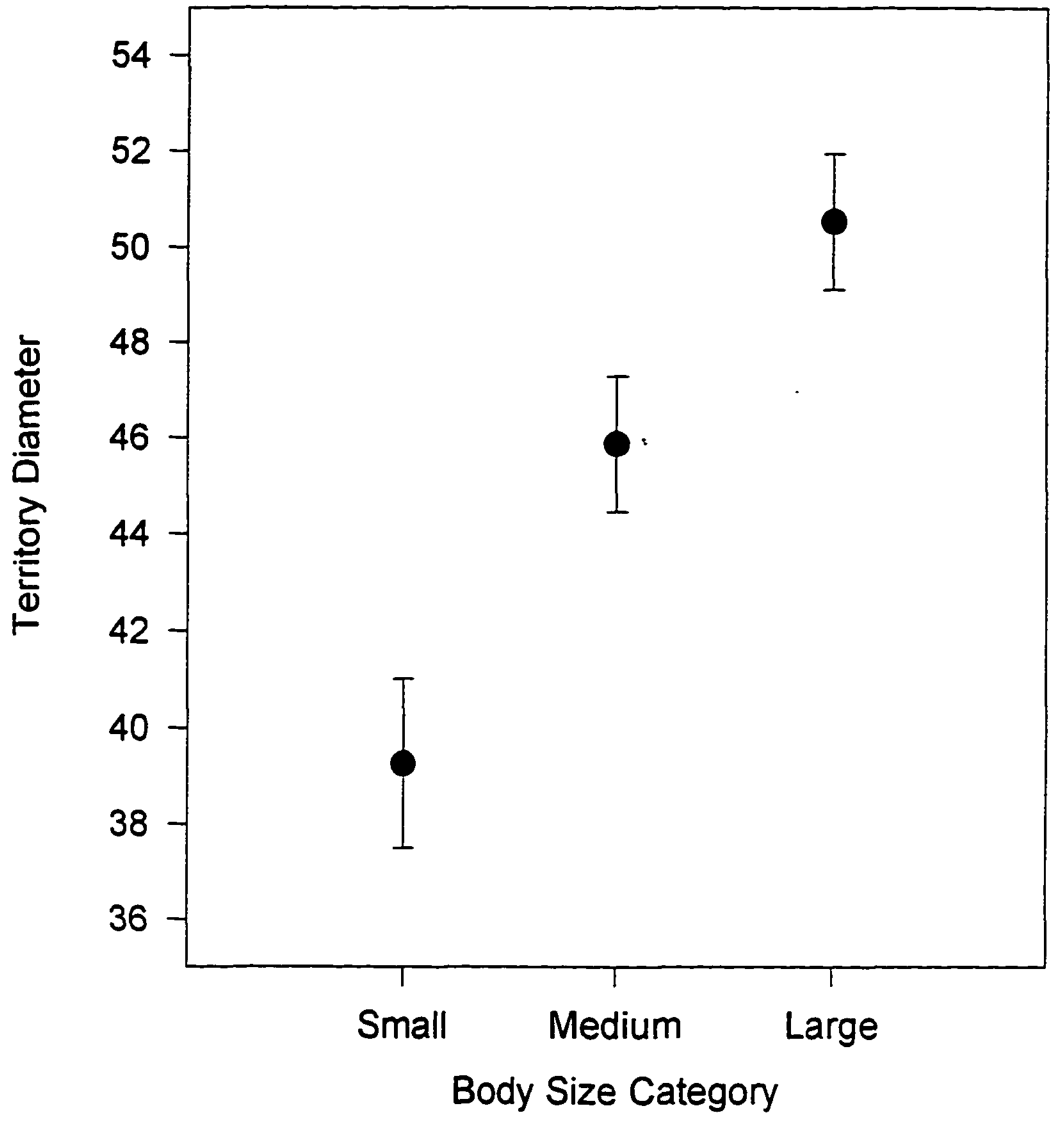

Figure 2.1. Mean territory diameter with standard error bars for the three size categories. (F(2,111) = 11.9, P < 0.0001)

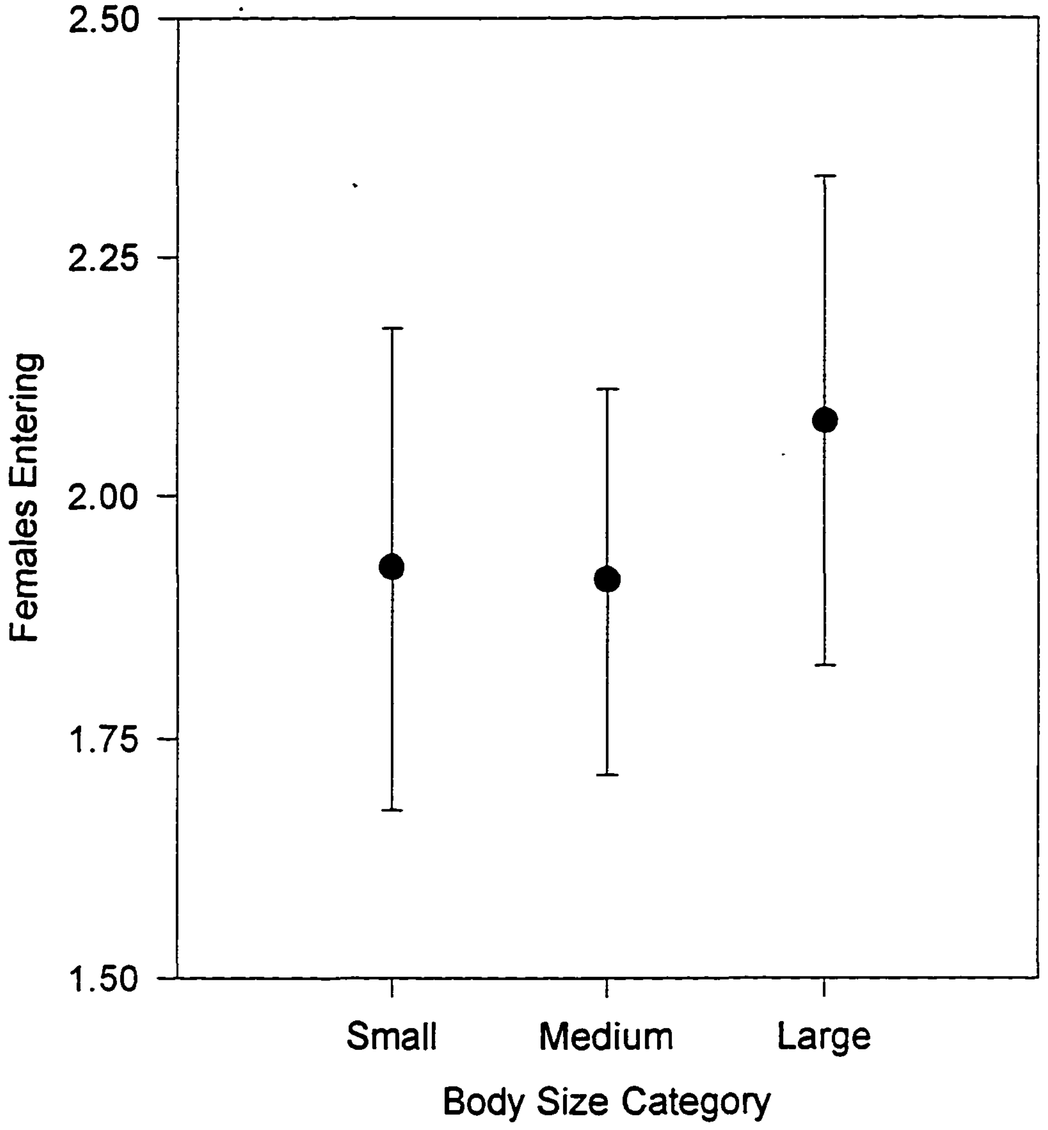

Figure 2.2. Mean number of females entering with standard error bars for the three body size categories. (F(2,111) = 0.16, P < 0.85)

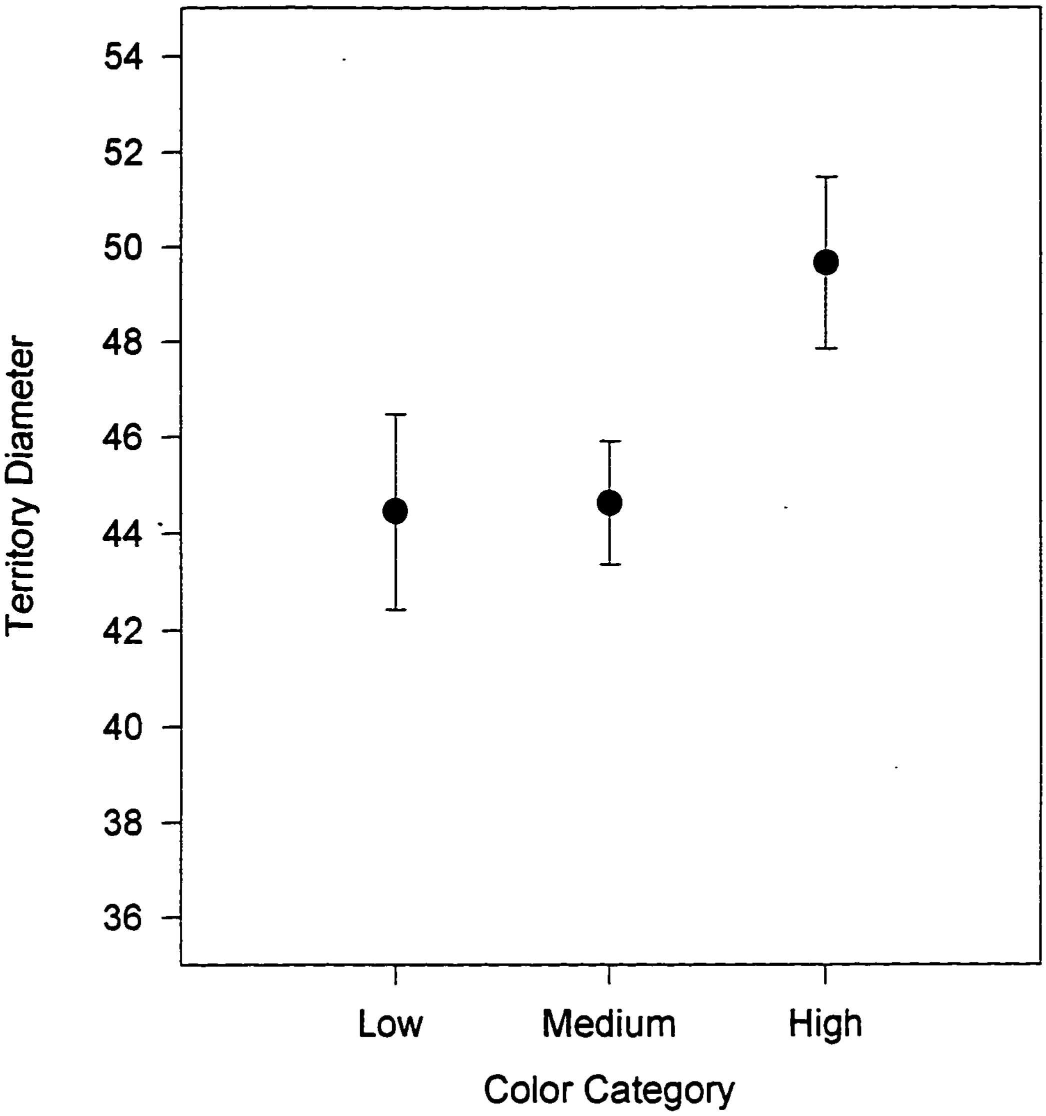

Figure 2.3. Mean territory diameter with standard error bars for the three color categories. (F(2,111) = 2.75, P < 0.14)

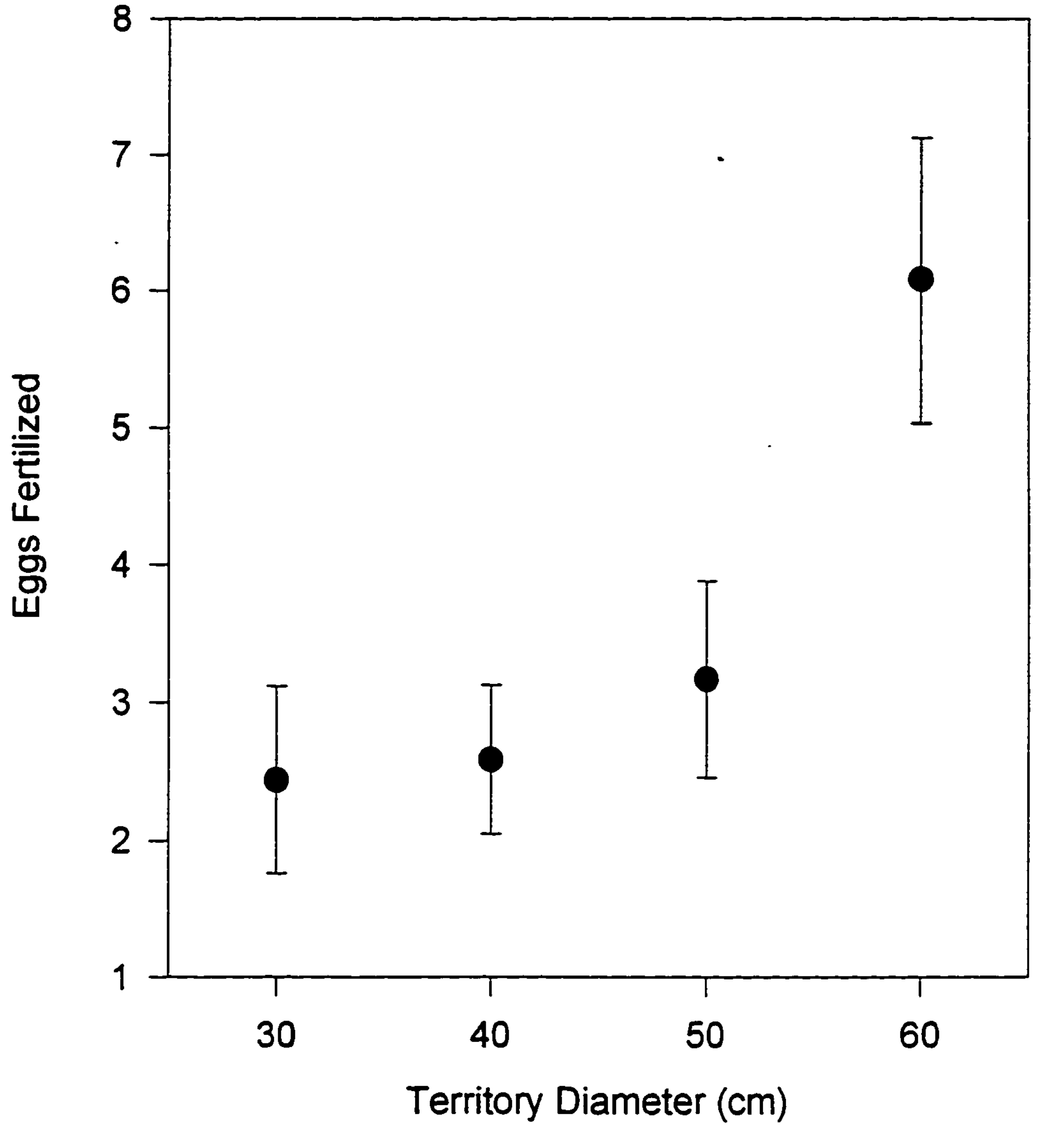

Figure 2.4. Mean number (+/- standard error) of eggs fertilized during the twenty minute observation period for males defending four territory diameter categories.(F(2,111) = 4.5, P < 0.01)

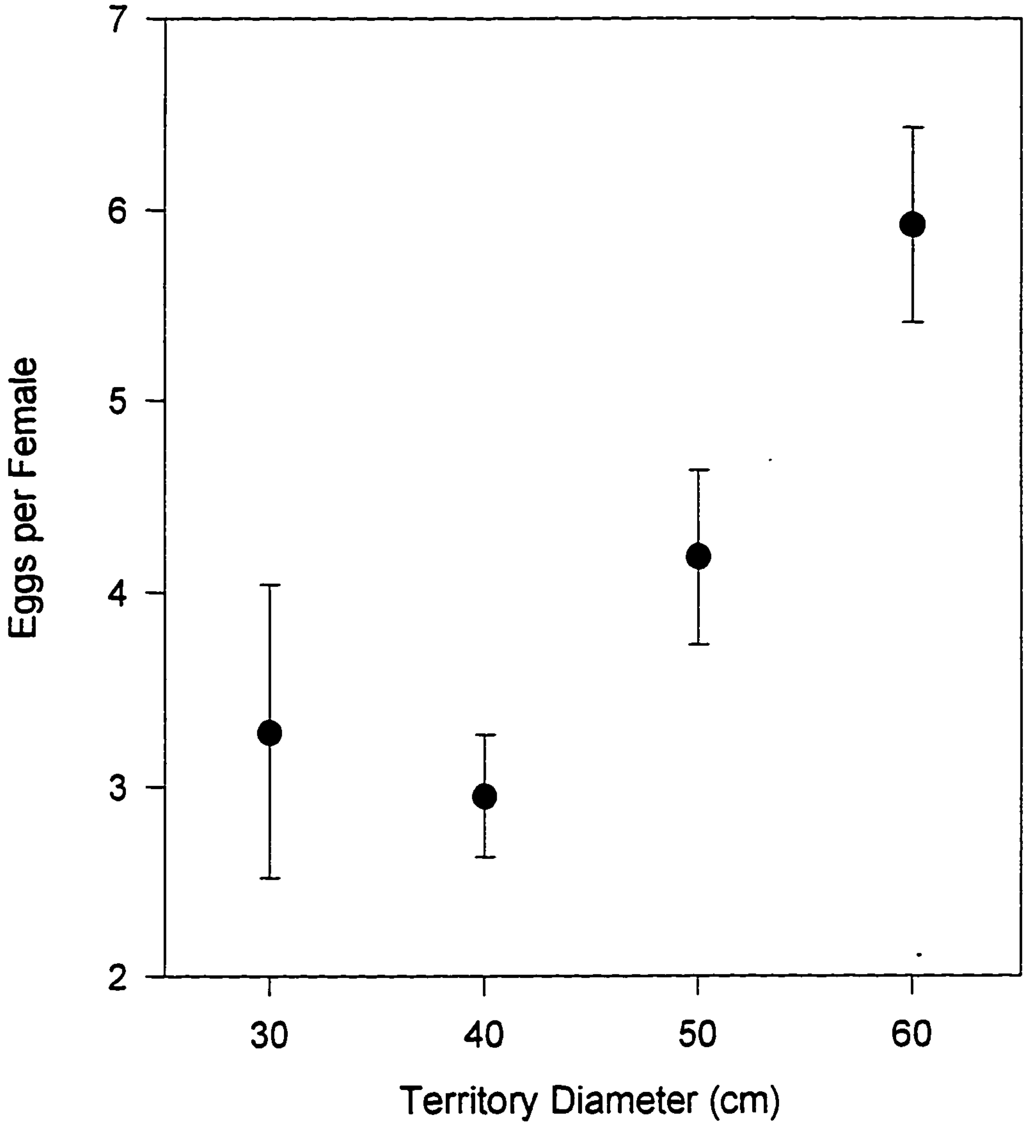

Figure 2.5. Mean number (+/- standard error) of eggs per female left in territories of different diameters. (F(2,68) = 8.22, P < 0.0002)

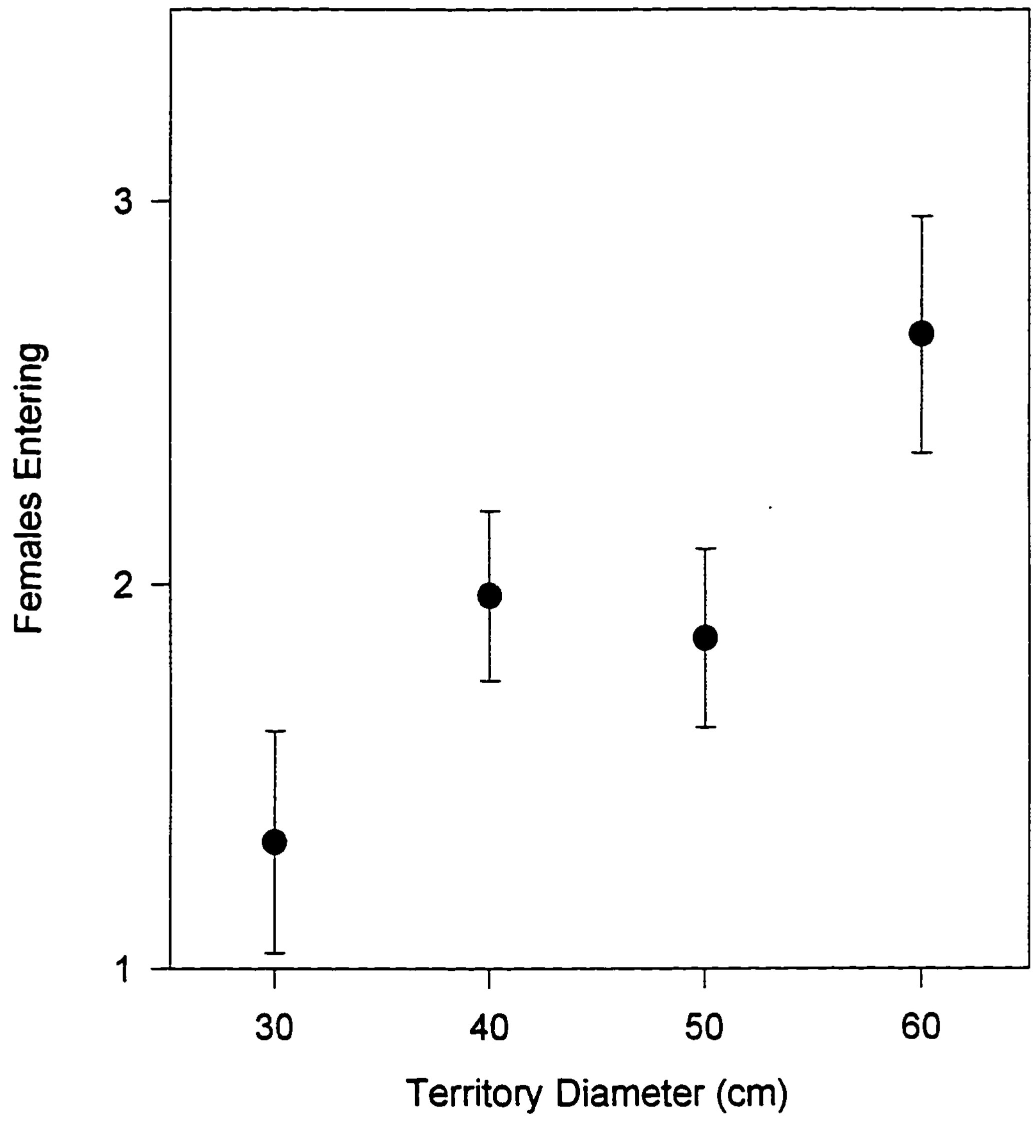

Figure 2.6. Mean number (+/- standard error) of females entering a male's territory for the four territory diameter categories. (F(2,111) = 3.27, P < 0.048)

Color Category	Description of Body Color
0	No color present. Silvery in appearance.
1	Blue color present on anterio-dorsal surface. Body silvery with dark vertical bars.
2	Blue color present on anterio-dorsal surface. Body uniform grey with dorsal and caudal fin bars.
3	Blue color present on anterio-dorsal surface. Body milky in appearance with dorsal, caudal, and suborbital bars. Rusty color present on ventrum.

Table 2.1. Definitions of the color categories used in this study.

		Small / Low Color	Medium Size & Color	Large / High Color	Total
Color	Spawns	9	8	10	27
	Eggs	30	23	25	78
Size	Spawns	8	11	8	27
	Eggs	20	33	25	78

Table 2.2. The number of spawning events and eggs allocated by females that visited multiple males to relative male phenotypes.

Chapter 3

Female choice and male-male competition in the pupfish, *Cyprinodon variegatus*: Are small males at a disadvantage?

Introduction

Reproductive success is typically more variable for males than females, apparently as a direct consequence of male-male competition and/or female mate choice (Clutton-Brock 1988; Andersson 1994). A major contribution to male reproductive variation is the failure of small sexually mature males to mate due to competition with larger males. This is especially evident in species that continue to grow after the onset of sexual maturity, because competitive ability usually increases with size. Therefore small males are often at a marked disadvantage in direct competition for mates (e.g., LeBoeuf 1974) or for critical resources needed for obtaining mates (e.g., Kodric-Brown 1986; Mathis 1991). Small males may also be discriminated against by females. Female mate choice is expected to evolve if the variation in male body size affects female fitness in a predictable fashion. For example, female sculpins prefer large males because they protect their eggs better than small males (Downhower and Brown 1980). Females may also prefer large males because they have demonstrated "good genes" by surviving to a given size (e.g., Cooper and Vitt 1993).

While field studies are useful in indicating whether small males have lower reproductive success, it is often difficult to determine whether this is generated by male-male competition or female choice or both (Andersson 1994). For this reason, laboratory studies have been designed to separate the affects of male body size on competitive ability and female mating preferences (e.g., Mathis 1991). In some cases, laboratory results have indicated female preference for a character that is not important in the field. For example, Hastings (1988) showed that angel blenny females preferred large males in laboratory studies, but male body size was not strongly correlated to reproductive success in the field. Basolo (1990) showed that female platy fish showed a mating preference for a sword, even though males of this species do not have one. These findings indicate that considerable care must be used in interpreting laboratory results.

In this paper I use laboratory experiments to determine the affects of male body size on intra-sexual competition and female choice in the pupfish, *Cyprinodon variegatus*. This species has a resource-defense polygynous social system. Males defend territories throughout the summer months, and females visit them daily to spawn. Females leave shortly after spawning and there is no direct paternal care for the eggs. Little is known of the importance of male body size in intra-sexual competition in this species, but field studies suggest that the smallest sexually mature males rarely defend territories and that territory size is positively correlated to male size. Therefore, I hypothesized that when introduced into a neutral "arena", that larger males would always defeat smaller males, and that larger "intruder" males would takeover the territories of smaller males who had prior-residence for 24 or 72 hours (e.g., Maynard Smith and Parker 1976; Hammerstein 1981).

A field study (Draud in prep) and a laboratory experiment (Itzkowitz 1978) indicate that females of this species mate at random, but there has never been a direct test of female choice for male body size. I predicted that females which were offered only one male, would spawn the same number of eggs regardless of the size of that male. (Non-choice experiment). I also predicted that females who were offered a choice between a large and small male would spawn equal numbers of eggs with both. (Choice experiment).

Methods

All fish used in these experiments were collected from pannes on Nummy Island, Stone Harbor, New Jersey. Fish were transported to the lab in large coolers and transferred to 70 gallon stock tanks which had no sand covering the glass bottom (to discourage spawning). Salinity was maintained at 20-25 ppt in all stock tanks and in experimental tanks. Fish were fed frozen *Artemia sp.* and various vegetarian flake foods four times per day to satiation.

Male-Male Territory Competition

The first set of experiments was designed to determine if body size was critical to the outcome of competition for territory space in a neutral arena. Two males and three females were netted from stock tanks and simultaneously placed into a 10 gallon aquarium (dimensions) with fine sand substrate and a small bubble filter. The males were either approximately equal length (within 3 mm) or differed in length by 15-20%. They were allowed to compete for territory space for twenty four hours, but were observed every two hours to determine the outcome of the competition. The first experiment used only small males (25-35 mm) and the second experiment used large males (45-55 mm).

The second set of experiments was designed to test the affect of a 24 or a 72 hour prior residency on the ability to defend a territory. The first experiment used small males as residents (25-35 mm) and the second experiment used large males as residents (45-55 mm). Ten gallon aquaria (dimensions) were used for both experiments. .

Two males and three females were placed in an aquarium and the males were allowed to compete for territory space for 24 hours. After this time period, the male who had lost was removed, and the three females remained with the winner. The winner (now the resident) was then allowed to interact with the females for either an additional 24 or 72 hours. After this time period, an intruder male was added who was either 15-20 % shorter (n=12), 15-20 % longer (n=12), or approximately the same length (< 5% different) (n=12) as the winner male. These two males were allowed to compete for twenty four hours and the victor was determined.

Female Mating Preferences

Non-Choice

This experiment was designed to determine if females will spawn with small males (24-34 mm) in the absence of a choice and further to see whether small males can fertilize eggs. Thirty males, ranging in size from 25-53 mm, with blue dorsal coloration (a good indication of sexual maturity) were chosen from bi-sexual stock tanks. In the evening prior to data collection, each male was placed in a 10 gallon aquarium (dimensions) with fine sand substrate (diameter < .5 mm) and a small bubble filter. Each male was fed *Artemia sp.* 30 minutes prior to lights-off. The following morning, three females (35-40 mm) were placed in each males aquaria. The four fish were allowed to interact for four hours, and then all fish were removed and returned to stock tanks. All of the sand from each tank was siphoned and passed through a sieve (pore diameter = .8 mm). This process allowed sand to pass through the sieve but the eggs were retained. Eggs were counted and gently transferred to a large petri-dish and examined periodically under dissection scope to determine if they were fertilized.

Choice

This experiment was designed to test the affects of relative male body size on female spawning preferences. To reduce the potential for intrasexual male competition influencing spawning choices, males were not permitted to physically interact. This was accomplished by tethering the males to the two ends of the aquaria (Figure 3.1). I inserted a small-diameter heat-sterilized hypodermic needle through the dorsal musculature of each male, and passed a length of fine monofilament line through the needle. The needle was removed and the two ends of the line were melted together using a hot metal object, to create a harness on each fish. This procedure took less than 3 minutes and was done with the fish wrapped in a wet paper towel to prevent scraping of scales and loss of mucous. Immediately following this surgery, the fish was placed into a one gallon container of water with a bubble stone. Fish coped very well with the stress of this surgical procedure as they typically fed within 30-60 minutes post-procedure. Harnesses were placed in a total of 36 males ranging in size from 35 mm to 55 mm. One fish died immediately after the surgical procedure, but the other 35 appeared to recover normally and survived past the end of the experiment.

Two plastic rulers were placed on the top of a 20 gallon tank, approximately 3 cm from the end. A 10 cm length of monofilament line was tied to the middle of each ruler and a small swivel was attached to the other end. A second length of monofilament (25 cm) had a small snap-swivel attached to one end and a small loop tied in the other end. The loop end was passed through the fish's harness and then the snap-swivel was passed through the loop. The snap-swivel was then attached to the swivel on the 10 cm suspended line to complete the tethering of the fish to the ruler.

Two males, either differing in length by 15-20 % (experimental group: n=8) or approximately the same length (within 5%) (control group: n=8) were placed together in an aquarium, each tethered to one side (sides chosen at random). Males were allowed to acclimate for 60 minutes. After acclimation, three females were added and were allowed to spawn with both males for two hours. The females were then removed, and the males remained. The sand was then sifted through a sieve, one half at a time, and the eggs deposited on each side were counted. The sifted sand was then returned to the tank and the following day three new females were allowed to spawn for two hours with the same two males. The males were then removed, their harnesses carefully cut away and they were returned to stock tanks. Each male was used only once. Again the sand from each side was sifted and eggs counted. The eggs collected on both days were combined for statistical comparisons.

Results

Male-Male Competition

Neutral Arena

Small Males

In this size category, larger males were always victorious and defended all of the available space. The outcomes of these staged fights were determined in less than 6 hours in all replicates. Eight of twelve replicates of the control condition had no victor, but rather both males successfully defended part of the available area, generally about 50%.

Large Males

In this size category, larger males always won and successfully defended all of the available space. In the control condition, only 3 of 12 replicates had shared ownership of the available area, and the other 9 had a single victorious male. This proportion is not significantly different from the small males (Fisher's Exact, n=12, p=0.0995).

Prior Residence

Small Resident

Residents always defeated intruders that were smaller or approximately the same size as themselves, regardless of the length of residency. Intruders were never capable of usurping any space. When intruders were larger than the resident, residents lost their territories every time regardless of the time of residency.

Large Resident

Residents always defeated intruders that were smaller or approximately the same size as themselves, regardless of the length of residency. Again, no intruders were able to usurp any space. Nine of 12 large residents lost to larger intruders with 48 hour prior residence. This proportion is not significantly different from the small males (Fisher's Exact, n=12, p=0.1087). However, only 2/12 residents lost to larger intruders with 72 hour prior residence. This proportion was significantly different from small residents (Fisher's Exact, n=12, p<0.0001).

Mating Preferences

No Choice

Females mated with males of all sizes. The correlation between male body size and total eggs fertilized was not significant (Correlation analysis: r = .1405; n = 30; p = 0.46) (Figure 3.2). All collected eggs were fertilized.

Choice

When offered a choice of a large and small male, females spawned more eggs with the larger male (ANOVA; F=11.86; p = .0039). When the two males were of approximately equal size, females spawned approximately the same number of eggs with both males (ANOVA; F=0.29; p=0.6032) (Figure 3.3).

Discussion

These laboratory experiments show that relative body size is important in male-male competition for territory space in *C. variegatus*. In a neutral arena, the larger of two males always won staged fights. The hypothesis that prior residence would not overcome the advantage of body size was partially supported. Small male residents always lost to larger intruders, regardless of the duration of prior residence. However, large male residents were occasionally able (3/12) to defend their territories against larger intruders after a 24 hour residence, and were often able to do so after 72 hours (10/12). Thus rather than an absolute rule for size and prior residence, there seems to be a relative rule. That is, size differences appear more important to small resident males than to large resident males. One possibility is that experience may play an important role in territory defense, as larger males presumably have more experience competing for and defending territories.

Prior residence was also important in competition with similar sized intruders. In neutral arenas, males of approximately the same size often shared the available space, but when one male had a prior residence, intruder males of approximately equal size were never successful in usurping even some of the territory. This was true for small and large residents, suggesting that prior residence is valuable in territory defense.

The prediction that females would mate randomly with respect to male body size was supported in the non-choice experiment, but not supported in the choice experiment.

When offered only one male, females spawned about the same number of eggs with all size males (Figure 3-2). This experiment demonstrates that small males are fully capable of spawning and fertilizing eggs. However, when offered a choice of a small and a large male, females spawned significantly more eggs with larger males (Figure 3-3). This is surprising since field and lab studies suggested that female *C. variegatus* mate at random (Draud in prep; Itzkowitz 1978). Perhaps when all other factors are held constant (i.e., territory size, prior residence, male-male competition, etc) as in this highly controlled experimental design, female discrimination becomes apparent. Under natural conditions however, female choice may be masked by intense male-male interference (e.g., Cox 1981). Intra-sexual interference can be strong in this species, as most spawning events observed in the field (87 %) ended due to interruptions by neighboring territorial males (Draud in review). Since active mate choice is likely to bear a cost (Pomiankowski 1987), when male-male interference is strong females may relax their preference and allow intra-sexual competition to determine the "most fit" mate.

Female mate choice may become more important with reduced male-male competition. Master (1989) has shown that wading birds can severely decrease the population density of *C. variegatus* in the panne habitats of southern New Jersey salt marshes. Intra-sexual competition may be reduced at low population densities, and under these conditions perhaps females do discriminate against smaller males. In other species, female mating preferences are known to be sensitive to environmental factors such as interspecific interference competition (e.g., McClain 1981) and predation risk (e.g., Hedrick and Dill

1993; Godin and Briggs 1996).

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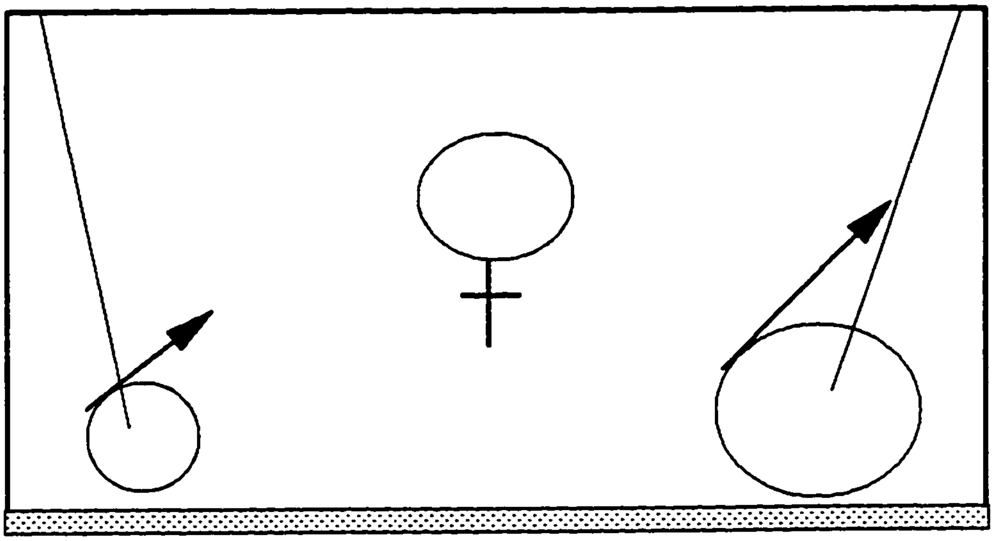

Figure 3.1. Illustration of the experimental design for the female choice experiment.

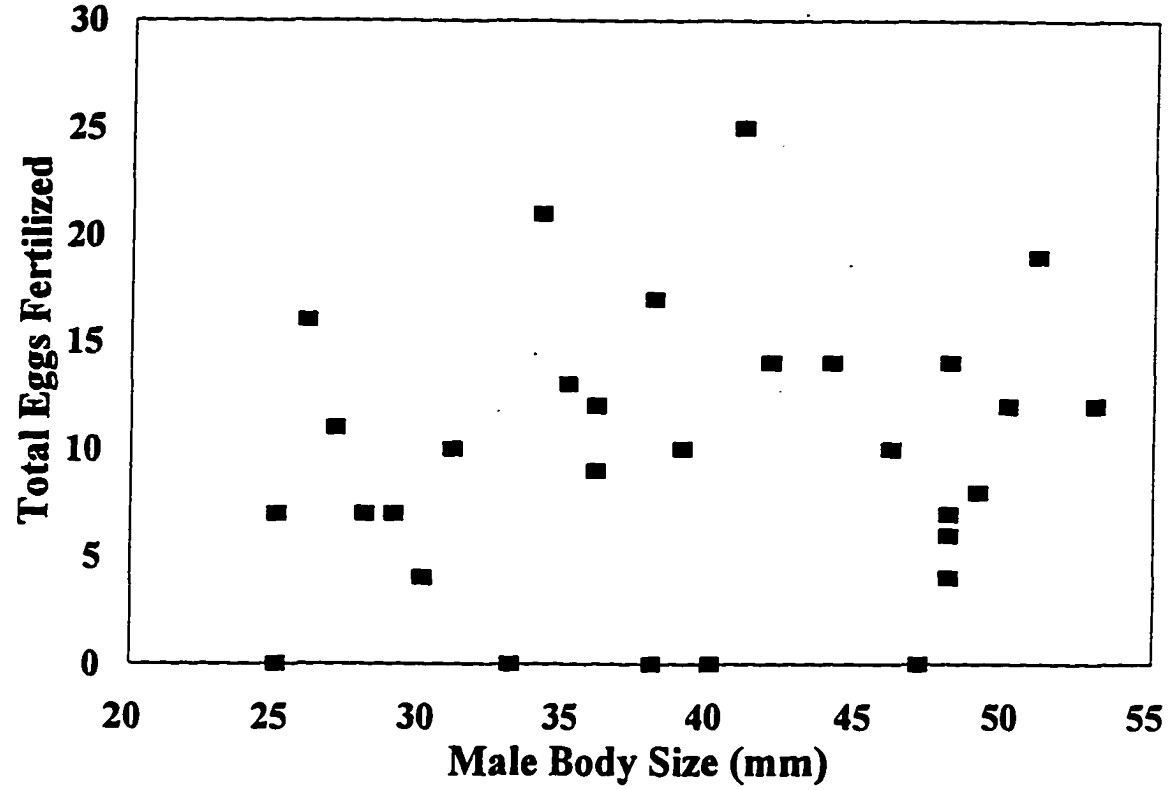

Figure 3.2. Results of the Non-choice experiment. Total eggs fertilized in four hours by males of different size. (Correlation analysis: r = .1405; n = 30; p = 0.46)

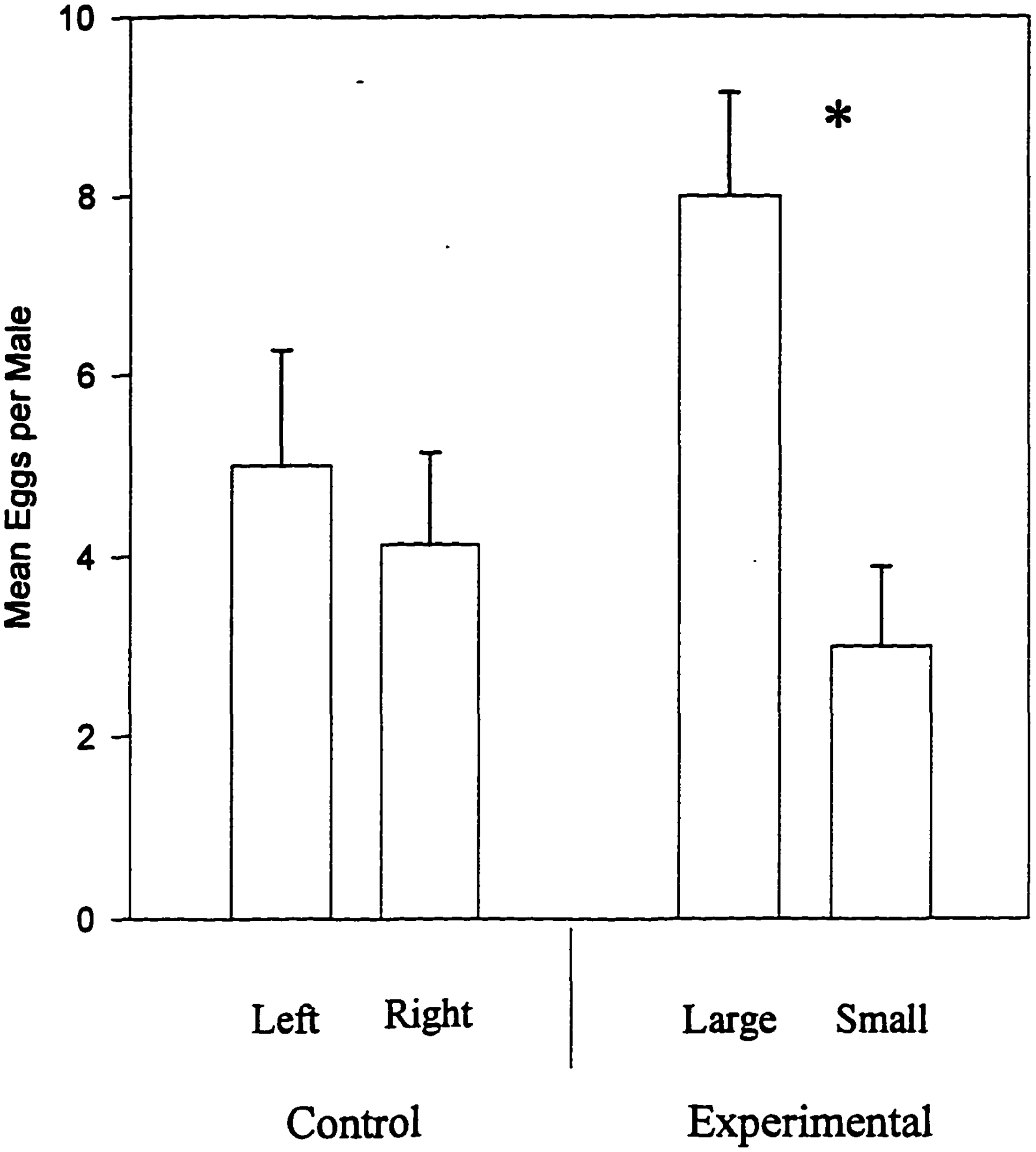

Figure 3.3. Results of the Choice experiment. Bars represent the mean number of eggs (+/- standard error) received by each category of males. Astericks represent significant difference. (Experimentals: ANOVA; F=11.86; p = .0039) (Controls: ANOVA; F=0.29; p=0.6032)

Chapter 4

Body size and the mating success of male and female pupfish.

INTRODUCTION

In resource-defense polygynous animals, females typically invest more in their offspring than males, leading to a basic difference in the reproductive strategies of the two sexes (Bateman 1948; Trivers 1972). Males tend to maximize reproductive success by increasing the number of matings, while females maximize reproductive success by increasing the quality of their mates. To maximize the number of mates, males must compete amongst themselves for access to a finite pool of females (or the resources needed to attract the females). The most ubiquitous male feature that determines competitive ability is body size, and thus it is not surprising that research on many different taxa has shown that small males are often unable to effectively compete against larger males for access to females (e.g., *insects* Severinghaus, Kurtak, and Eickwort 1981; *fish* Downhower and Brown 1980; Kodric-Brown 1986; *frogs* Wells 1977; Howard 1978, 1984; *salamanders* Mathis 1991; Verrell 1991; *lizards* Cooper and Vitt 1987). In addition, in some species females directly discriminate against small males (e.g., *insects* Simmons 1986; *fish* Downhower and Brown 1980; Bisazza and Marconato 1988; Cote and Hunte 1989; *frogs* Woodward 1982; Morris and Yoon 1989; *salamanders* Mathis 1991; *lizards* Cooper and Vitt 1993). Thus, intra-sexual competition and female choice often enable large males to secure a disproportionately high amount of the total matings, while causing small males to mate less frequently or not at all.

On the other hand, since males are typically not limited to the number of females with which they can mate, females are not expected to compete amongst themselves for access to males. Further, since males tend to maximize the quantity rather than quality of mates, they are expected to be less choosy than females. Therefore, theory predicts that body size should not affect the ability of females to mate as it does males. However, few empirical studies have explicitly tested this prediction, and in fact some studies suggest that males may be more selective than previously thought (e.g., Sargent et al. 1986; Cote and Hunte 1989; Van den Berghe and Warner 1989). Since fecundity often increases with increasing body size, males may be selected to prefer larger females when faced with a simultaneous choice or when they are limited to the number of females with which they can mate (Sargent et al. 1986).

In this paper, I examine the significance of body size in the mating success of male and female pupfish, *Cyprinodon* variegatus, at a field site in southern coastal New Jersey. Pupfish reside in shallow marsh pools called "pannes" in this portion of their range. I predicted that body size would be an important component to male mating ability but not female mating ability. Specifically, I hypothesized that the smallest sexually mature males would be under-represented in the breeding population of males, but that the smallest sexually mature females would be as likely to mate as larger females.

The social system is resource-defense polygyny, with males defending territories that incorporate oviposition sites and females depositing eggs only within these bounds. Females leave the territory after spawning, and although the male continues to defend the area against conspecific and heterospecific egg predators, there is no direct paternal care of the eggs. The breeding season is prolonged and females often breed with more than one male per day and probably breed multiple days in a season. Non-territorial males, females, and juveniles remain in schools and are found in the same pannes as the territorial males.

METHODS

Study Sites:

Data were collected during the summer of 1992. The study sites were located in the Marmora Marsh Wildlife Management Area, near the town of Stone Harbor, in southern New Jersey. The marsh in this area is dominated by salt marsh cordgrass (*Spartina alterniflora*) and there are numerous tidal creeks and salt marsh pannes throughout the area. Pannes are isolated pools of salt water located in the salt marsh.

These pannes vary considerably in circumference (from < 1 m2 to > 50,000 m2) and depth (from < 2 cm to > 1.5 m) as well as shape and morphology. Master (1989) defined two basic panne morphotypes; overhang and non-overhang. Overhang pannes have precipitous sides around the entire perimeter, while non-overhang pannes have gradually sloping sides. They are inundated with salt water only during full moon flood tides, and they receive fresh water from time to time from rain storms. Because they are isolated from tidal influence through most of the month and because they are relatively shallow areas, the pannes fluctuate widely in temperature, salinity, dissolved oxygen and water level.

I observed and collected pupfish from 8 pannes from June to August, 1992. Three of these pannes were randomly chosen for behavioral observations, and the remaining five pannes were used solely for collecting animals for measurement and sex determination. Even though these pannes are isolated from one another during most of the month, Master (1989) has shown that pupfish commonly move between pannes on the monthly full moon flood tide.

Fish Collections

I collected fish with seine and dip nets about twice per month from June through August. The seine and dip nets had 0.125 inch mesh. Each seine haul was done parallel to the shoreline with one end of the seine at the water's edge and ranged from 3-8 m in distance. Dip nets were used as well to catch fish that were hiding under the precipitous sides of the pannes. Live fish were separated visually based on color and morphology into male, female, and unknown. The fish were then preserved in alcohol and the unknowns later dissected to determine maturation and sex. Fish from the three pannes were combined and treated as a single sample. All fish were measured to the nearest millimeter.

Territorial Pannes

Behavioral observations were done by approaching one of the five pannes slowly and sitting near the edge (less than 0.5m from the water). Several small rectangular pieces of white acrylic (6 cm x 2 cm) ("plastic rulers") were tossed at random into the immediate area in front of the observer. These pieces were marked off at 1 cm intervals on both sides and were attached to a length of monofilament line so that they could be moved and retrieved after the observation period. The fish were often startled by the approach, but quickly acclimated to the observer and usually returned to their normal activities within several minutes.

Males that returned to the immediate area and resumed territory defense were compared to the closest plexiglass ruler. They were then classified into four groups; <31 mm, 31-40 mm, 41-50 mm, > 50 mm. Females that were courted by males in the area of the rulers were also observed. Females that subsequently spawned were compared to the nearest ruler and classified into three groups; < 35 mm, 35-40 mm, > 40 mm. After all of the males in the area had been measured, the rulers were retrieved and the observer moved several meters (to prevent measuring the same individuals) and again tossed the rulers into the water.

Data Analysis

To test whether small males and females were under-represented in the breeding population, I compare the relative proportions of fish in each size category between the breeding population and the total population. I assume that if males and females are recruited to the breeding population at random, that the relative proportions should be very similar. If body size affects the ability of fish to enter the breeding population then the proportions will be significantly different. I use a Chi-Square Test for Goodness of Fit to test whether the relative proportions in the breeding population are significantly different from those of the total population.

Results

Sexually mature males ranged in total length from 22 - 55 mm, while sexually mature females ranged from 27-47 mm (Figure 4-1). All fish were sexually mature by 30 mm. There were a total of 455 sexually mature males collected by seine; 39 (9%) were less than 31 mm, 178 (39%) were between 31- 40 mm, 164 (36 %) were between 41-50 mm, and 74 (16 %) were greater than 50 mm. There were 126 territorial males observed, of which none (0 %) were smaller than 31 mm, 45 (20 %) were between 31-40 mm, 73 (44 %) were between 41-50 mm, and 55 were larger than 50 mm (36 %). Figure 4-2 shows the size distribution of sexually mature males in the field collections (referred to as "total population") and the territorial population. A Chi-Square Test for Goodness of Fit indicated that the observed frequencies of territorial males in the four size categories were significantly different from the expected frequencies from the total population samples (Chi-Square; df=3, χ^2=36.86, p < .005).

There were 501 sexually mature females; 167 (33 %) less than 35 mm, 175 (35 %) between 36-40 mm, and 159 (32 %) larger than 40 mm. I observed 113 females spawning in territories, of which 35 (31 %) were less than 35 mm, 40 (35 %) were between 36-40 mm, and 38 (34 %) were larger than 40 mm. Figure 4-3 shows the size distribution of sexually mature females in the collections (total population) and the females observed spawning. A Chi-Square Test for Goodness of Fit indicated that the observed frequencies of breeding females in the three size categories were not significantly different from the expected frequencies from the total population samples (Chi-Square; $df=2$, $\chi^2=0.26$, $p > .1$).

Discussion

The hypothesis that small males would be under-represented in the breeding population was strongly supported. First, the smallest sexually mature males (those less than 30 mm) were never observed defending territories. Second, males between 31-40 mm were twice as common in the total population as they were in the territorial population. Furthermore, males larger than 40 mm were relatively over-represented, especially those over 50 mm, which were more than twice as common in the territorial population as compared to the total population. (Figure 4-2). It seems likely that the under-representation of small males is due to competitive exclusion by larger males, since in the lab, in the absence of large males, small males (as small as 25 mm) have been shown to aggressively defend territories, court and spawn with females, and are fully capable of fertilizing eggs (Draud in prep). Thus, it appears that intra-sexual male competition eliminates the possibility of males reproducing as soon as they reach sexual maturity, and forces a reproductive delay.

The hypothesis that small females would be just as likely to spawn as large females was also strongly supported. First, the size range of sexually mature females collected in the field entirely overlaps the range of females observed spawning in male territories. Second, the percentages of females in each size category from the total population and from those observed spawning were remarkably similar (See Figure 4-3). These data support the prediction that body size is relatively insignificant to the ability of females to mate, suggesting that they do not actively compete amongst themselves for access to males and that males are not discriminating against small females. Thus, females reproduce as soon as they are sexually mature.

It remains unclear why males begin developing testes at 22 mm when they are unlikely to be able to defend territories until they are considerably larger. Theoretically, if males did not invest energy in gonads, they could invest more in somatic growth and thus attain a size sufficient to acquire and defend territories sooner. However, since the actual cost of producing and maintaining testes is unknown, it is possible that there is no substantial selective advantage to delay the onset of sexual maturity for males. Perhaps small males do mate in the field when larger males are absent, or population density is very low. Master (1989) has shown that wading birds, primarily the snowy egret (*Egretta thula*), can severely deplete *Cyprinodon* numbers in small pannes in New

Jersey. Other work has shown that *E. thula* prefer large fish when presented with a choice (Itzkowitz 1986). Perhaps in some pannes, overall population density, or the number of large males, is reduced enough to permit small males to defend territories and breed.

In other species of *Cyprinodon*, small males are also inferior competitors. However, in several species these small males adopt alternate reproductive tactics that allow them to side-step intra-sexual competition and achieve some reproductive success, albeit lower than the larger territorial males (*C. macularius;* Barlow 1961; *C. pecosensis;* Kodric-Brown 1986; *C. elegans*; Itzkowitz pers. com.). These size-dependent strategies were not observed in this study and have never been reported in *C. variegatus* (Raney et al. 1953; Itzkowitz 1974) In other species of *Cyprinodon*, the success and frequency of these opportunistic mating strategies are affected by ecological and social parameters such as habitat and population density (Kodric-Brown 1986). Perhaps small *C. variegatus* use alternative tactics under different field conditions.

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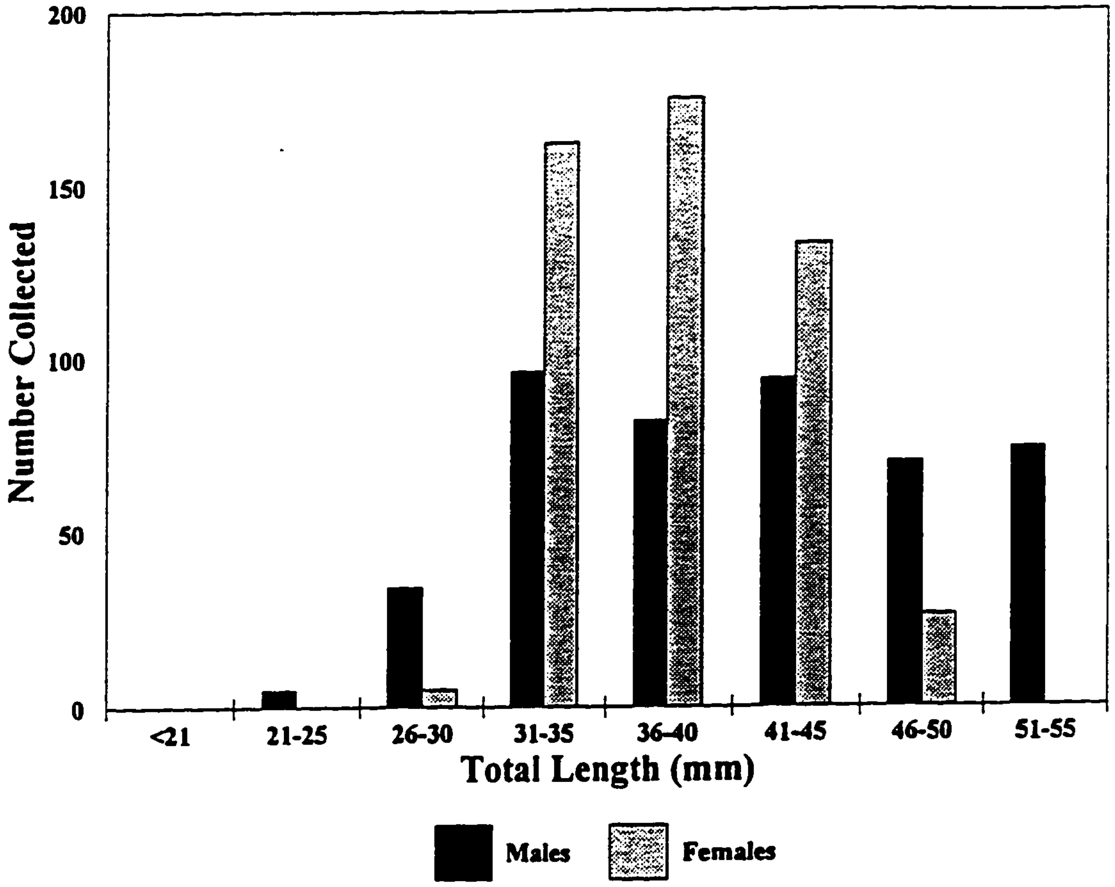

Figure 4.1. Number of male and female pupfish collected in each of eight size categories.

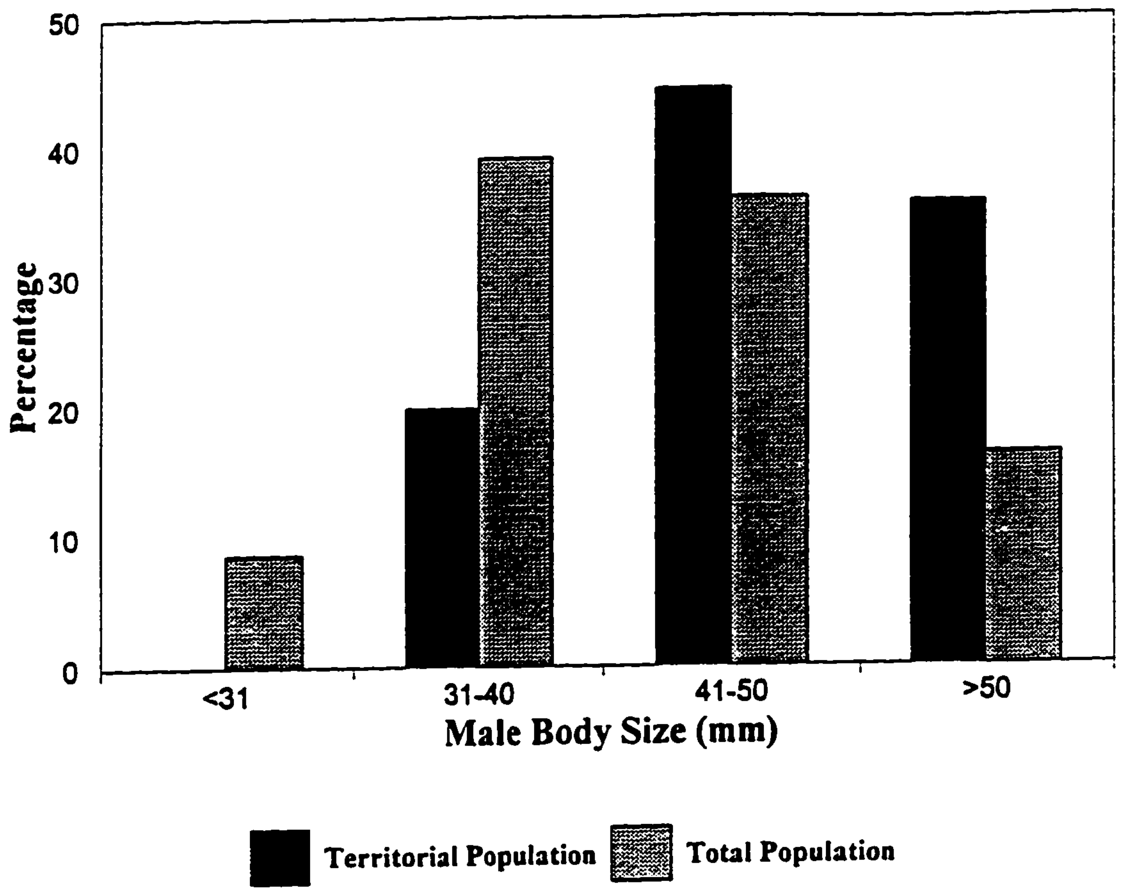

Figure 4.2. Proportions of male pupfish in each size category from the total population samples and the territorial population.

(Chi-Square; df=3, χ^2=36.86, p < .005)

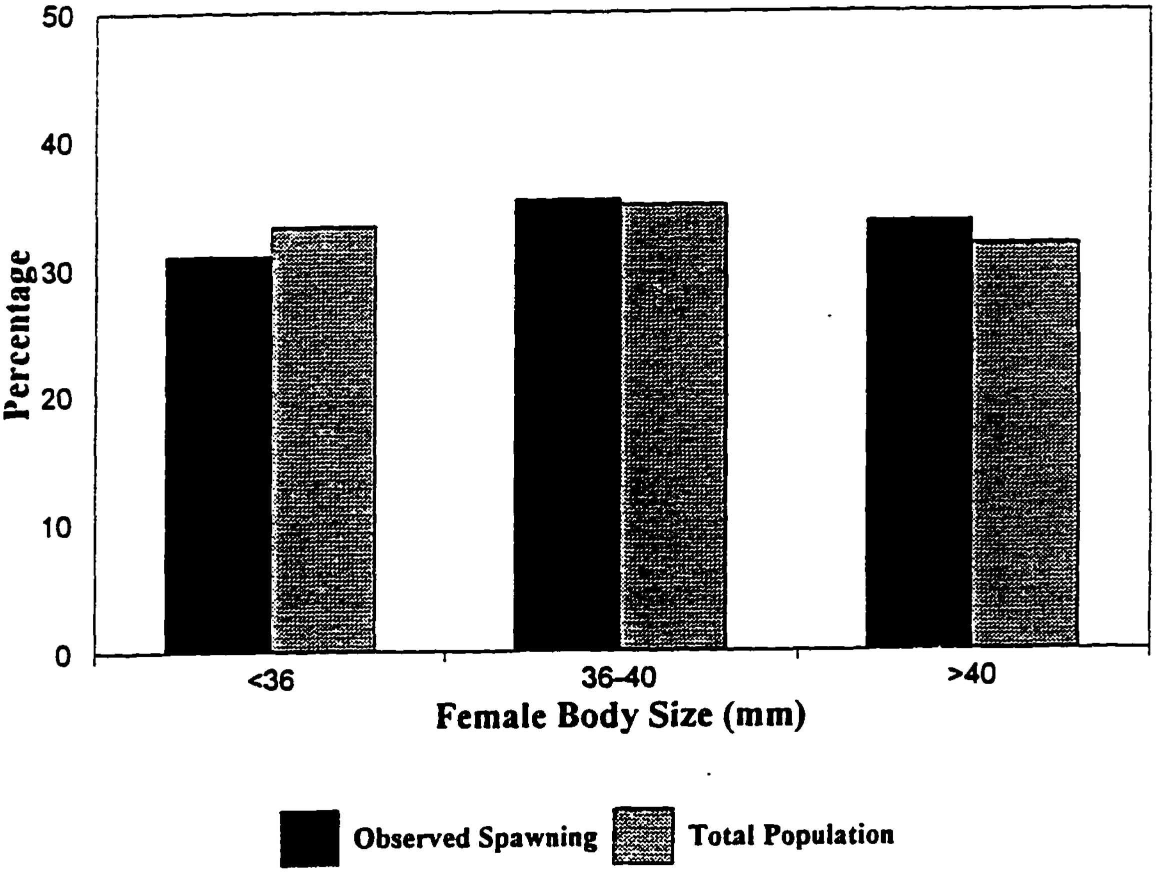

Figure 4.3. Proportions of female pupfish in each size category from the total population samples and the spawning population. (Chi-Square; df=2, χ^2=0.26, p > .1)

Chapter 5

Summary of Findings

These field observations and laboratory experiments were designed to examine female mate choice and male-male competition in *Cyprinodon variegatus*. The results indicate that male-male competition is very important in determining male reproductive success in this species. Territory size was found to be highly variable in the field, and was significantly related to the number of eggs fertilized by males. Males that defended larger territories received more eggs from each female with which they spawned. Observations indicated that this pattern was caused by intense male-male interference competition, in the form of spawning interruptions. Nearly 90% of all spawning events observed in the field were interrupted by neighboring males. It appears that females were able to spawn more eggs in larger territories before they were detected by neighboring males and interrupted. Thus, a male's ability to acquire and defend a large territory is very important to his reproductive success.

Both field and laboratory evidence suggests that male body size is very important in determining the ability to acquire and defend territories. In the field data from 1993, the relationship between male body size and territory size was highly significant. In addition, field data from 1992 showed that the smallest sexually mature males (< 30 mm) were entirely absent from the territorial population, indicating that they were competitively excluded from breeding. Laboratory evidence corroborates this notion, since these small males were able to defend territories in the absence of large males, and were fully capable of spawning and fertilizing eggs. Further, the largest sexually mature males were twice as common in the territorial population as they were in the total population. This over-representation is also assumed to be due to the increased competitive ability of the large males.

In the lab, prior residence was found to contribute to the ability to defend a territory. All males that had 24 or 72 hours to defend a territory, never lost any of their space to intruder males that were approximately equal to their size or smaller. Further, prior-residence conferred an advantage in competition with larger intruders as well. Large residents were occasionally able to defend their territories against larger intruders after a 24 hour occupancy, and were often able to do so after a 72 hour period. Small residents however were never able to defend their territories against larger intruders, regardless of the duration of prior-residence. These data suggest a relative rule concerning body size and competitive ability, rather than an absolute rule. That is, body size differences are more important to small males than to large males.

The field observations of males and females revealed no evidence of female mate preference for large or brightly colored males. Quite possibly this was due to the intense male-male interference competition that effectively overpowered it's expression. In the laboratory, females did not discriminate against small males when they had only one male from which to choose. However, when females were provided with a choice between a large and small male, they did spawn significantly more eggs with the larger male. Male-

male interference was prevented in these choice experiments by tethering the male to opposite ends of the aquaria. Perhaps the absence of male spawning interruptions allowed for the expression of the female mate preference for large males. Female choice may also become important in the field if male-male interference is reduced.

VITA

Matthew Jay Draud was born on February 22, 1967, in Covington, Kentucky, the son of Leroy and Hazel Draud. He graduated from Covington Latin High School in 1983, and received a Bachelor of Art degree in Biology from Thomas More College in 1987. In 1989, Matt married Michelle Lynn Kordes, and in 1990, he received a Master of Science in Biology at the University of Southwestern Louisiana. Matt and Michelle moved to Bethlehem, Pennsylvania where he began working on a Ph. D. at Lehigh University. Their first son, Travis Edward, was born in December of 1993. Matt joined the Office of Technology Assessment of the Congress of the United States in 1994, and worked there until it closed in October of 1995. Matt received a Ph. D. At Lehigh University in October of 1996, and is currently teaching at Northern Kentucky University and Clermont College.