Courtship and parental care in the biparental convict cichlid fish (Archocentrus nigrofasciatus): A test of their relationship.

Citation

Bockelman, Angela K. - Lehigh University. *Courtship and Parental Care in the Biparental Convict Cichlid Fish (Archocentrus nigrofasciatus): A Test of Their Relationship*. 2004, https://preserve.lehigh.edu/lehigh-scholarship/graduate-publications-theses-dissertat
theses-dissertations/courtship.

Courtship and parental care in the biparental convict cichlid fish (*Archocentrus nigrofasciatus*): A test of their relationship

By

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A Dissertation

Presented to the Graduate Research Committee

of Lehigh University

in Candidacy for the Degree of

Doctor of Philosophy

in

Biological Sciences

Lehigh University

Approved and recommended for acceptance as a dissertation in partial fulfillment of the requirements for the degree of Doctor of Philosophy

4/26/04

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ACKNOWLEDGMENTS

I would like to thank my dissertation committee, Dr. John Nyby, Dr. Colin Saldanha, and Dr. Robert Jaeger, for the assistance and advice they have given me over the course of my work at Lehigh. I especially thank my advisor, Dr. Murray Itzkowitz, not only for his guidance, but also for his unending enthusiasm for my ideas. Thanks also to the other graduate students in the Itzkowitz lab, who were a great sounding board.

Special thanks to Kelly Maloney, not only for reading multiple drafts and statistical advice, but also for lending a frequent shoulder to lean on and for keeping me sane.

And finally, I thank my parents, Paul and Darlene Bockelman for always supporting any endeavor I chose, and for giving me every opportunity to find my way.

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ABSTRACT

This dissertation examined courtship and parental care in convict cichlids (*Archocentrus nigrofasciatus*), and how behaviors involved in courtship affected subsequentparental behavior. Courtship has several proposed functions, one of which is the establishment and maintenance of a pair bond to aid in offspring care in biparental monogamous species.

My first experiment examined and compared courtship and parental care in both the field and laboratory. Behaviors appeared under laboratory conditions also appeared under field conditions, validating the use of convict cichlids as an animal model in laboratory experiments. Laboratory pairs courted at a similar frequency to field pairs. However, increased variability in offspring defense was seen in the lab.

The second experiment explored whether courtship duration was related to long-term pair bond formation and whether disrupting courtship affected the parents' abilities to coordinate activities during offspring care. To shorten courtship, I removed the male when the female neared spawning-readiness, and replaced him with a novel male. Pairs did not require an extended courtship in order to produce and rear offspring successfully. Pairs with shortened courtship did show more aggression and more courting behaviors early in the parental phase. Additionally, females appeared able to retain viable eggs for later spawning for at least one week following the disappearance of the mate.

The third experiment further investigated the relationship of courtship to parental care by interrupting the male's courtship. The female mate when was removed she was near spawning, and a novel female introduced. Males generally accepted the new female, but required significantly longer to spawn. Courtship behaviors were higher in experimental than control pairs only early in the parental phase.

In both the second and third experiments, courtship behaviors continued in both groups throughout the parental phase. Thus, I infer that individuals assess the parental capabilities of a mate during the long courtship period. Males appeared more attracted to the mate, while females appeared more attracted to reproducing. I suggest that despite the sex differing attraction/priorities, continuing "courtship" allows parents to coordinate activities as the needs of the offspring change.

CHAPTER I. GENERAL INTRODUCTION

Courtship has received considerable attention from evolutionary biologists, including Charles Darwin (1859), who noticed that in some species "successive males display their gorgeous plumage and perform strange antics before the females, which standing by as spectators, at last choose the most attractive partner". Darwin noticed that the plumage and "antics" often did not increase an individual's survival, but rather did increase mating success. The selection for traits that increase an individual's mating success was termed sexual selection.

The intensity of sexual selection depends on the degree of competition for mates, which in turn depends on two factors: 1) the operational sex ratio (OSR), and 2) parental investment (Krebs & Davies 1993). The influence of OSR on sexual selection is a matter of logistics. For example, if many females are breeding at a time, there is a low chance for a few males to control access to the females. Conversely, if few females are breeding, competition for access to them will be high, and likewise, so will selection on male courtship. Sexual selection is also expected to be highest in species with large differences in parental investment (PI) between the sexes.

The term parental investment was first coined by Trivers (1972), and can be defined as "anything done for the offspring that increases its chance of survival while decreasing the parents' ability to produce additional offspring." Although the definition is very open, some PI can be measured, primarily the physiological cost of gametes, and (to some degree) effort expended on offspring (Trivers 1985). Trivers noted Bateman's (1948) work on *Drosophila* in which most females produced offspring, but fewer males did. He concluded that males mated indiscriminately because the cost of producing sperm was minimal, and additional matings typically resulted in additional offspring. Eggs, on the other hand, were physiologically more expensive for the female to produce. Additional matings by the female did not result in additional offspring. Therefore, each mating was more valuable to the female than to the male.

Trivers expanded on the intrinsic differences in the cost of gametes. PI theory states that the sex investing less physiologically in offspring production will compensate by investing in physical ornaments (to obtain matings) and/or behavioral expenditure in the offspring. In polygamous species with no parental care, or only female care, females invest more in the offspring. In these species, more sexual dimorphisms are exhibited, primarily in the form of male ornaments or elaborate displays (Trivers 1985). For any given encounter with a member of the opposite sex, males are expected to be favored if they mate, while females are favored if they do not (Krebs & Davies 1993). Females are expected to be choosey, and to show a preference for males with elaborate displays, while males are expected to be indiscriminant in mating.

An obvious extension of parental investment theory relates to courtship. When females invest more in the offspring physiologically and/or through offspring care, they should be expected to require that males increase their parental expenditure in the form of courtship. Males are not expected to exhibit the same requirement from females, and might even attempt to shorten courtship themselves in an attempt to achieve subsequent matings with other females. In biparental species, males and females have similar post-copulatory offspring investment, and are predicted to therefore have similar courtship requirements. This dissertation examined courtship using a novel experimental design that decreased the courtship period for males and females. Unlike polygamous species where males and females are expected respond differently to changes in courtship, P.I. theory predicts that males and females of biparental species should respond similarly. Much like courtship, PI theory predicts that the sexes may have different tactics regarding offspring care. For example, in polygamous species the theory predicts that one sex will attempt to off-load its parental obligations onto the other parent. However, there are no studies, either theoretical or empirical, suggesting that the courtship interactions of these species can influence parental behavior. This is not the case in biparental species where courtship is predicted to assist in the maintenance of the pair bond and in the organization of parental activities (Keenleyside, 1979). Thus, the tactics each parent uses to modulate its parental investment during offspring care may be organized during the courtship period.

While it is obviously in the best interest of both parents for the offspring to survive, the sexes may not use the same parental tactic. For example, PI theory predicts that each sex is expected to exploit the other in order to decrease its own PI in a given reproductive bout (Krebs & Davies 1993). One example of differing ideal strategies is seen in the blue tits, described in Gowaty (1996). Adult female parents have better post-breeding survival if the young hatch synchronously, while male parents survive better if the young hatch asynchronously. Thus, if males and females of biparental species have different investment patterns, changes in the courtship period may influence a sex's commitment to the pair bond and its tactics in raising the offspring. In this dissertation, I examined whether the parental behavior of males or females are influenced by modifying the duration of the courtship period.

In summary, this dissertation examined courtship behaviors and the influence they have on parental care in the biparental convict cichlid (*Archocentrus nigrofasciatus*), and was composed of three primary parts. The first part examined courtship and parental care in both the field and the laboratory. No previous study of this species had quantitatively studied either reproductive stage, nor had field behaviors been compared to those in the laboratory to determine whether differences exist due to the inherent restrictions of captivity. Part 2 of this study investigated how females respond to the pre-spawning loss of her mate, and subsequent effects on parental care. The third part of this study examined how males respond to the pre-spawning loss of his mate.

The Animal Model:

The convict cichlid, *Archocentrus nigrofasciatus*, is a monogamous, biparental freshwater fish native to Central America. This fish exhibits the typical reproductive behaviors of a substrate brooding cichlid (Baerends & Baerends-van Roon 1950). A male and female form a pair and after courting for several days choose a spawning site upon which eggs are laid. This site is usually a protected depression under a rock/small rock formation. The pair shares in site preparation and subsequent offspring care. After 3 days, the eggs hatch as yolked-sac larvae called wrigglers. The yolk is absorbed within 4-6 days after hatching, resulting in free-swimming fry. During the egg and wriggler stages, the father spends more time defending the nest site while the mother spends more time caring directly for the young (fanning the eggs, removing fungused eggs) (see Baerends & Baerends-van Roon 1950). Later, both parents defend the fry equally.

General Laboratory Methods:

The convict cichlids were housed in single sex stock aquaria, fed dry food daily, and kept on a 15: 9 h light: dark period. Unless otherwise stated, a male and a female pair were placed in a 250 l aquarium with a fine gravel substratum. A terra-cotta flowerpot at one end of the aquarium served as a spawning substrate. At the opposite end, a transparent plastic partition 10 cm from the end of the aquarium created an intruder compartment (Fig. 1.1). A conspecific intruder was placed in the compartment to facilitate pair-bond formation and spawning (Itzkowitz & Draud 1992). Juveniles were used as intruders, in order that the intruder not be a possible mate. Because convict cichlids can be very aggressive, all fish were observed regularly. Any fish subjected to excessive attack was removed and the replicate terminated.

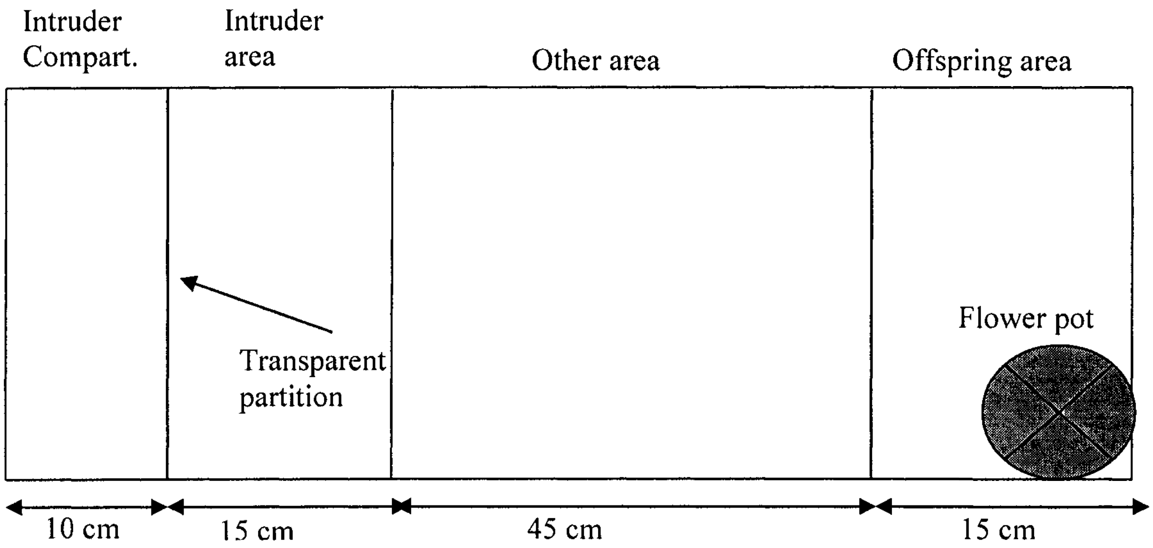

Figure 1.1. Experimental aquarium. The transparent partition created the intruder compartment. The terra cotta flower pot provided a spawning substrate.

Behavior Definitions:

The following is the list of behaviors that I recorded and their definitions. Most are established in the cichlid literature (Baerends & Baerends-van Roon 1950; Barlow 1970; Baylis 1975; Baerends 1986). I have operationally defined behaviors marked with an asterisk (*)

Typical Courtship Behaviors

Tailbeat: Deep, slow undulation of the tail, which is directed toward the other fish.

Brush: Male and female approach and swim past each other, and sometimes make lateral contact.

Circle: Male and female swim in a circle formation.

Lateral Display: Individuals swim past each other with unpaired fins extended.

Quiver: Individual orients anterior end toward substrate and twitches.

Greet: After an absence (due to foraging, patrolling) the members of a pair engage in displays. This can be circle, brush, lateral or frontal display or any combination.

Aggressive Behaviors

Bite: Individual contacts the other (or partition) with an open mouth. May or may not close jaws.

Chase: One individual charges and the other flees.

Mouthfight: Both actors lock maxilla, and tug back and forth.

*Face-off** : Low-level aggressive display in which male and female orient toward each other, without moving.

Frontal Display: One individual faces the other with branchiostegal flaps extended.

Role exchange: The individual defending the territory begins direct offspring care (e.g. fanning eggs), allowing the animal caring for the young to leave the nest, or vice versa.

Role agreement: Both individuals perform either different or the same roles, in the absence of intrapair aggression.

Disagreement Behaviors

Butt: One animal rams the other with its head. This usually results in the recipient changing direction or engaging an intruder.

Failed exchange attempt:* One member of the pair begins to perform the role of the other fish, but is prevented from doing so by the other, which results in each continuing to perform its previous role.

E.g. The male returns from patrolling and attempts to enter the flower pot, but the female positions herself between the male and the flower pot. The male then returns to patrolling.

Role disagreement: Both individuals perform the same role (e.g. both male and female provide offspring care while an intruder is present), resulting in aggression from one of the mates toward the other.

CHAPTER II. COURTSHIP AND PARENTAL CARE IN THE CONVICT CICHLID, AND A TEST OF ITS USE AS A MODEL SYSTEM

Introduction

Cichlid fishes have become popular research animals, in large part because they are easy to maintain under laboratory conditions and, perhaps, because Baerends and Baerends-van Roon's (1950) monograph popularized their elaborate courtship and biparental care patterns. In spite of numerous publications describing cichlid behavior since that classic monograph, most studies have been laboratory-based usually emphasizing some segment of courtship behavior (e.g., male-male aggression, mate choice; pair competition; mate switching) or parental care (e.g., division of roles, mate desertion) with no attempt to assess how the aquarium conditions influences social behavior. Field studies on cichlids have rarely considered courtship or parental care but rather have emphasized mate choice and offspring defense. The intent of this study was two fold: First, to provide the first detailed account under both field and laboratory conditions describing both courtship and parental care in a biparental cichlid and second, to determine whether activities seen under laboratory conditions are an accurate reflection of behavior under natural condition. I used the convict cichlid (*Archocentrus nigrofasciatus*), one of the most studied of the biparental cichlid species.

In spite of many studies examining mate selection in cichlids (e.g. Keenleyside 1985; Beeching & Hopp 1999), few have examined pre-mating behavior (i.e., courtship). Baerends (1986) reported that, in some cichlids species, certain behaviors were more likely to occur early in the pre-spawning phase (frontal and lateral displays, chasing, mouthfighting), while others occurred later (quivering, digging). Baylis (1975) similarly observed that certain behaviors were more likely early vs. later in courtship, but the shift in behaviors was not coordinated between the two individuals of a pair. Despite the lack of coordination, positive correlations were seen between the male behavior and the female's performance of the same behavior, and vice versa for some courtship behaviors (*Tilapia melanotheron*; Barlow & Green 1970).

Substantial laboratory work has been performed on substrate-brooding cichlid biparental care seen in substrate-brooding cichlids. The primary parental behaviors were direct offspring care (e.g. fanning the eggs), guarding the young, and defending the territory. Although both perform all roles, males and females typically show a division of labor, in which the female performs more direct offspring care, while the male tends to defend the territory (Keenleyside 1978; Smith-Grayton & Keenleyside 1978; Itzkowitz & Nyby 1982; Itzkowitz 1984; Itzkowitz 1985; Barlow 1991; Itzkowitz et al. 2001). Moreover, both parents will alter their behavior to perform at least some of an absent mate's role (Itzkowitz 1984; Lavery & Reebs 1994; Itzkowitz et al. 2001).

Although most studies investigating parental care in biparental cichlids have focused on division of labor and defense of young from intruders (FitzGerald & Keenleyside 1978; Itzkowitz 1985; Lavery & Colgan 1991; Galvani & Coleman 1998), no measures of intra-pair behaviors are typically reported. Determining intra-pair behaviors could help illuminate how parents coordinate their activities. Texas cichlid pairs show high levels of aggression toward each other when first introduced (Itzkowitz & Draud 1992). Intra-pair aggression could be later detrimental when offspring are present by diverting attention from offspring defense. The agonistic behaviors seen early in courtship in the convict cichlid occur less often as courtship progresses. Thus the courtship period might serve to diminish the aggressive tendencies apparent at the onset of courting. However, certain behaviors, typically considered courting behaviors, also reappear throughout the parental stage (e.g. behaviors involved in "greet", Keenleyside et al. 1990). I hypothesize that these behaviors might allow members of a pair to coordinate their parental behaviors and minimize intra-pair aggression. To test the hypothesis it is necessary to quantify intra-pair behaviors during courtship and parental care to determine how these behaviors change during a breeding cycle.

Laboratory research sometimes yields results that are not applicable to the natural ecoloty of a species (de la Maza et al. 1999; Mahady & Wolff 2002; Sloman & Armstrong 2002; McPhee 2003; Milius 2003; Wolff 2003). Although most work on cichlids has occurred in the laboratory, some field work has been undertaken. For example, McKaye (1977) examined how several cichlid species in Lake Jiloá, Nicaragua competed for breeding sites. Ninety percent of all breeding sites were lost prior to breeding cycle completion, but pairs with sites in shallower water were more successful.

Neil (1984) described parental defense of the firemouth cichlid (*Cichlasoma meeki*) toward intruder fish, and found increased predation if the parents were distracted from their parental duties. The increased predation lent support for the hypothesis that both parents are required to rear offspring successfully.

Wisenden (1994a) extensively studied convict cichlids in the field, and measureed several aspects of reproductive success. For example, males were most likely to desert their mates at sites with the highest brood survivorship or when fry were close to independence. These finding supported the need for biparental care to insure offspring survival in areas with high predation pressure. Brood survival was correlated with the female parent's size, but not the male's. Habitat played a primary role in reproductive success in the field, such that fry survivorship was higher in shallow habitats than in deeper one. Wisenden hypothesized that the lower light level in deeper water inhibits the parents' abilities to see predators. Wisenden also found that during the fry stage, females performed more provisioning (fin-digging and leaf lifting) than males, and that both sexes provisioned more when mated than when widowed (Wisenden et al. 1995). However, none of Wisenden's field studies specifically examined intra-pair behaviors.

Here I quantitatively describe intra-pair behaviors during courtship and parental care. Although convict cichlids have been studied under both field and laboratory conditions, this is the first study directly compare behavior in the field to that in the laboratory. Therefore, my hypotheses are not specific due to the lack of a published theoretical framework. The restrictions imposed by the laboratory setting could result in quantitative differences between the laboratory and field. I hypothesized that the frequency of courtship behaviors in the laboratory would increase due to the lack of conspecific distractions or predators. Males and females were both expected to display higher frequencies of courtship behavior counts, since neither had other mate options. Alternatively, there might be no difference in courtship, or even a decrease in courtship behavior counts. Without conspecific competitors, there may be less need to engage in displays designed to keep the attention of the mate.

During parental care in the laboratory, I expected decreased vigilance since there would be no offspring predators on a regular basis. When confronted with an intruder, I hypothesized that laboratory parents would respond with higher aggression. The male, who typically spends more time on offspring defense, might increase the time spent near the intruder as an attempt to ward off the threat. Conversely, the male could be expected to increase his time with the offspring, since the confined intruder will not flee and will be closer to the offspring than typically occurs in the field. Finally, I hypothesized that intrapair aggression would increase. An intruder confined to one section of an aquarium is unable to flee, which could induce both parents to attack in an attempt to allay the threat. Both parents attacking an intruder could interrupt the typical parental division of labor, resulting in intrapair aggression. Despite expected quantitative differences between the laboratory and the field, I did not expect to observe novel behaviors in the laboratory.

Methods

Field Methods: Observations took place at 3 streams in and near the Lomas Barbudol Biological Reserve in Guanacaste Province, Costa Rica. These sites are described in greater detail in Keenleyside et al. (1990). Convict cichlids in Costa Rica breed during the long dry season (December through May). I spent 7 weeks during the dry season (January 30-March 20, 2001) to observe convict cichlids in their native habitat.

Courtship Study: At each field site, I arbitrarily selected pairs that had not yet spawned. I observed each pair (n=30) for 5 min and recorded: 1) the time each member spent away from the other (> 2 body lengths), 2) interactions with one another, and 3) interactions with other fish. I included the number of aggressive and courtship behaviors exhibited by the pair in the observations.

Parental Care Study: In each stream, I constructed artificial caves with native rocks as possible spawning sites. Pairs that spawned in those caves (n=14) were observed every other day through the immobile (egg, wriggler) and mobile (fry) stages. I recorded intra-pair courtship and aggressive acts and behaviors toward conspecifics and heterospecifics that entered their territory.

Laboratory Methods: I compared the field observations to laboratory observations made at Lehigh University in Bethlehem, Pennsylvania. I assembled aquaria as described in the General Laboratory Methods (chapter 1).

Courtship Study: After assembling the aquaria, for 3 days I made 5 min observations twice daily (resulting in 90 observations), and recorded courtship behaviors as well as aggressive acts within the pair and directed toward the intruder. The 6 observations per pair were averaged and the mean numbers per pair were used in the analysis.

Parental Care Study: I did not use the same pairs used in the courtship laboratory observations. Aquaria were assembled, and once eggs were laid, the juvenile intruder was removed. Real-time videotaping was conducted on the second day of the egg stage, and on the second and fifth days of the wriggler stage. Each of these tapings consisted of 15 min with an adult male intruder placed in the intruder compartment. The presence of an intruder stimulates a sexual division of labor (Itzkowitz et al. 2001) by presenting a possible danger to the offspring. Behavior rates per minute were calculated to equate differing recording times between the laboratory (time=15 min) and field (time=5 min).

Data from the videotapes entered into an event recorder (BEAST Professional, v1.01). Due to many low counts, nonparametric statistics were necessary. I used a Kruskal-Wallis ANOVA by ranks to analyze field vs. laboratory behaviors, and a Median test to analyze aggression directed toward various intruders in the field for the courtship experiment, and for male vs. female tests for the parental care experiment.

Results

Courtship Study

Field Courtship

Both males and females exhibited aggression toward other fish (fig. 2.1). Females chased female intruders significantly more than did males ($\chi^2_1=4.50$, $P<0.05$). A sex difference in chasing of intruder males ($\chi^2_1=0.05$, $P>0.05$), juveniles ($\chi^2_1=3.16$, $P>0.05$) or heterospecific fish ($\chi^2_1=0.16$, $P>0.05$) was not seen.

Field vs. Laboratory

All behaviors measured during courtship in the laboratory also occurred in the field, and vice versa. Additionally, few quantitative differences were seen between the laboratory and field.

Laboratory females chased their mates more than field females ($H_1=5.03$, $P=0.025$). This difference was not seen in males ($H_1=2.03$, $P=0.15$). Females in the laboratory spent more time away from their mates than those in the field(fig. 2.2, $H_1=6.13$, $P=0.013$), but laboratory males did not($H_1=2.35$, $P=0.13$)

When comparing the laboratory to the field, neither females nor males differed in the number of tailbeats (fig. 2.3) directed toward the mate ($H_1=1.78$, $P=0.18$; $H_1=0.51$, $P=0.47$, respectively). There were no differences in the number of circle ($H_1=0.02$, $P=0.90$) or greet ($H_1=0.02$, $P=0.88$) performed by pairs. Field pairs engaged in the brush significantly more than laboratory pairs (H_1=5.56, P=0.02). When all courtship behaviors were added together, total courtship was significantly higher in field pairs than in laboratory pairs (fig. 2.3b; H_1=9.14, P=0.003).

Due to the inherent differences, aggression toward an intruder was not directly comparable between the field and laboratory. In the field, other males, females, juvenile conspecifics, and heterospecific fish interacted with a given pair. Laboratory pairs had only a juvenile intruder constrained behind a partition. However, a qualitative assessment showed that both laboratory and field pairs showed aggression towards "intruder" fish.

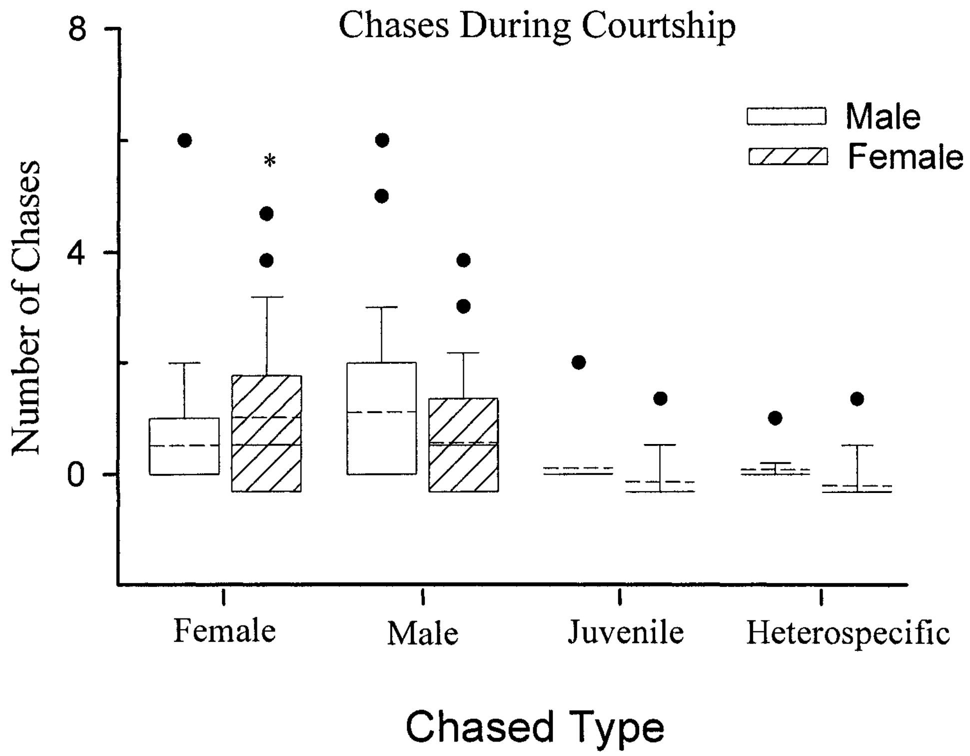

Figure 2.1. Number of chases by males and females directed toward other fish in the field during courtship. Only female chases toward females differed significantly. Boxes = 25th and 75th quartiles, whiskers = 5th and 95th percentile, * $p<0.05$., ●=outlier, solid line (—) represents median, dashed line (– –) is mean.

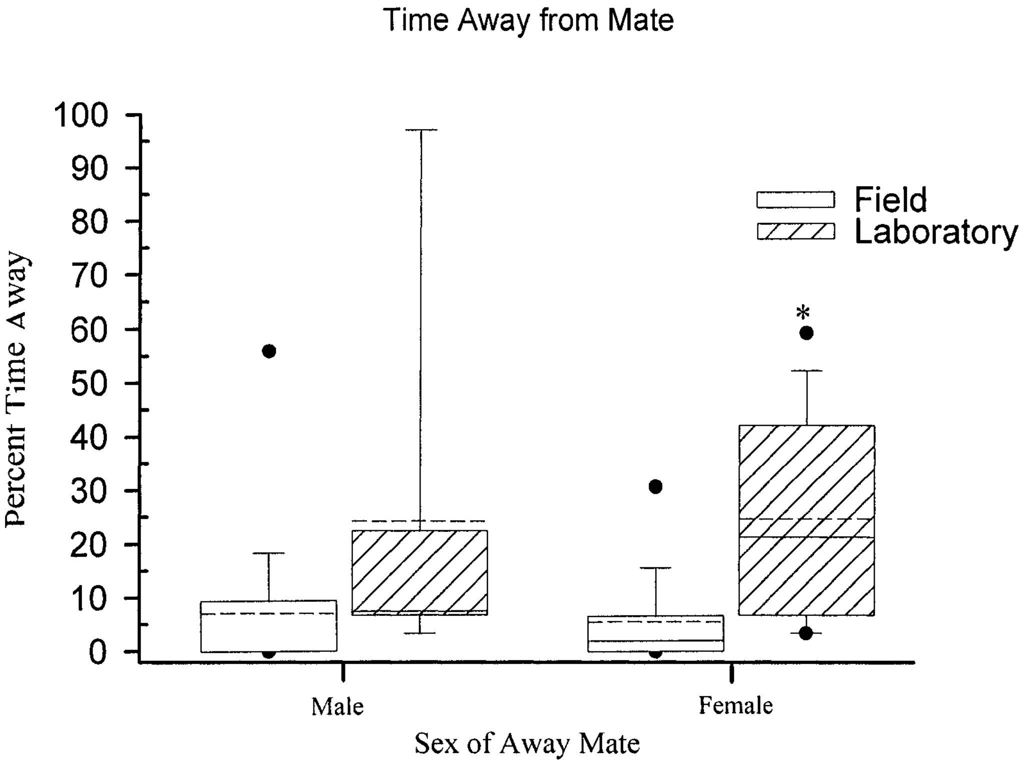

Figure 2.2. . Percent of time per 5 min spent more than 2 body lengths away from the mate during courtship Boxes = 25th and 75th quartiles, whiskers = 5th and 95th percentile, * = $p<0.05$., ●=outlier, solid line (—) represents median, dashed line (– –).

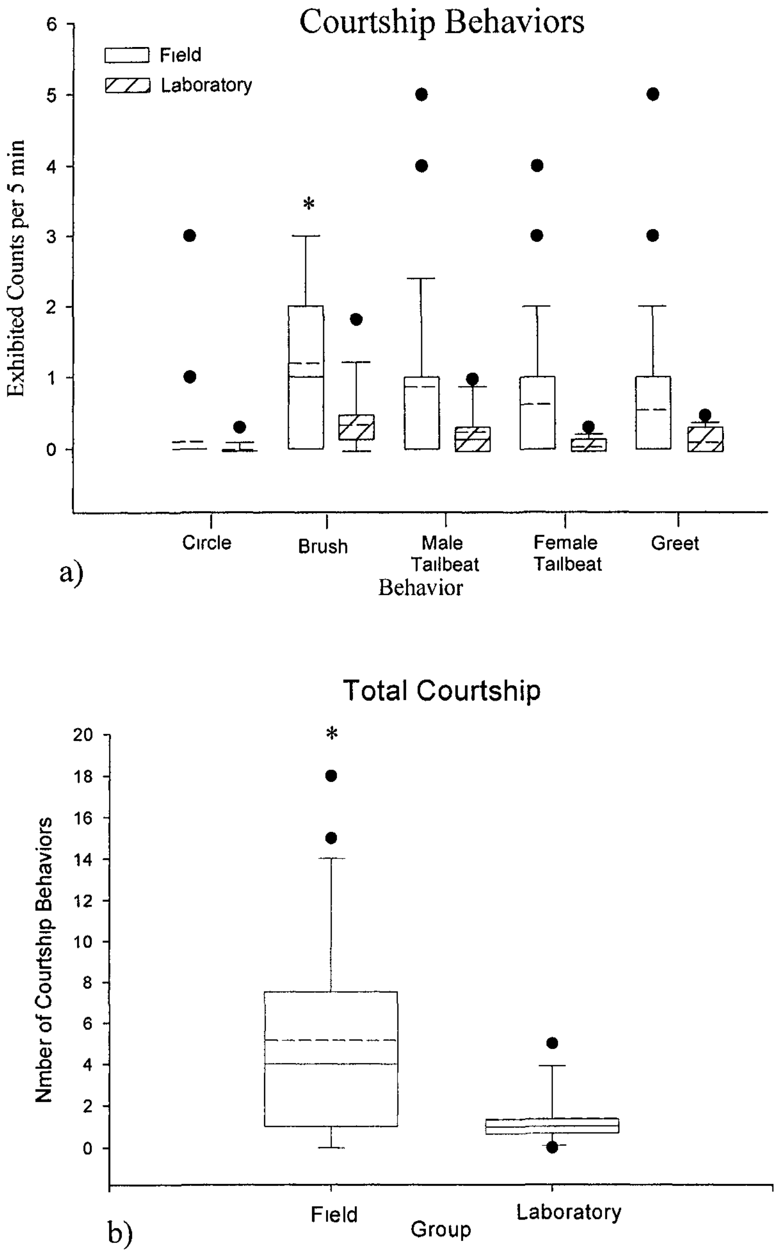

Figure 2.3 a) Counts of individual courtship behaviors seen in the lab and in the field during courtship b) Total courtship. Individual courtship behaviors were combined. Boxes = 25th and 75th quartiles, whiskers = 5th and 95th percentile, * = $p<0.05$., ●=outlier, solid line (—) represents median, dashed line (– –) is mean.

Parental Care Study

Field Parental Care with Immobile Offspring

Chases directed toward male or heterospecific intruders did not differ significantly between male and female parents, although males showed a trend toward more chases directed to both (male intruder: χ^2_1=3.59, P=0.058; heterospecific intruder: χ^2_1=3.39, P=0.065, fig. 2.4). Males and females did not differ in chases directed toward intruding females or juveniles (χ^2_1=0.84, P=0.36; χ^2_1=0.15, P=0.70 respectively).

Males left the nest area more times than females (fig. 2.5; χ^2_1=9.14, P=0.003), and spent more time away from the nest (χ^2_1=9.14, P=0.003).

Field Parental Care with Mobile Offspring

Males and females did not differ in the number of chases directed toward males (fig. 2.4; χ^2_1=1.29, P=0.26), females (χ^2_1=0.14, P=0.70), or heterospecific fish (χ^2_1=2.29, P=0.13). Females chased juvenile intruders more than did males (χ^2_1=9.14, P=0.003).

Males spent more time away from the offspring than females (fig. 2.5, χ^2_1=14.29, P=0.0002). Females were more likely to leave the offspring immediately following the return of the mate than were males (χ^2_1=9.96, P=0.002)

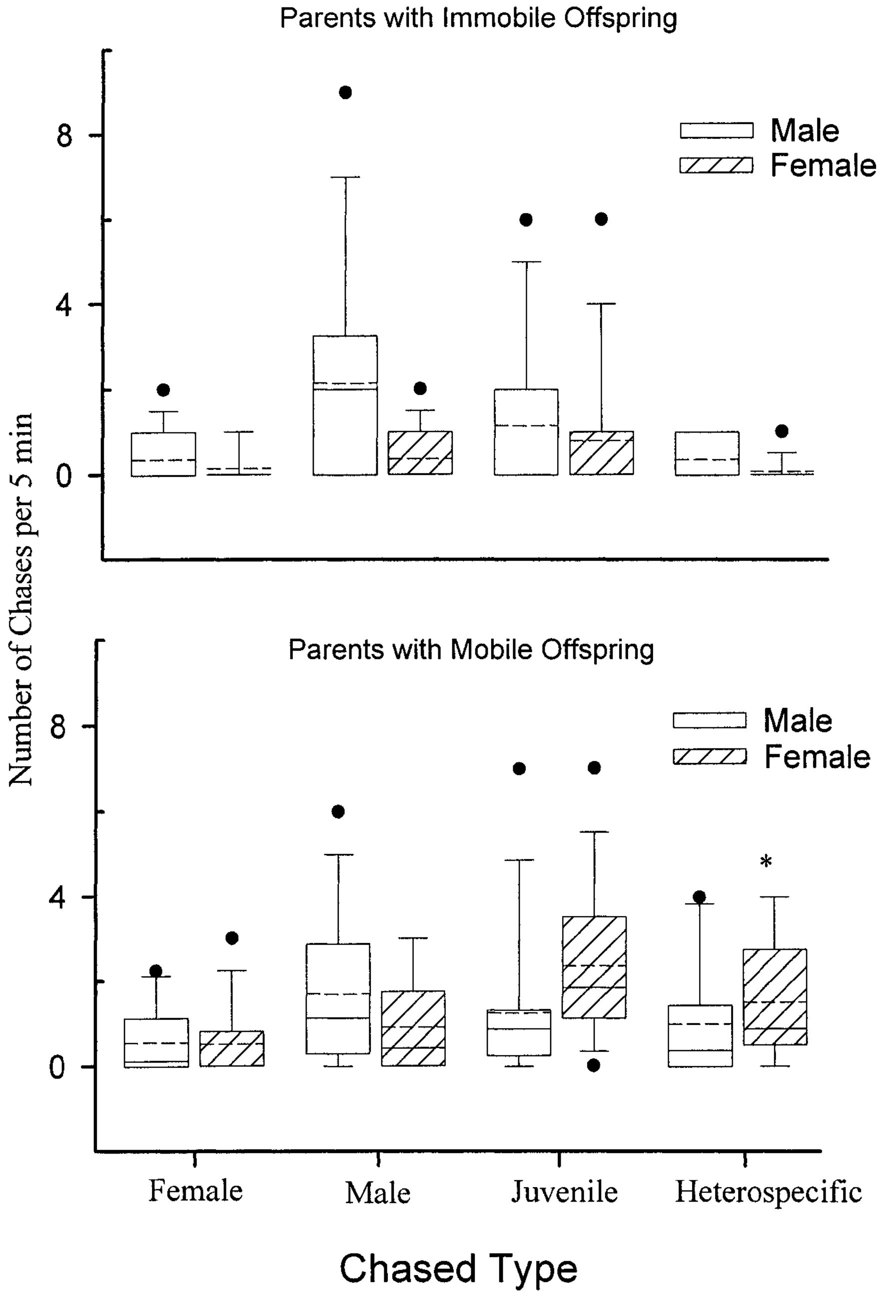

Figure 2.4. Number of chases male and female parents directed toward other fish while the offspring were either immobile (egg, wriggler) or mobile (fry). Boxes = 25th and 75th quartiles, whiskers = 5th and 95th percentile, * = $p<0.05$., ●=outlier, solid line (—) represents median, dashed line (– –) is mean.

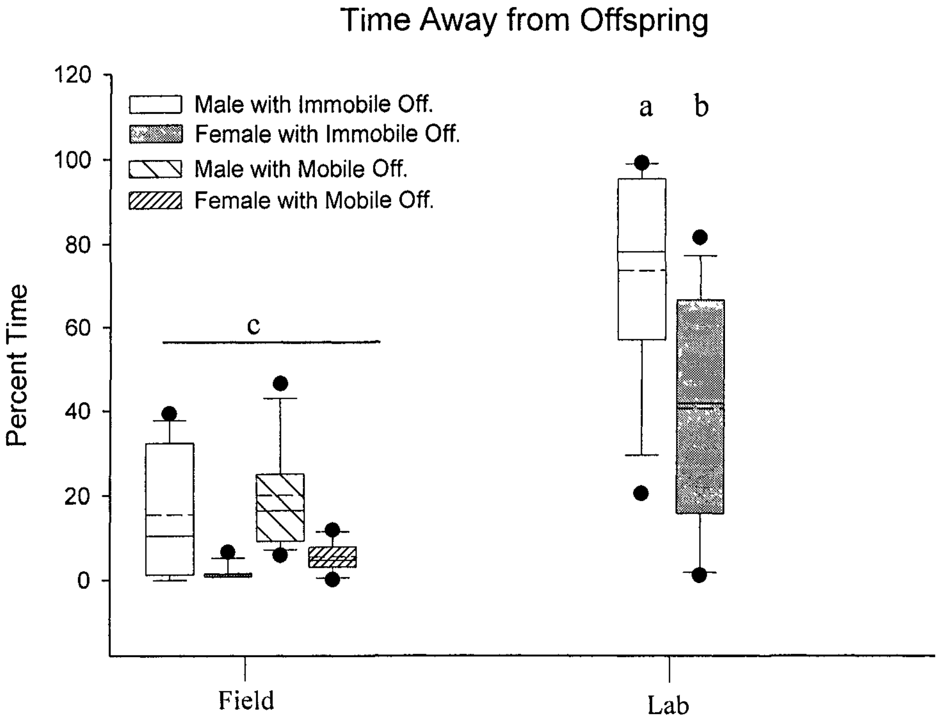

Figure 2.5. Percent of time parents spent away from the offspring in the field and lab. Both males (a) and females (b) in the lab were away more than those in the field (c) Boxes = 25th and 75th quartiles, whiskers = 5th and 95th percentile, •=outlier, solid line (—) represents median, dashed line (– –).

Field vs. Laboratory

Similar to the courtship study, behaviors that were detected during parental care in the laboratory were also observed in the field, and vice versa. Additionally, few quantitative differences were observed between the two groups.

There were no significant differences in the number of occurrences of courtship behaviors between the field and the laboratory. The only behaviors typically considered to be "courtship" behaviors exhibited more than once per comparison were brush (H_1=0.552, P=0.46) and greet (H_1=2.70, P=0.10). Aggression was higher among laboratory pairs but not quite significantly so (H_1=3.69, P=0.055).

Field and laboratory pairs differed significantly in time spent with and away from the offspring (fig. 2.5). In the laboratory, both males and females spent a greater percentage of time away from the offspring (H_1=17.94, P=0.00 and H_1=19.74, P=0.00 respectively). Additionally, pairs in the laboratory spent more time together engaging an intruder (H_1=14.84, P=0.0001).

Discussion

My hypothesis that courtship behaviors would occur more frequently in the laboratory was not supported. Total courtship was higher in the field. The only difference seen in individual behaviors was brush, which occurred more often in the field. This difference could be a result of a high density of fish in streams, and the brush might allow aired individuals to recognize one another. During courtship, laboratory females chased their mates more, and spent more time away from the mates than did field females. In the field, there may be a female sex-bias, which makes males a more valued resource (Cleveland 2003). Additionally, not all females breed, and those that do, breed less often than males (Wisenden 1995). Thus, females in the field might be less inclined to be aggressive towards a potential mate, and more likely to stay in closer proximity to him in order to mate-guard him from other females.

As in previously published accounts (Mackereth & Keenleyside 1993), field females during courtship chased other females more than males chased females. Males, however, did not show the same intrasexual aggression. Male chases directed toward intruder males did not differ from female chases of males. This might be a direct result of a female bias in the field, where the males may be a limited resource and do not experience the competitive selection for mates.

Based on time spent away from the offspring, the hypothesis that parents in the laboratory might decrease vigilance was supported. During the immobile offspring stage, laboratory parents spent more time away from the offspring than field parents. Most notably, both parents were away from the nest more, leaving the offspring vulnerable. Time away from the offspring explained most of the increased behavioral variability seen in laboratory pairs. This variability may be a result of laboratory methods in which intruders only appear in one area.

Although both parents were away from the nest more in the laboratory, I did not see the predicted increase in intrapair aggression at alpha=0.05, and therefore rejected that hypothesis. I did, however, see a trend toward increased intrapair aggression. A previous study (Itzkowitz et al. 2003) suggested that individuals of a pair use aggression to maintain a division of labor. As in that study, there could be disagreement over role division when both individuals are performing the same behavior (e.g. attacking an intruder), and warrants further investigation.

Both parents in the field chased intruders with few sex differences in behavior. When the offspring were mobile, females chased juvenile intruders more than did males, which could indicate that females might consider juveniles a greater threat to offspring than did males. Juveniles do prey upon egg and larval conspecifics (pers. obs.).

In the field during both parental stages, males spent significantly more time away from the offspring than females. Although I personally did not bigamy, males are facultatively bigamous (Keenleyside 1985) and might use time away from the offspring to search for new additional mates.

My most important finding was that no unique behaviors were observed during courtship or parental care in the laboratory. This validates the use of laboratory experiments to explore the social behaviors of convict cichlids.

CHAPTER III. THE IMPACT OF COURTSHIP DURATION ON THE PARENTAL CARE OF THE MONOGAMOUS CONVICT CICHLID. PART I: MALE REMOVAL

Introduction

Courtship services one or more of the following functions: 1) species and sex recognition; 2) determination of potential mate quality; 3) triggering the reproductive physiology of the mate; 4) appeasement of aggression; 5) synchronous release of gametes; and 6) establishment and maintenance of a pair bond to aid in offspring care (Barlow 1970; Baylis 1975; Keenleyside 1979; Baerends 1986; Barlow 1991). The first five functions seem applicable to most species. In polygamous species with no parental care, only physiological priming for gametic exchange and indications of genetic quality may be relevant. In species with uniparental care, individuals select mates that will become good parents (e.g. sticklebacks, (Bastock 1967), sunfish, (Keenleyside 1979), damselfish, (Knapp & Kovach 1991). Many such species often perform relatively short courtship, lasting only seconds to hours (Itzkowitz 1974; Keenleyside 1979). Thus, polygamous animals judge potential mate quality without a lengthy courtship.

Monogamous animals (those that remain together socially during the course of a reproductive cycle) with biparental care typically have a much longer courtship than polygynous species, perhaps reflecting that courtship is related to offspring care. For example, courtship behavior in biparental species often appears to mimic offspring care (Baerends & Baerends-van Roon 1950; Gowaty 1996) and may allow parents to synchronize their behavior such that only one parent is away from the offspring at a time. This coordination is especially important when one parent is necessary to shield the offspring from harsh environmental conditions. The need to coordinate parental behavior seems especially important when both parents can perform all parental roles but each sex emphasizes different ones. For example, in the convict cichlid, *Archocentrus nigrofasciatus*, the male typically spends more time defending the territory while the female provides more direct offspring care. However, the male, on occasion, returns to the nest, in effect "relieving" the female to leave the nest to forage (Keenleyside et al. 1990). If both sexes are capable of performing both roles, they must have a means to determine which parent will perform a given role, and how these roles change with changing offspring needs.

Finally, parental roles are not static and in many species the roles change as the offspring mature (Sasvari 1986; Gowaty 1996; Szekely & Cuthill 2000). The changing parental roles suggest that the process that may have started during courtship would continue after the offspring are present. The need to continue determining parental roles may explain why males and females from a number of monogamous species continue to display "courtship" behavior even after the young have arrived (Epple 1978; Erickson 1978; Anderson 1984; Moreno et al. 1994; Geissmann 1999; Geissmann & Orgeldinger 2000; Johnson et al. 2000; Wachtmeister 2001). Although "courtship" displays prior to pair formation may serve in mate selection, after the pair has formed, such assessment seems unnecessary, and wasteful. For example, pigeons and ring doves that remain together for multiple breeding cycles court and display each cycle (Erickson 1978). The reason for the continued 'courtship behavior' after pair-formation has confused investigators (Geissmann 1999).

I investigated how a disruption of courtship might affect both the pair bond and offspring care. Under natural conditions, such disruptions could occur due to predation or injury. I formed several hypotheses (not all of which are mutually exclusive): First, if courtship serves simply to physically prepare individuals to mate, those pairs with a disrupted courtship would not produce offspring. Shortening courtship might affect the mate selection process, resulting in no offspring. Second, if courtship coordinates offspring care, a female should require that a new male undergo a complete courtship before mating with him. Third, if courtship is required for coordination, and a female copulated more quickly than is typical with a new mate, the pair would show parental behavioral abnormalities due to abbreviated courtship. If courtship coordinates offspring care, then pairs with attenuated courtship should extend courtship behavior into the parental phase. If courtship does not coordinate offspring care, no differences would be expected during the parental phase between control and experimental pairs.

Methods

Exp. 1 – Effects of shortened courtship on parental care

In order to test the effects of a disrupted courtship, I shortened the courtship duration. Aquaria were prepared according to the general laboratory methods (chapter 1).

The pair was allowed to interact until the female was within several hours of spawning, as determined by the extension of the female's ovipositor. When the female neared spawning-readiness, the paired male was removed and immediately replaced with another male of the same size (total length, ±2 mm). Because females show a preference for males based on size (Wisenden 1995), the replacement male was likely as attractive as the original. In the control pairs, I removed the male and immediately returned him. Pairs were videotaped for 15 min after male introduction/reintroduction, which allowed the fish to interact freely without the presence of an observer. After the initial 15 min videotaping, experimental the video camera was set to record 1 second every 50 seconds, until eggs were laid. This extended videotaping allowed a determination of whether eggs had been laid and consumed, or if none were laid. Once eggs were laid, the juvenile intruder was removed from its compartment. Additional videotaping occurred on the second day of the egg stage, and on the second and fifth days of the wriggler stage. Each of these tapings consisted of 15 min with no intruder in the intruder compartment, and 15 min with an intruder. The presence of an intruder stimulates a sexual division of labor (Itzkowitz et al. 2001) by presenting a possible danger to the offspring. The manipulations were repeated until 15 pairs in both the experimental and control groups that successfully reared offspring through the wriggler stage.

Data taken from the videotapes were entered into an event recorder (BEAST Professional, v1.01). I quantified courtship, aggressive, and disagreement behaviors within the pair, the time each parent spent near the offspring and near the intruder, latency to spawn, and attacks upon the intruder.

Many behaviors occurred infrequently, thus for statistical analysis, the various courtship, aggressive and disagreement behaviors were added together into a courtship coefficient, an aggression coefficient, and a disagreement coefficient. Analyses were done using the median test followed by chi-squared tests, unless otherwise stated.

Exp. 2 – Must physiologically primed females spawn?

The experimental females of Experiment 1 often spawned very quickly. Thus, to ascertain whether the females that had extended their ovipositors had reached a physiological point at which they committed to spawn or lose the eggs, an additional experiment was conducted. To test whether a female was committed to spawning once the ovipositor was extended, a female, a male and a juvenile were placed in an experimental tank as described in Experiment 1. When the female neared spawning-readiness (n=19), I placed her into a different 250 L aquarium partitioned into 3 compartments (see Fig. 3.1). This partitioning was to preserve tank space and allow 3 females to be observed simultaneously. Each aquarium section contained a flowerpot as a spawning substrate. I then videotaped each female daily at 1 sec per 50 sec intervals for 1 week to determine if she spawned. Since a female with a male mate present would have spawned within 24 hr, one week was adequate to determine if she was physiologically committed to spawn.

To eliminate the stress placed on females by removing them from their original aquarium, I performed the experiment once again, under conditions less stressful to the female. This time I placed a female, male and juvenile into an aquarium as described earlier (n=10). Once the female extended her ovipositor, the male was removed. The female was then videotaped at intervals of 1 sec every 50 sec for 7 days. After 7 days the male was returned to the aquarium. The pair was then videotaped at intervals of 1 sec every 50 sec.

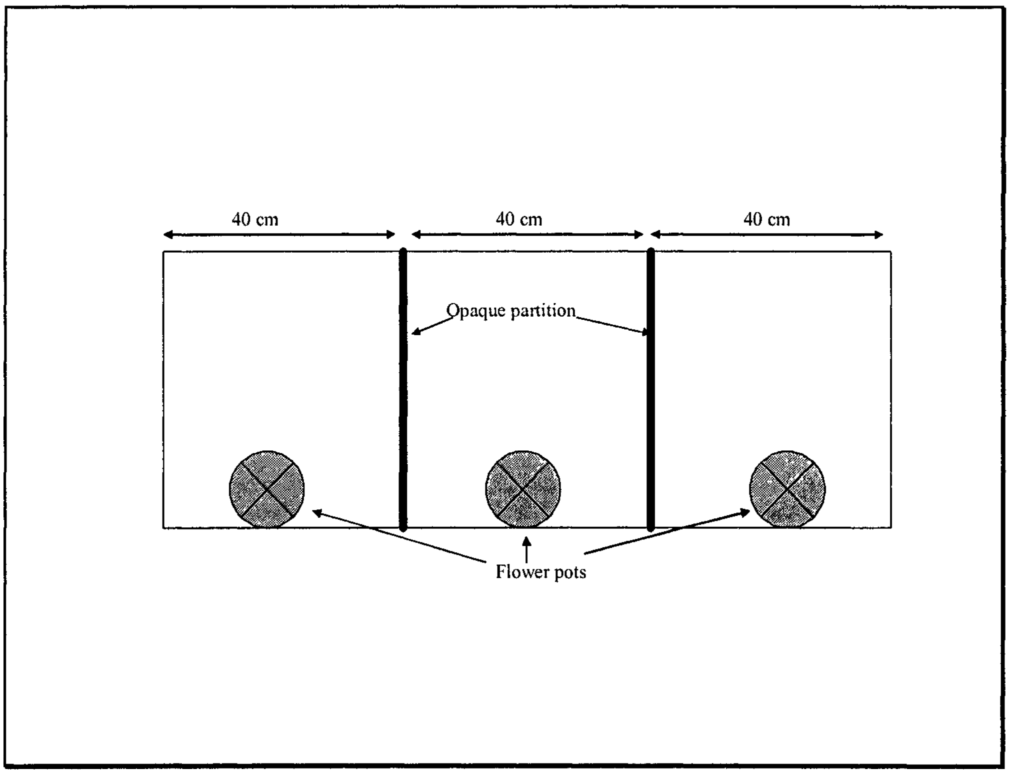

Figure 3.1. Aquarium for Exp. 2. The aquarium was divided into 3 sections by placing opaque plastic partitions into the tank. The flower pots functioned as spawning substrates.

Results

Experiment 1

There was a significant difference (ANOVA: $F_{1,41}$=4.69, P<0.05) in pair success (the pair reared offspring to the fry stage), with the control group showing a higher success rate (90%) than the experimental group (63%) (Fig. 3.2). To test whether this significance was a result of the pair formation rate with an unfamiliar individual, I added the individuals that never formed pair bonds to the control group. There was no difference in pair formation with an unfamiliar individual (72%: ANOVA:$F_{1,46}$=0.50, NS) between the control pairs after initial set-up and experimental pairs after the female had received a new male. The following analyses used data from the successful pairs (n=15 for each group, 3 additional control pairs were not included in the analysis due to mechanical malfunction of the videorecorder).

There was no difference in latency to spawn of the successful pairs (Fig. 3.3; t_{28}, P=0.36). Most spawnings in each group occurred within 24 hr of the introduction/reintroduction of the new/paired male.

Intra-pair behavior

Aggression was much higher in the experimental pairs following the introduction of the new male than after the control males were removed and reintroduced to the female (χ^2_1=22.53, $P<0.05$). None of the control pairs, but 53% of experimental pairs exhibited mouthfighting (χ^2_1=10.91, $P<0.05$). Within the experimental pairs, females were more aggressive than males (Wilcoxon matched pairs, Z=3.107, $P<0.05$). The higher female aggression likely reflected that the females did recognize the new male was not her mate. Courtship behaviors also occurred significantly more often in experimental pairs (χ^2_1=10.99, $P<0.05$), with experimental males courting more than experimental females (Wilcoxon matched pairs, Z=3.17, $P<0.05$.

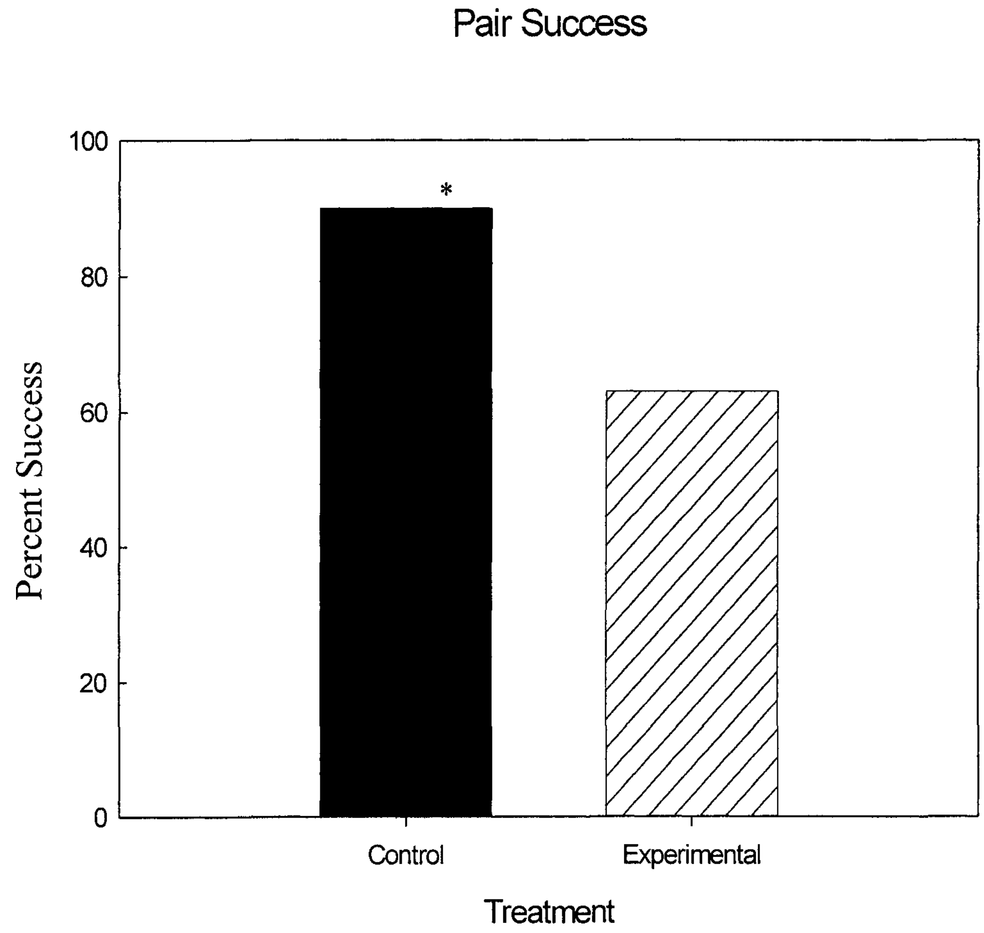

Figure 3.2. Pair Success. Pairs were successful if they reared offspring to the fry stage.

* = $p<0.05$.

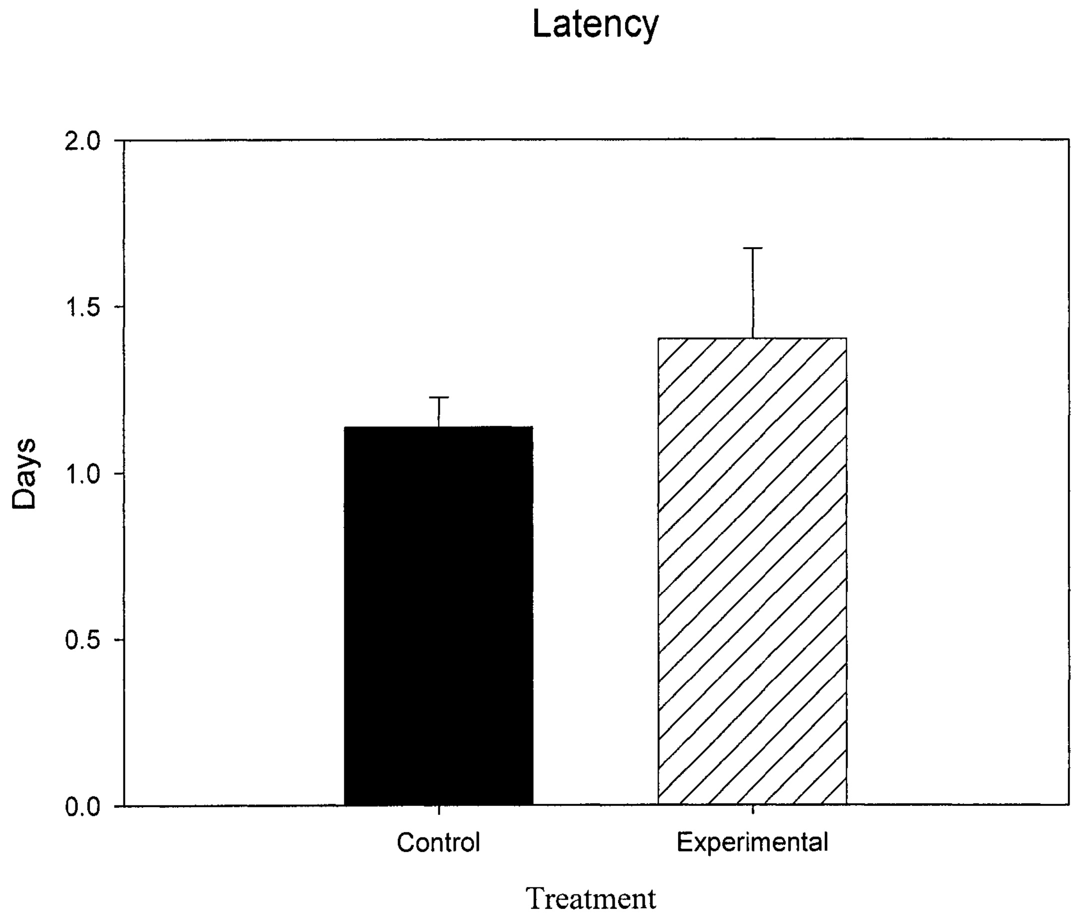

Figure 3.3. Latency to spawn for control and experimental pairs, as measured in days from the experimental manipulation to spawning.

Table 3.1. Descriptive statistics and results of chi-square analysis on aggressive, courtship, and disagreement behaviors directed toward the mate in the presence and absence of an intruder. An * denotes significance.

				Without Intruder			
		Control Mean	Median	Experimental Mean	Median	X^2	P
Aggression	Egg 2	0.07	0.00	1.60	0.00	6.14	0.01*
	Wrig 2	0.20	0.00	1.20	0.00	3.97	0.05*
	Wrig 5	0.00	0.00	1.57	0.00	4.36	0.04*
Courtship	Egg 2	0.80	0.00	0.67	0.00	0.60	0.44
	Wrig 2	0.93	1.00	0.93	1.00	0.19	0.67
	Wrig 5	1.54	1.00	1.43	1.00	0.30	0.58
Disagreement	Egg 2	0.13	0.00	0.40	0.00	2.16	0.14
	Wrig 2	0.13	0.00	0.47	0.00	1.68	0.20
	Wrig 5	0.00	0.00	0.50	0.00	4.36	0.04*
				With Intruder			
		Control Mean	Median	Experimental Mean	Median	X^2	P
Aggression	Egg 2	0.00	0.00	1.31	1.00	7.40	0.01*
	Wrig 2	0.40	0.00	1.13	0.00	0.13	0.72
	Wrig 5	1.31	0.00	2.36	0.50	3.50	0.06
Courtship	Egg 2	1.00	0.50	2.77	3.00	2.16	0.14
	Wrig 2	3.67	1.00	3.93	4.00	0.13	0.72
	Wrig 5	4.54	3.00	3.64	3.00	0.08	0.78
Disagreement	Egg 2	0.00	0.00	1.46	1.00	7.40	0.01*
	Wrig 2	4.00	0.00	2.00	1.00	0.13	0.72
	Wrig 5	3.38	0.00	4.64	2.00	0.54	0.46

In the absence of an intruder, aggression was higher in the experimental pairs during the entire parental bout than in control pairs (Egg 2: χ^2_1=6.14, P=0.01; Wriggler 2: χ^2_1=3.97, P=0.05; Wriggler 5: χ^2_1=4.36, P=0.04). When an intruder was introduced, aggression (combined male and female: mate aggression) was higher within the experimental pairs only in the Egg day 2 stage (χ^2_1=7.40, P=0.01) and the Wriggler day 5 stage (χ^2_1=3.50, P=0.06). Significantly more disagreement was seen in experimental pairs than control pairs only in Egg day 2 (χ^2_1=7.40, P=0.01).

Courtship behaviors were seen throughout the parental bout in both intruder absent and present groups (Table 3.1). There were no significant differences between the two groups on any of the parental days, whether an intruder was absent (Egg day 2: χ^2_1=0.60, P=0.44; Wrig. day 2: χ^2_1=0.19, P=0.67; Wrig. day 5: χ^2_1=0.30, P=0.58) or present (Egg day 2: χ^2_1=2.16, P=0.14; Wrig. day 2: χ^2_1=0.13, P=0.72; Wrig. day 5: χ^2_1=0.08, P=0.78).

Experimental pairs exhibited higher disagreement than controls (Table 3.1) during the Egg day 2 stage in the presence of an intruder (χ^2_1=7.40, P=0.01), and in the absence of an intruder on Wriggler day 5 (χ^2_1=4.36, P=0.04).

Offspring defense

Control and experimental pairs differed little in their offspring defense (Figs.3.4-3.6). There was no difference in time spent near the intruders when compared to controls

(Fig. 3.5) for males (Egg day 2: χ^2_1=0.42, P>0.05; Wrig. day 2: χ^2_1= 1.16, P>0.05; Wrig. day 5: χ^2_1= 0.31, P>0.05) or females (Egg day 2: χ^2_1=0.42, P>0.05; Wrig. day 2: χ^2_1= 1.16, P>0.05; Wrig. day 5: χ^2_1= 0.91, P>0.05. There was also no difference in the time spent with the offspring for males (fig 3.6, Egg day 2: χ^2_1=1.00, P>0.05; Wrig. day 2: χ^2_1=0.13, P>0.05; Wrig. day 5: χ^2_1=2.92, P>0.05) or females (Egg day 2: χ^2_1=1.01, P>0.05; Wrig. day 2: χ^2_1=0.13, P>0.05; Wrig. day 5: χ^2_1=1.73, P>0.05). Although the total percent of time females spent with either offspring or intruders was not different, experimental females spent more time at the intruder in the absence of her mate during the Egg day 2 (χ^2_1=3.84, P=0.05) and Wriggler day 5 (χ^2_1=6.08, P<0.05) stages (Fig. 3.5) than did control females.

There was no difference in the total number of bites directed toward the intruder for control or experimental males (Egg day 2: χ^2_1=0, P>0.05; Wrig. day 2: χ^2_1=1.1, P>0.05; Wrig. day 5: χ^2_1=0.04, P>0.05) or females (Egg day 2: χ^2_1=0.03, P>0.05; Wrig. day 2: χ^2_1=0.13, P>0.05; Wrig. day 5: χ^2_1=0.03, P>0.05). Bites at the intruder in the absence of the mate differed only on the fifth wriggler day for both males (Egg day 2: χ^2_1=1.0, P>0.05; Wrig. day 2: χ^2_1=0.13, P>0.05; Wrig. day 5: χ^2_1=4.30, P<0.05) and females (Egg day 2: χ^2_1=2.36, P>0.05; Wrig. day 2: χ^2_1=3.22, P>0.05; Wrig. day 5: χ^2_1= 4.27, P<0.05).

Table 3.2. Bites at the intruder. Mean and median number of bites directed toward the intruder by control and experimental malee and females, both total (a), and in the absence of the mate (b).

Total Bites

a)		*Control* Mean	*Control* Median	*Experimental* Mean	*Experimental* Median
	Egg 2	105.5	102	14.75	70.5
Male	Wrig 2	127.9	117	30	76.5
	Wrig5	137.8	103	41.5	80
	Egg 2	50.5	52	63.6	62.5
Female	Wrig 2	47.7	52	63.5	44.5
	Wrig5	44.2	28	60.5	13

Bites Alone

b)		*Control* Mean	*Control* Median	*Experimental* Mean	*Experimental* Median
	Egg 2	51.6	34.5	14.75	10.5
Male	Wrig 2	81.1	69	30	25.5
	Wrig5	84.2	71	41.5	46
	Egg 2	8.9	0	6.9	2
Female	Wrig 2	11.8	1	4.6	1.5
	Wrig5	0.77	0	4.8	2

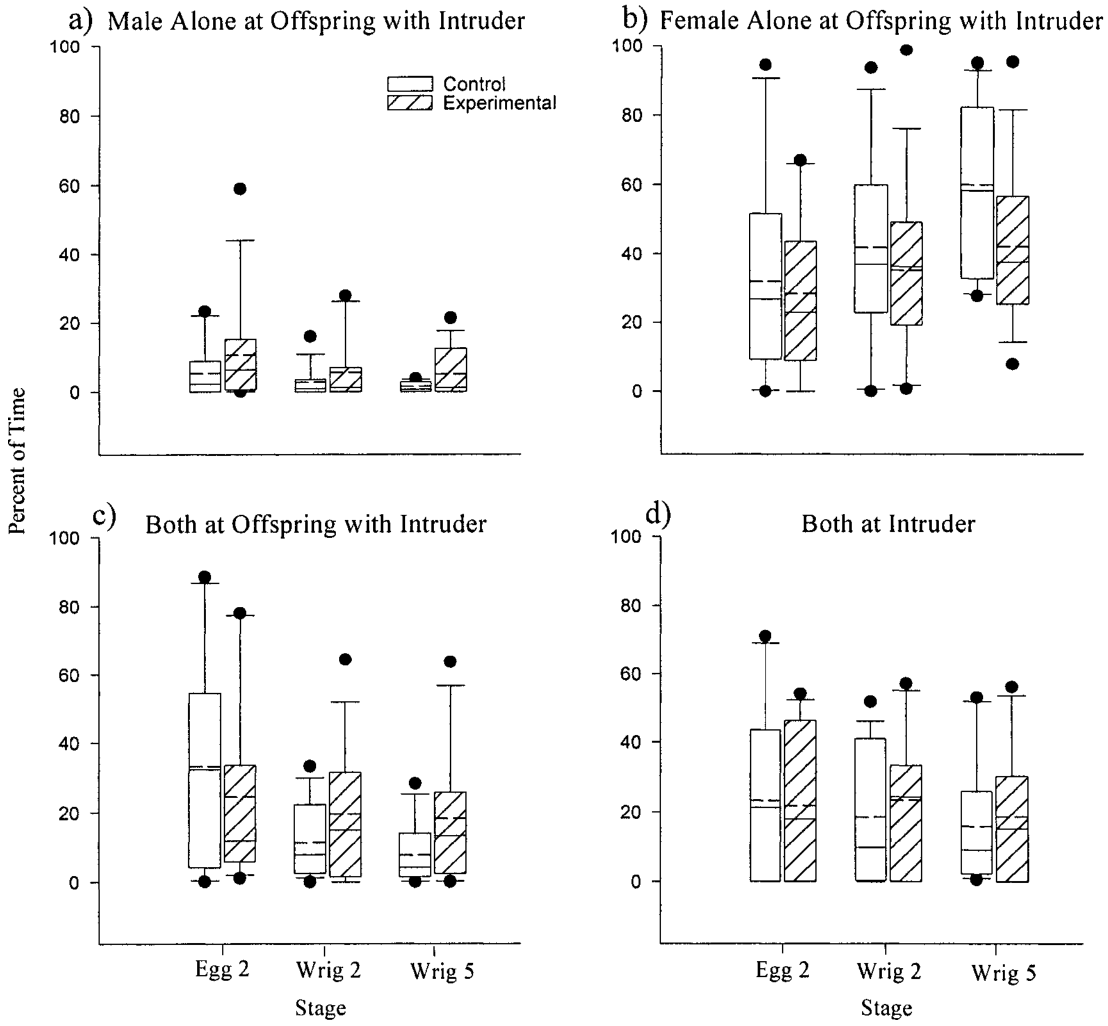

Figure 3.4. Percent of time per 5 min observations during the Egg day 2 (Egg 2) Wriggler day 2 (Wrig 2) and Wriggler day 5 (Wrig 5) stages that a) experimental and control males spent alone with the offspring with an intruder present, b) experimental and control females spent alone with the offspring with an intruder present, c) experimental and control males and females spent together with the offspring with an intruder present, and d) experimental and control males and females spent together near the intruder. Boxes = 25th and 75th quartiles, whiskers = 5th and 95th percentile, •=outlier, solid line (—) represents median, dashed line (– –).

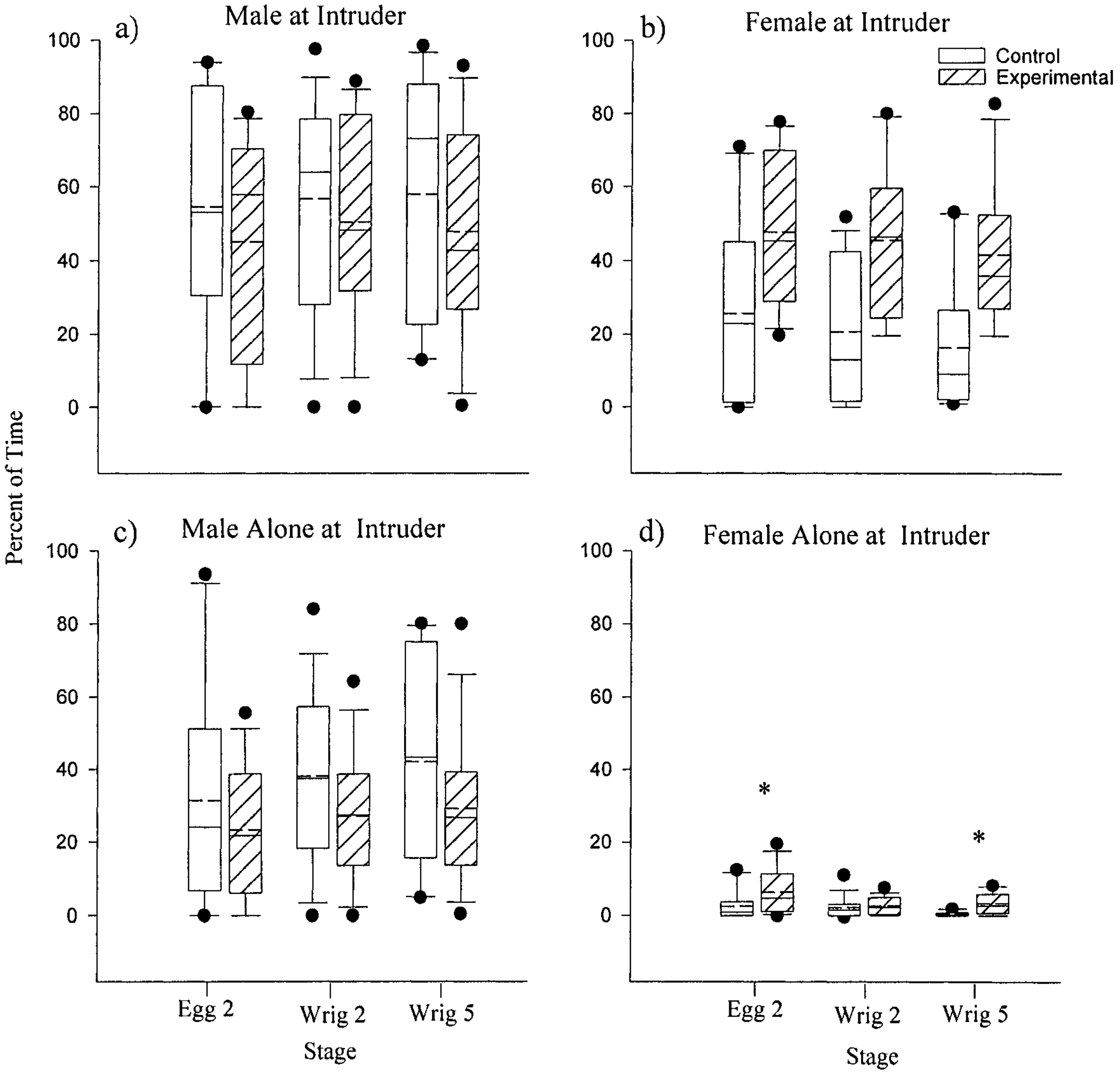

Fig. 3.5. Percent of time per 5 min observations during the Egg day 2 (Egg 2) Wriggler day 2 (Wrig 2) and Wriggler day 5 (Wrig 5) stages that a) experimental and control males spent near the intruder, b) experimental and control females spent near the intruder, c) experimental and control males spent without the female mate near the intruder, and d) experimental and control females spent without the mate near the intruder. Boxes = 25th and 75th quartiles, whiskers = 5th and 95th percentile, •=outlier, solid line (—) represents median, dashed line (– –).

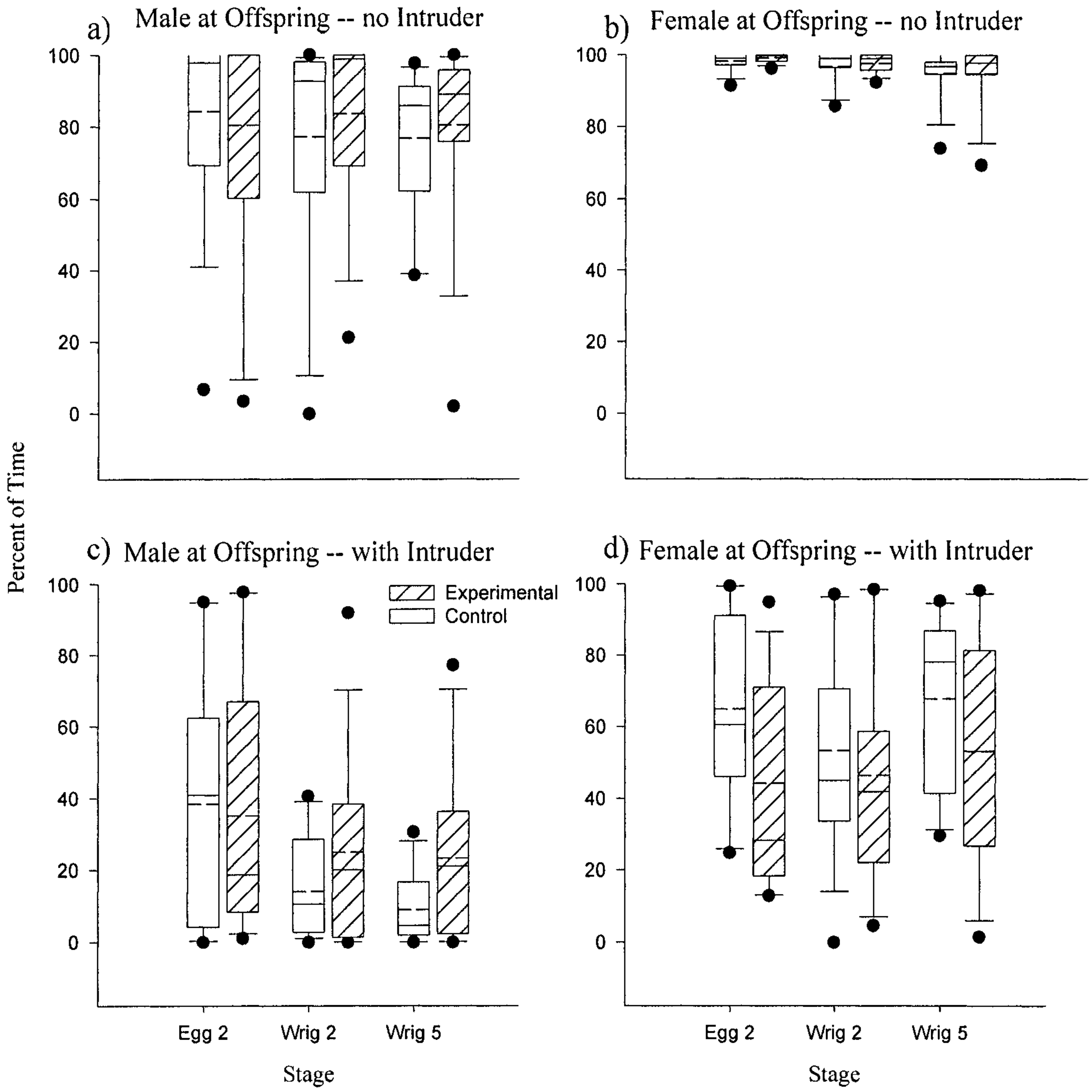

Fig. 3.6. Percent of time per 5 min observations during the Egg day 2 (Egg 2) Wriggler day 2 (Wrig 2) and Wriggler day 5 (Wrig 5) stages that a) experimental and control males spent near the offspring, intruder absent, b) experimental and control females spent near the offspring, intruder absent, c) experimental and control males spent near offspring, intruder present, and d) experimental and control females spent near the offspring, intruder present. Boxes = 25th and 75th quartiles, whiskers = 5th and 95th percentile, •=outlier, solid line (—) represents median, dashed line (– –).

Experiment 2

In the first part of Experiment 2, 5% of females removed from their males spawned. In the second part, 0% females laid eggs after the male was removed. In contrast, 6 of 10 females spawned within five days of the male's return to the aquarium. Three of the six spawned within two days of the male's return.

Discussion

My first hypothesis, that an extended courtship period is necessary for individuals to release gametes, was rejected after 15 of 24 pairs with abbreviated courtship spawned and successfully reared offspring. Itzkowitz (unpublished data) found that the typical likelihood of pair formation in randomly paired convict cichlids is 70-75%. Although experimental pairs had a significantly lower success than control pairs, they did not differ significantlyfrom the typical success of unfamiliar individuals. Females readily re-paired with an unfamiliar male after being on the verge of spawning with a previous male. The quick acceptance of the new mate suggests that mate selection is not the primary reason for the extended courtship of convict cichlids. The pair bond can be broken, and mate switching can occur, at any point prior to spawning. Switching sometimes occurred under laboratory conditions when pairs were mismatched, then allowed to re-pair (Triefenbach & Itzkowitz 1998). My data show that even seemingly matched pairs may switch. The possibility for mate switching could explain the pre-spawning mate guarding seen in these fish (Mackereth & Keenleyside 1993).

The acceptance of a new mate in this experiment likely was not the result of a physiological commitment of the female to expel her eggs. The results of Experiment 2 demonstrated that females do not have to expel eggs once primed. Females are able to forego spawning until a suitable mate is available. 60% of the females in experiment 2 laid eggs when the males were returned after 7 days. The ability to postpone spawning would allow a female to find a suitable mate in the event of the pre-spawning death or injury of a mate.

As previously stated, monogamous animals tend to exhibit longer courtship than do polygamous species. Their longer courtship period may give bonded pairs the opportunity to coordinate their parental roles before offspring production. For example, in the black wheatear, *Oenanthe leucura*, both members of a pair, but especially the male, carry stones to the nest before the eggs are laid (Moreno et al. 1994). The stones do not play a role in nest construction. Moreno et al. hypothesized that stone-carrying might allow the female to adjust her later foraging for the young according to her partner's foraging capability. Similarly, convict cichlids might assess the parental capabilities of the potential mate in preparation of offspring care. During the pre-spawning period, paired convict cichlids often chase conspecifics and (to a lesser degree) heterospecific fish (Mackereth & Keenleyside 1993; pers. obs.) in a fashion similar to that seen during parental care, which might allow each to assess the mate's future offspring defense ability.

Despite the shortened courtship, most experimental pairs reared offspring successfully to the fry stage. If courtship allows a pair to assess and coordinate each member's subsequent parental activity, then a pair would need to complete "courtship", even if a portion of the behaviors happened subsequent to spawning. Although experimental pairs did not exhibit significantly higher courtship levels during parental care, there was a trend. Sixty-nine percent of experimental pairs exhibited courtship behaviors during the Egg day 2 stage, while only 50% of control pairs did so. This trend did not continue in later parental stages. This suggests an attempt to compensate for lost courtship time. Experimental pairs showed more intra-pair aggression during the entire parental bout in the absence of an intruder. With an intruder present, intrapair aggression was higher during the Egg day 2 stage, but not during the Wriggler day 2 stage. This finding suggests that once a full courtship period has commenced, intrapair aggression may decrease while an intruder is present because the pair might focus on offspring defense. However, in the absence of an intruder, intrapair aggression still exists. This aggression indicates that pairs do need to complete courtship in order to eradicate lateraggression within the pair.

In both the control and experimental groups, courtship behaviors continued to be seen during the parental phase, albeit at a low rate. The courtship behaviors may serve to maintain the pair bond. Males and females of other monogamous species continue to display "courtship" behavior even after the young have arrived. For example, in the monogamous siamang (*Hylobates syndactylus*), Geissmann (1999) determined that the duets ("songs") that occur throughout the course of the pair bond (Geissmann 1999;

Geissmann & Orgeldinger 2000; Wachtmeister 2001) began upon pair introduction, and as the pair spent more time together the song changed until it reached a point of certain stability. Copulations did not begin until nearly two months after the beginning of duetting, and conception did not occur until the pair reached a particular stage in song formation. Intriguingly, the songs varied between pairs. When one member of a mated pair was given a new mate, each individual changed his/her song according to how the new mate also sang. Although there were species-typical general patterns in the songs, the songs themselves were pair-specific. Each pair sang a recognizably different song that was from those of other pairs. Again, this pair specificity began before conception but after pair formation. Such pair-specific displays may reflect the developing coordination needed for offspring care.

Convict cichlids exhibit similar pair specificity in parental care. Although males defend more while females spend more time with the offspring, the extent differs between pairs. However, within pairs there is a high degree of coordination (Itzkowitz et al. 2002). I hypothesize that the continuing performance of courtship behaviors throughout the parental bout allows parents to coordinate their activities as the offspring develop.

In summary, following an experimentally abbreviated courtship, pairs were able to spawn and rear offspring. Aggression and disagreement were subsequently higher in experimental pairs early in the parental phase, but not later. Courtship behaviors continued to be seen in both groups throughout the parental phase. I suggest that individuals of a pair assess the parental capabilities of the mate during the protracted courtship. Additionally, I suggest that the “courtship” behaviors seen later during parental care might allow the parents to reassess their activity as offspring requirements change (e.g. transition from egg care to offspring provisioning).

CHAPTER IV. THE IMPACT OF COURTSHIP DURATION ON THE PARENTAL CARE OF THE MONOGAMOUS CONVICT CICHLID. PART 2: FEMALE REMOVAL

A fundamental difference between males and females has its basis in anisogamy. Males produce large amounts of sperm at minimal physiological cost, while females expend considerable energy in the production of eggs (Trivers 1972; Krebs & Davies 1993). This difference in gamete cost has led to the belief that females should be choosy about mates. In contrast, males should be comparatively indiscriminant, since an unsuccessful copulation should have little impact on a male's fitness. In some species, males have elaborate ornaments or perform premating behaviors such as nuptial feeding of the female, which Trivers (1972) developed into the theory of parental investment. According to parental investment theory, the sex investing less into the offspring, typically the male, invest more in physical ornaments involved in sexual selection, or by assisting the female and/or offspring. As the behavioral investment of the male in the offspring increases, the level of ornamentation decreases, and the sexes become less dimorphic. However, even in monogamous, biparental species, a level of sexual dimorphism often exists (de Lope & Møller 1993; Mateos & Carranza 1997). Sexual dimorphism may indicate that although both sexes invest in the offspring, they might not use the same tactics. For example, in the monogamous biparental termite *Zootermopsis nevadensis*, males prefer females with large body mass and lipid stores (related to fecundity), while females select males for large heads (related to defense) (Shellman-Reeve 1999).

Convict cichlids (*Archocentrus nigrofasciatus*) also display sexual dimorphisms. For example, only females have patches of orange/red on their ventrum, whereas males have elongated dorsal fins compared to females. It is therefore possible that male and female convict cichlids employ different reproductive strategies. Although the convict cichlid is considered monogamous, the male is facultatively bigamous. Under field conditions some males occasionally have two mates, and in the laboratory males will sometimes pair with two females under female-biased conditions (Keenleyside 1985; Barlow 1991). Additionally, males in the natural habitat typically mate more frequently than females (Wisenden 1994b). Therefore, males may be more apt than females to accept a new mate if the first is lost, since males might more readily form new pair bonds.

A male that has lost his mate before copulation might be physiologically prepared to re-mate quickly (Adler 1978). In Atlantic salmon, *Salmo salar*, an increase in courtship intensity can accelerate the breeding sequence (de Gaudemar et al. 2000). A male who has previously courted (but not spawned with) a female might be physiologically primed and may attempt to accelerate the courtship period with a new female. An accelerated courtship pace in the convict cichlid would likely present itself as an increased frequency of courtship behaviors. In spite of the accelerated pace, both individuals will have undergone a courtship period, and thus might not exhibit abnormal intra-pair behaviors.

I hypothesized that males would court new females at elevated levels, compared to how the original females were courted. Elevated male courtship levels might be an attempt to hasten a new female's spawning-readiness, thereby abbreviating courtship duration. If true, I expected that males presented with new females would spawn more quickly than males with original females. However, females might not respond to an elevated courtship, requiring a courtship of typical duration in order to spawn. Alternatively, the males might not increase courtship intensity, and pairs would exhibit typical courtship periods. Whether or not males attempted to accelerate courtship, and whether or not females responded to the male's possibly accelerated courtship, I predicted typical parental behaviors because both individuals of the parental pair would be involved in a courtship period. Conversely, if both members of a pair require an uninterrupted courtship, disagreements (see Definitions, chapter 1) could occur since the male's original courtship was interrupted.

Methods

Aquaria were assembled as described in the General Laboratory Methods (chapter 1). When the female was within 24 hours of spawning, she was removed and a novel female of the same size introduced into the aquarium (termed "original" and "new" females, respectively). For controls I removed the female from the aquarium and immediately returned her. I videotaped for 10 min each day for the first three days after the male and female were introduced (first 3 days for each female in experimental pairs) in order to measure the aggressive and courting behaviors. Once eggs were laid, I videotaped for 15 min without an intruder and 15 min with an intruder on the second day of the egg stage, and on days 2 and 5 of the wriggler stage.

Data were taken from the videotapes and entered into an event recorder (BEAST Professional, v1.01). I quantified courtship, aggressive, and disagreement behaviors within the pair, the time each parent spent near the offspring and near the intruder, latency to spawn, and attacks upon the intruder. The study concluded with N=15, however, due to one experimental pair laying the eggs on the filter box in the middle of the "other" region, the analysis was concluded with 15 control and 14 experimental pairs. Due to malfunctions of the video recorder, I had complete courtship data for 13 experimental pairs. For the analysis of experimental courtship behaviors, the Wilcoxon Matched Pairs Test was performed. Unless otherwise stated, Median tests followed by chi-square tests were used to analyze the parental data. Due to many low counts, the categories were also lumped into an aggression coefficient, courtship coefficient, and disagreement coefficient.

Results

Experimental pairs' success at rearing the offspring through the wriggler stage (83%) did not differ from controls (88%, fig.4.1, $\chi^2_1=1.06$, $P>0.05$). Both were not significantly different than the success rate (73%) typically seen in our laboratory (unpub. data).

Latency to spawn was measured from the day of first introduction of the male and female. For control pairs, day 1 was the day the aquarium was set up, while for experimental pairs, day 1 was the day the new female was introduced to the aquarium. The experimental pairs took significantly longer to begin spawning than control pairs (fig. 4.2, χ^2_1=6.53, P=0.01).

Courtship Phase

Pairs including the original female spent a significantly larger percent of time together at the flower pot than pairs with a new female (fig. 4.3, Z=2.55, P=0.01). New females spent more time at the intruder (Z=2.97, P=0.002) and at the other area (Z=3.11, P=0.001), and subsequently less at the flower pot (Z=2.06, P=0.04).

Males chased the new females more than the original females (Z=2.85, P=0.004). Pairs with the new female had higher overall aggression coefficients (fig. 4.4, Z=2.85, P=0.004).

There were no significant differences in the performance of individual courtship behaviors or in the courtship coefficient (fig. 4.4, Z=0.97, P=0.33).

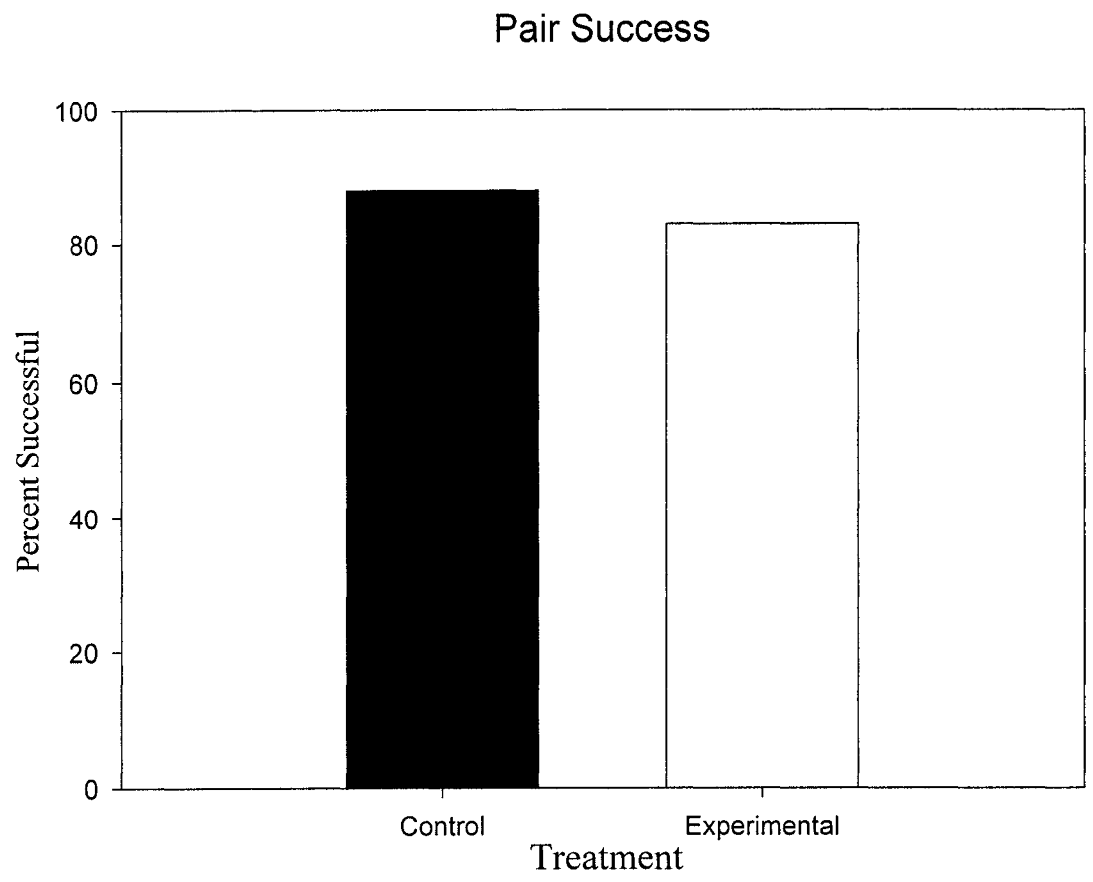

Figure 4.1. Pair Success. Pairs were successful if they reared offspring to the fry stage.

P=NS

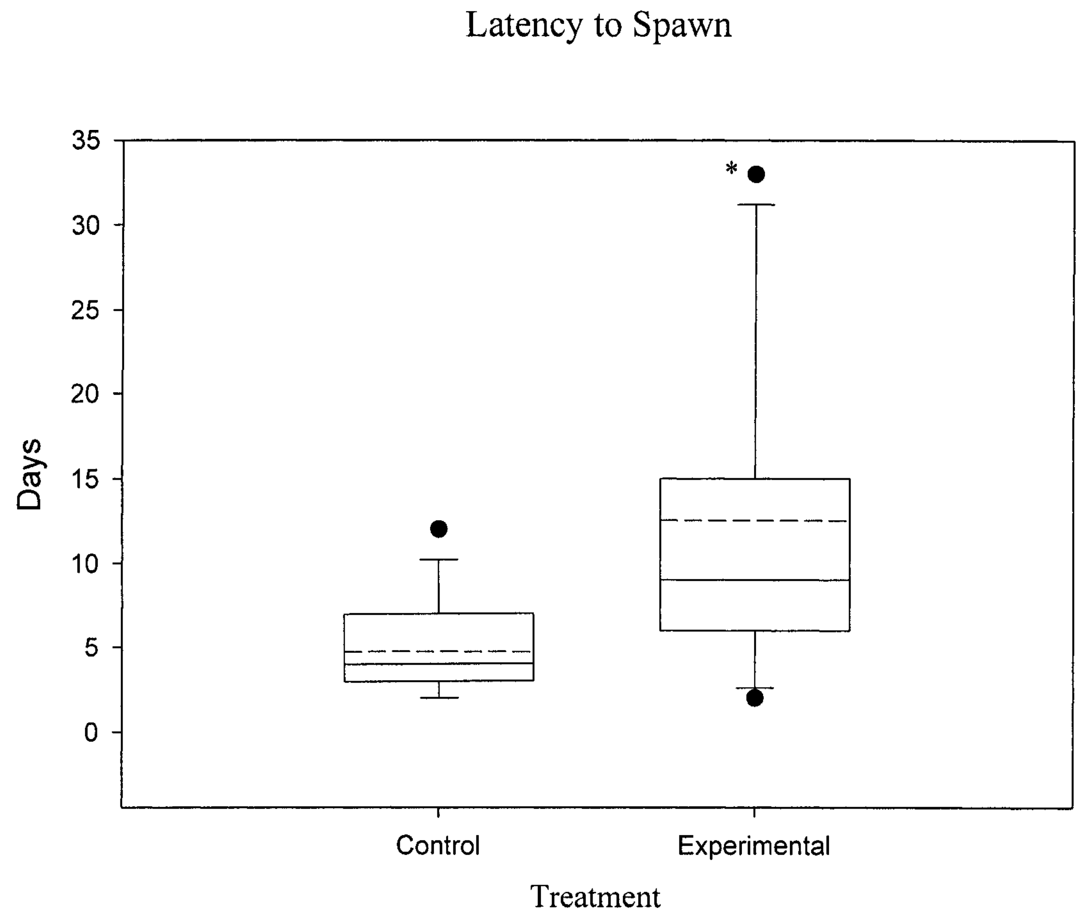

Figure 4.2. Latency to spawn, as measured by the number of days from first introduction of a male and female until spawning occurred. Boxes = 25th and 75th quartiles, whiskers = 5th and 95th percentile, * = $p<0.05$., •=outlier, solid line (—) represents median, dashed line (– –).

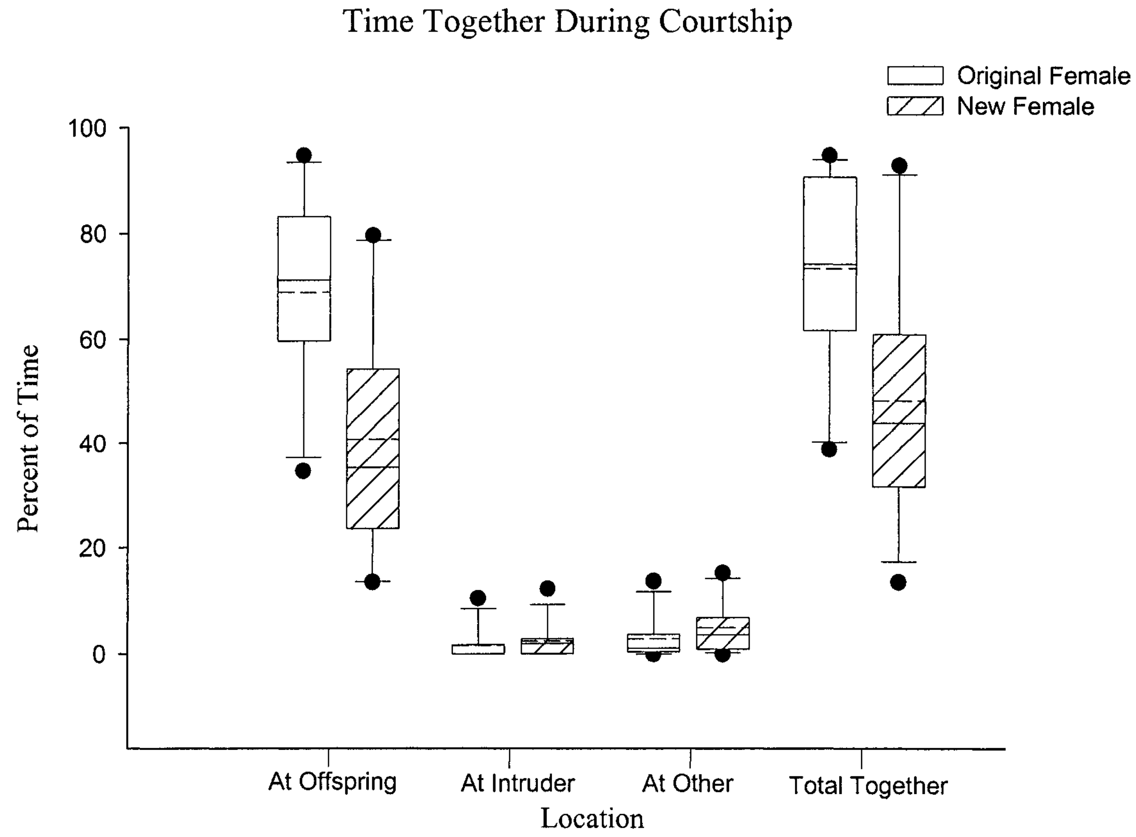

Figure 4.3. Time spent together during the courtship phase near the offspring area (no offspring present), the intruder area, the other area, and the combined total time together. Boxes = 25th and 75th quartiles, whiskers = 5th and 95th percentile, * = $p<0.05$., ●=outlier, solid line (—) represents median, dashed line (– –).

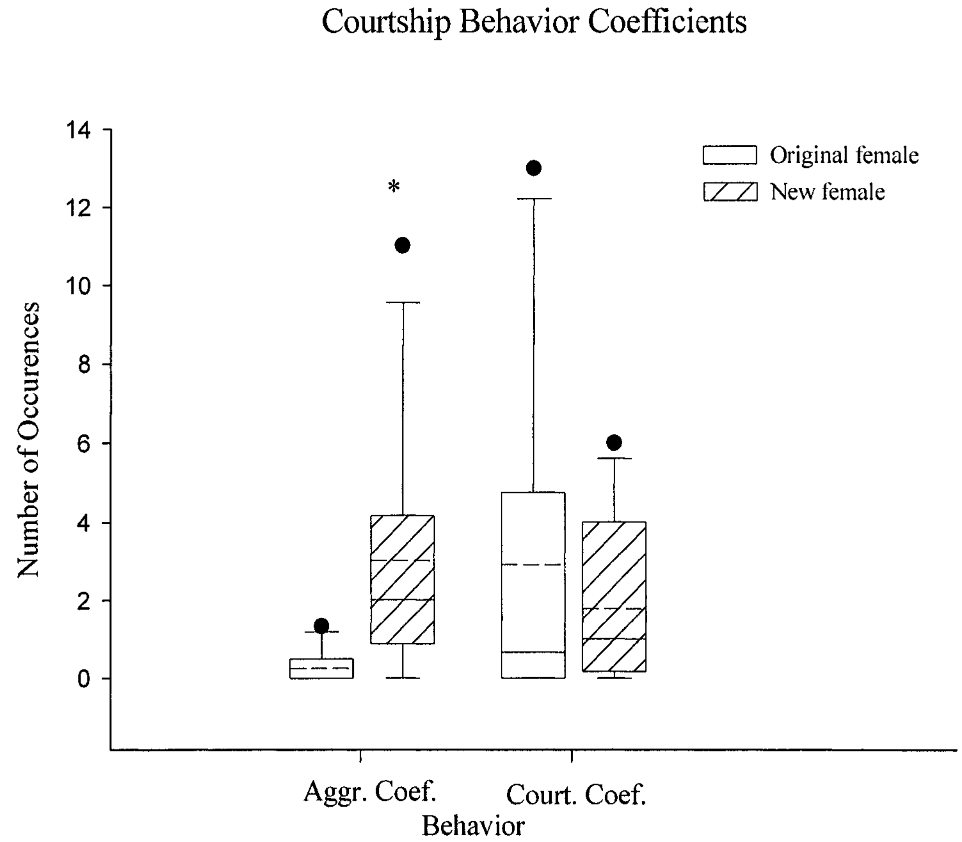

Fig. 4.4. Aggression (Aggr.) and courtship (Court.) coefficients (Coef.) during courtship in experimental pairs while either the original or new female is in the aquarium. Boxes = 25th and 75th quartiles, whiskers = 5th and 95th percentile, * = $p<0.05$., ●=outlier, solid line (—) represents median, dashed line (– –).

Parental Phase

During the second day of the egg stage, in the absence of an intruder, experimental males spent a larger percent of time at the pot (fig. 4.5, χ^2_1=3.85, P=0.05) and in the other area (χ^2_1=3.85, P=0.05) than control males. Females did not exhibit this trend (at pot χ^2_1=0.15, P=0.69; at other χ^2_1=1.42, P=0.23). With an intruder present, experimental pairs spent more time with both individuals in the other area (χ^2_1=6.74, P=0.01). There were no differences during subsequent stages (Wrig. 2, χ^2_1=0, P=1.0; Wrig 5, χ^2_1=2.38, P=0.12 . There were no differences seen in time spent at the intruder for any stages (fig. 4.6).

No significant differences in intrapair aggression were seen during any of the parental stages in the absence (fig. 4.7; Egg 2, χ^2_1=0.01, P=0.93; Wrig. 2, χ^2_1=0.04, P=0.84; Wrig. 5, χ^2_1=0.10, P=0.76) or presence (fig. 4.8) of an intruder.

Experimental pairs exhibited a significantly higher courtship coefficient during the egg day 2 stage in the presence of an intruder (fig. 4.8, χ^2_1=5.00, P=0.03), but not in the absence of the intruder (fig. 4.7, χ^2_1=0, P>0.99). No significant differences were seen during the other parental stages.

Experimental pairs during the egg day 2 stage had a higher disagreement coefficient both with no intruder (fig. 4.7, χ^2_1=4.89, P=0.03), and with an intruder present (fig. 4.8, χ^2_1=6.77, P=0.01). Additionally, during the second day of the egg stage in the absence of an intruder, experimental females butted their males more than did control females both without an intruder present (χ^2_1=4.72, P=0.03), and with one present (χ^2_1=5.15, P=0.02). Males showed no difference in butting during the egg stage (χ^2_1=2.17, P=0.14, χ^2_1=2.36, P=0.12, respectively). During the wriggler day 2 stage, experimental males butted their mates more than control males did only in the presence of an intruder (χ^2_1=5.51, P=0.02), but females did not (χ^2_1=0.10, P=0.76). There were no differences during the wriggler day 5 stage.

During the second day of eggs, experimental females displayed more bites at the intruder, both total (χ^2_1=5.54, P=0.02), and in the presence of the mate (χ^2_1=3.95, P=0.05). No significant differences were seen during the wriggler stages.

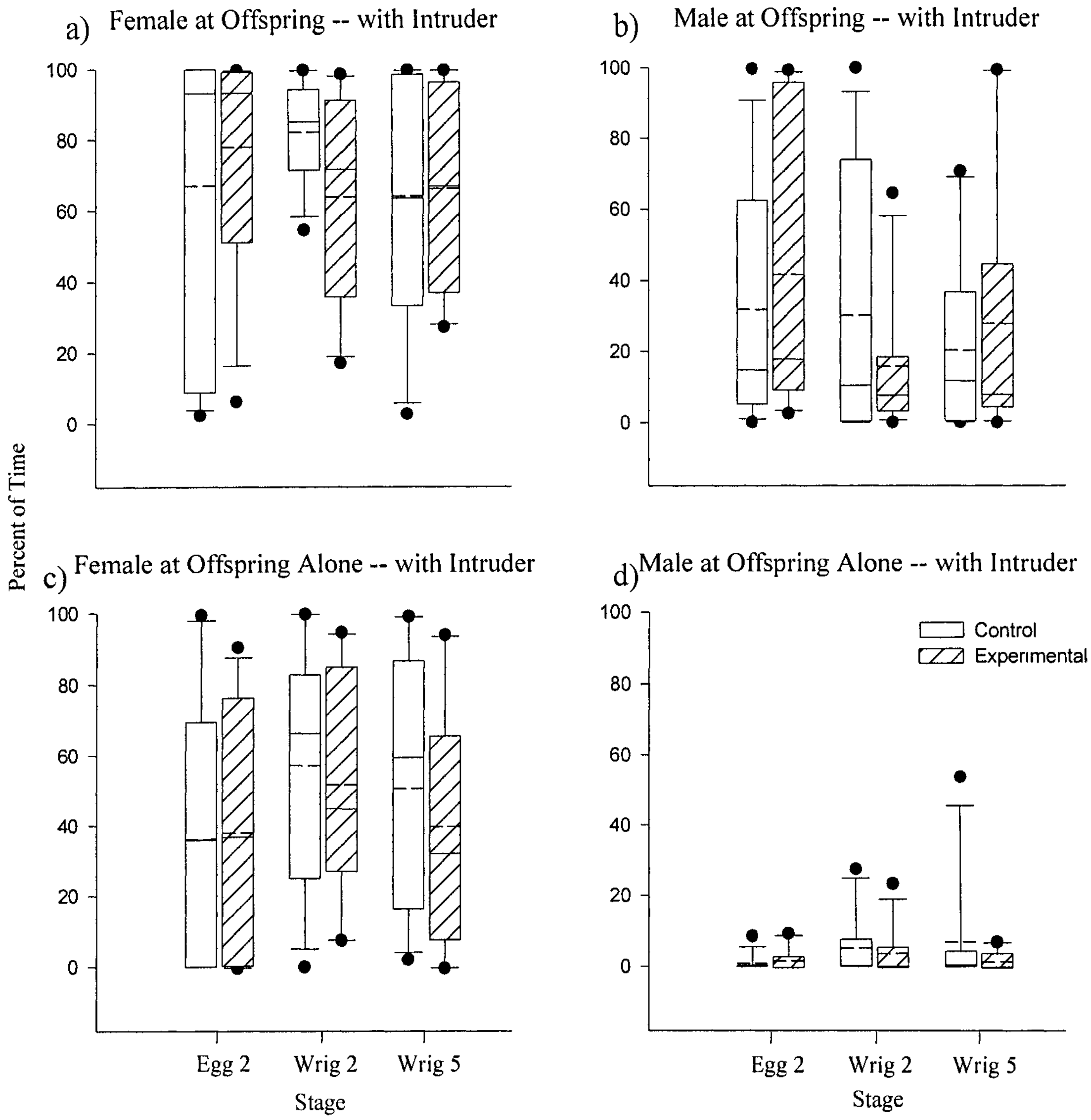

Fig. 4.5. Percent of time per 5 min observations during the Egg day 2 (Egg 2) Wriggler day 2 (Wrig 2) and Wriggler day 5 (Wrig 5) stages that a) experimental and control females spent near the offspring, b) experimental and control males spent near the offspring, c) experimental and control females spent without the male mate near the offspring, and d) experimental and control males spent without the female mate near the offspring. In all cases the intruder was present in the intruder compartment. Boxes = 25th and 75th quartiles, whiskers = 5th and 95th percentile, •=outlier, solid line (—) represents median, dashed line (– –).

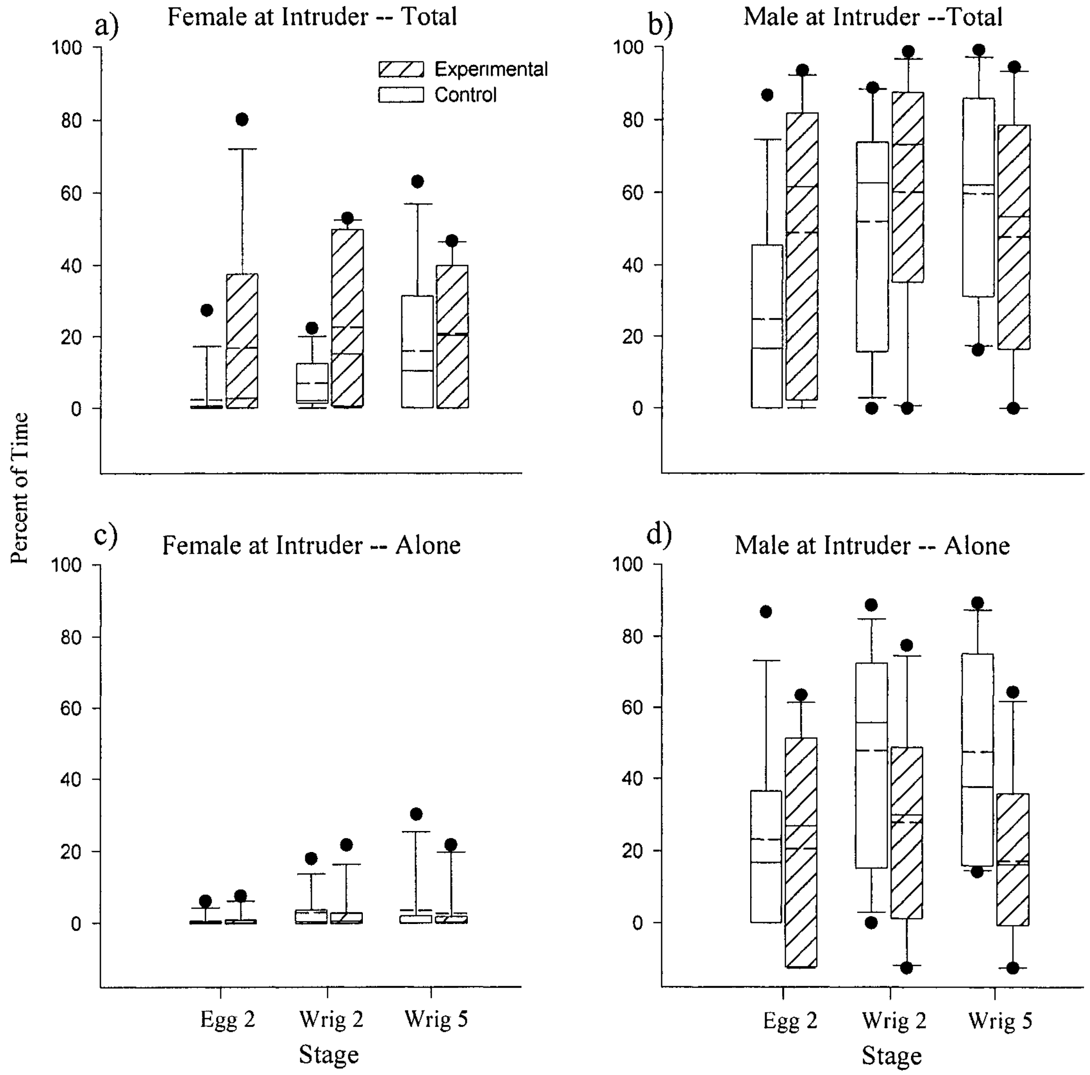

Fig. 4.6. Percent of time per 5 min observations during the Egg day 2 (Egg 2) Wriggler day 2 (Wrig 2) and Wriggler day 5 (Wrig 5) stages that a) experimental and control females spent near the intruder, b) experimental and control males spent near the intruder, c) experimental and control females spent without the male mate near the intruder, and d) experimental and control males spent without the female mate near the intruder. In all cases the intruder was present in the intruder compartment. Boxes = 25th and 75th quartiles, whiskers = 5th and 95th percentile, •=outlier, solid line (—) represents median, dashed line (– –).

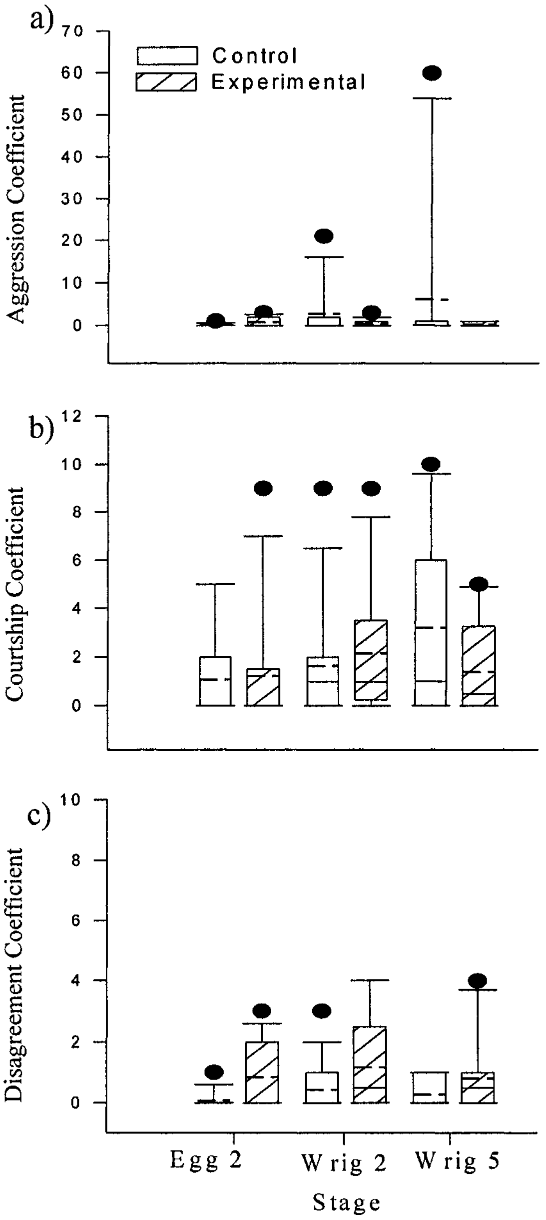

Fig. 4.7. Behavioral counts per 5 min observations during the Egg day 2 (Egg 2) Wriggler day 2 (Wrig 2) and Wriggler day 5 (Wrig 5) stages in the absence of an intruder for a) experimental and control intra-pair aggression, b) experimental and control courtship, c) experimental and control disagreement. Boxes = 25th and 75th quartiles, whiskers = 5th and 95th percentile, •=outlier, solid line (—) represents median, dashed line (– –).

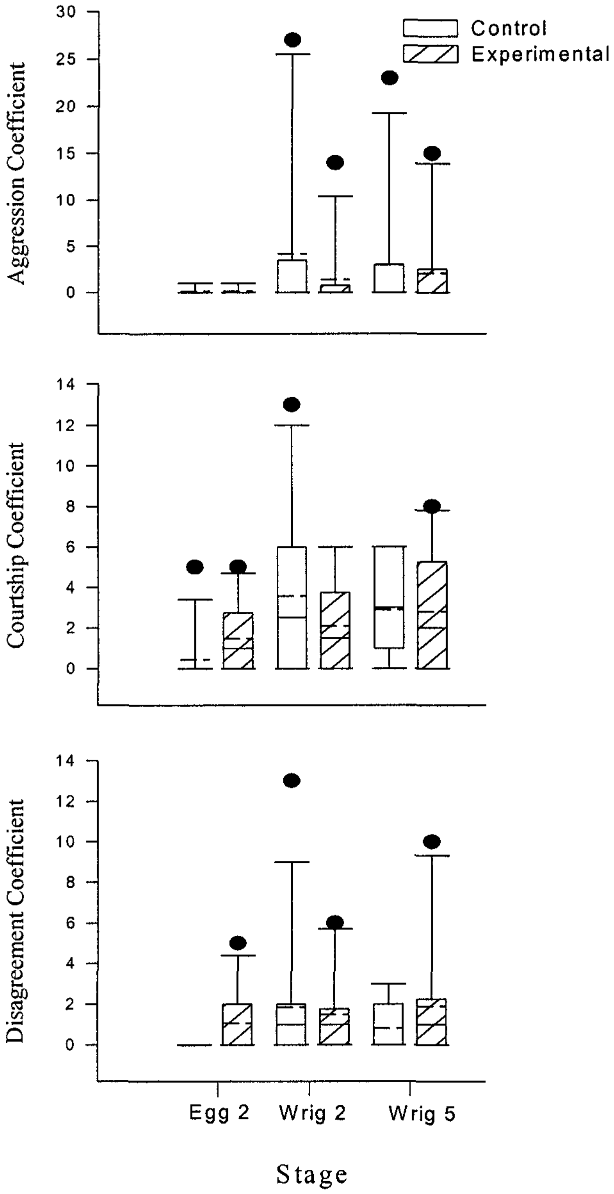

Fig. 4.8 . Behavioral counts per 5 min observations during the Egg day 2 (Egg 2) Wriggler day 2 (Wrig 2) and Wriggler day 5 (Wrig 5) stages in the presence of an intruder for a) experimental and control intra-pair aggression, b) experimental and control courtship, c) experimental and control disagreement. Boxes = 25th and 75th quartiles, whiskers = 5th and 95th percentile, •=outlier, solid line (—) represents median, dashed line (– –).

Discussion

Although experimental and control pairs did not differ in mating success, experimental pairs showed a much longer latency to spawn. Additionally, experimental males showed no differences in courting behaviors from control males, despite being within hours of spawning with the original female and thus, presumably, had primed physiologies. I rejected my original hypothesis that males would court new females at a higher rate. Males also showed increased aggression toward the new females. This aggression toward new females indicates that males typically undergo courtship with only one female at a time, and may require intervining time before courting a new female. Keenleyside (1985) found that bigamous males averaged 7 days between spawnings, roughly the time required for eggs to develop into fry. Perhaps bigamous males stagger courting females in a way that insures having only one brood of immobile offspring at a time.

My results differ from those of removing a male mate and introducing a new male to a female primed to spawn (chapter 3.). In both studies, aggression was increased after the introduction of a new mate, but, in the previous study, latency to spawn was not different between control and experimental groups. The present study suggests that males require more time to accept a new female as a mate than females require to accept a new male as a mate. This requirement might indicate that males form lasting attachments to the female, whereas females may be more concerned with reproduction. Females perform most of the early offspring rearing behaviors, which could lead to a stronger attachment to the offspring. The differing attachment of the sexes is supported by a previous finding (Itzkowitz et al. 2003) that male parents are more attached to the females while females are more attached to the offspring. Attachment to the female could increase a male's vigilance while guarding the nest during the egg and wriggler stages while the female may be in the more vulnerable position of providing direct offspring care.

In the present study, experimental (disrupted) pairs showed higher disagreement during the egg stage. The increased disagreement did not support my hypothesis that pairs would not exhibit differences in parental care. Experimental females directed more total bites at the intruder and in the presence of the mate. Increased female bites might indicate that individuals' roles were yet unclear, with the experimental female more likely than control females to "back up" her male against the intruder. Both parents attacking the intruder could cause intrapair aggression (Itzkowitz et al. 2003). If parents have not yet determined their respective roles, intrapair aggression could be even more intense. In the presence of an intruder, courtship was also more intense. If courtship helps to coordinate parental roles, courting may allow pairs to determine their roles. If respective roles are not yet determined, individuals of a pair might attempt to do so under a threat to the offspring.

In the present study, the differences in behavior seen during the egg stage were not seen during the wriggler stages, which indicates that, as in the previous study (chapter 3), pairs were able to determine their roles. Under predation pressure in the natural habitat, it would be important for pairs to coordinate their roles, particularly before the offspring are mobile. Once mobile, the pair provides both direct care and protection. Disagreement over roles could lead to unprotected fry. In the field, such unprotected offspring are quickly predated (Keenleyside 1978). As in Chapter 3, both control and experimental pairs continued to display "courtship" behaviors throughout the parental phase. I suggest that the performance of "courtship" behaviors after spawning is one method by which parents determine their roles as offspring needs change.

In summary, after males lost their mate before spawning, the newly formed pairs were able to spawn and rear offspring although latency to spawn was longer in experimental pairs than in control pairs. Courtship behaviors were higher in experimental pairs early in the parental phase, but were not different later. Courtship behaviors continued to be seen in both groups throughout the parental phase. I suggest that individuals of a pair assess the parental capabilities of the mate during the long courtship period. Additionally, I suggest that the "courtship" behaviors seen later during parental care might allow the parents to coordinate their activity as offspring needs change.

CHAPTER V. GENERAL DISCUSSION

This dissertation examined the relationship between courtship and parental care in the convict cichlid. Despite extensive use of convict cichlids in laboratory experiments, no one had previously validated their use. Chapter 2 was the first study to compare laboratory behaviors to field behaviors during the courtship and parental phases. I determined that convict cichlids do not exhibit novel behaviors when used in laboratory experiments, and are therefore valid laboratory animal models.

In the laboratory, parents decrease vigilance in offspring defense by leaving the young unattended more than in the field. Time away from the offspring explained most of the increased variability seen in laboratory pairs, which may be a result of laboratory methods in which intruders only appear in one area.

In chapter 3, I explored the relationship of courtship duration to parental care by attenuating courtship. For this experiment, males were removed and replaced by a new male when the female was within hours of spawning. A normal, extended courtship was not necessary for pairs to rear offspring successfully to the fry stage. The success rate of experimental pairs did not differ from that of control pairs, and reflected that females on the verge of spawning would readily re-pair with an unfamiliar male. The quick acceptance of the new mate suggested that mate selection is not the primary reason for extended courtship in convict cichlids. The pair bond can be broken, and mate switching can occur, at any point prior to spawning. The possibility for mate switching could explain the pre-spawning mate guarding seen in these fish (Mackereth & Keenleyside 1993).

The quick acceptance of a new mate was not the result of a physiological requirement of the female to spawn. The results of experiment 2 demonstrated that reproductively primed females do not have to spawn, but are able to retain their eggs until a suitable mate is located. The ability to postpone spawning could allow a female adequate time to find a suitable mate in the event of the pre-spawning death or injury of a mate.

For the final experiment (chapter 4), I disrupted courtship by removing females near spawning from the males, and introducing new females. Although no difference existed in success between experimental and control pairs, experimental pairs showed a longer latency to spawn after mate introduction. Additionally, experimental males showed no differences in courting behaviors from control males, despite being within hours of spawning with the original female and thus had primed physiologies. Males also showed increased aggression toward the new females compared to the original females. This aggression toward new females indicates that although males may become bigamous if conditions allow, they only undergo a courtship with one female at a time, and may require time before committing to a courtship with a new female.

In both studies (chapters 3 and 4), aggression after the introduction of a new mate was increased, but males require more time to accept a new female as a mate if pair bonded. The slow acceptance of a new mate by males might indicate that males form attachments to the female, whereas females may be more concerned with reproduction. Females perform most of the early offspring rearing behaviors, which could lead to a stronger attachment to the offspring. The respective male and female attachments are supported by a previous study (Itzkowitz et al. 2003) which found that male parents are more attached to the females while females are more attached to the offspring. Attachment to the female could increase a male's vigilance while guarding the nest during the egg and wriggler stages while the female may be in a more vulnerable position while providing direct offspring care.

In chapters 3 and 4, experimental pairs with disrupted courtship showed either increased aggression or disagreement early in the parental phase. Also in both experiments, courtship behaviors occur more in experimental pairs during the egg stage. If courtship helps a pair to coordinate parental roles, and if respective roles have not been determined prior to spawning, individuals of a pair might attempt to do so post-spawning, especially when confronted by a threat to the offspring.

In all groups, courtship behaviors continued to be seen during the parental phase, albeit at a low rate. The continuation of courting behaviors may maintain the pair bond. Males and females of other monogamous species continue to display "courtship" behavior even after the young have arrived (Epple 1978; Erickson 1978; Anderson 1984; Moreno et al. 1994; Geissmann 1999; Geissmann & Orgeldinger 2000; Johnson et al. 2000; Wachtmeister 2001). Although male convict cichlids in general defend more while females spend more time with the offspring, the extent to which these generalities occur differ between pairs. However, within pairs there is a high degree of coordination (Itzkowitz et al. 2002). I propose that the continuing performance of courtship behaviors that I found throughout the parental bout allows the parents to coordinate their activities as the offspring develop.

In summary, following a manipulated courtship period, pairs were able to spawn and rear offspring. Courtship behaviors continued to be seen in both groups throughout the parental phase. I suggest that individuals of a pair assess the parental capabilities of the mate during the long courtship period. Additionally, I suggest that the "courtship" behaviors seen later during parental care might allow the parents to coordinate their activity as offspring needs change.

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