Title

MALE QUALITY INFLUENCES INTERSEXUAL DYNAMICS, BUT NOT FEMALE INTRASEXUAL COMPETITION, IN A MONOGAMOUS, BIPARENTAL FISH

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MALE QUALITY INFLUENCES INTERSEXUAL DYNAMICS, BUT NOT FEMALE INTRASEXUAL COMPETITION, IN A MONOGAMOUS, BIPARENTAL FISH

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in

ECOLOGY AND EVOLUTIONARY BIOLOGY

by

Ashley R. Robart

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The Dissertation of
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Abstract

Male quality influences intersexual dynamics, but not female intrasexual competition,
in a monogamous, biparental fish

by

Ashley R. Robart

Female preference for higher quality males can influence both intrasexual and intersexual dynamics. In species with biparental care, male quality can influence not only the female's initial gametic investment but also the amount of care each parent provides to the offspring. Here, I describe studies of female reproductive investment in response to male size, an indicator of quality, and the effect of female intrasexual selection on parental behavior in the convict cichlid (*Amatitlania siquia*), a monogamous, biparental fish.

In Chapter 1, I observed breeding patterns in a natural population in Costa Rica and found that females increased their parental care when paired with larger males. Male size was positively correlated with offspring number, indicating a benefit to females from pairing with larger males. In Chapter 2, using a controlled breeding experiment, I investigated trade-offs in female fecundity and parental care within and between breeding events in response to male size. I found that females initially paired with small males had a greater probability of failing to successfully breed. Females did not increase their fecundity when paired with large males, but did increase their parental care and defensive behaviors. However, females did not benefit from pairing with larger males because they had fewer offspring. Male size did not significantly affect female parental care behavior during the second breeding, and fecundity again did not differ between females paired with small and large males. In Chapter 3, I presented breeding pairs with non-reproductive and reproductive female conspecific intruders. I found that parental females behaved more aggressively towards reproductive intruders, which were a threat to their mating status, compared to non-reproductive intruders, which were only a threat to their offspring. Female size, rather than male size, predicted parental female response to intruders, with small females behaving more aggressively. Males preferred to associate with the reproductive intruder, as it represented a potential new mate.

The results of this dissertation demonstrate that females increase their parental care, but not their fecundity, for larger males. Moreover, females appear to use their prior breeding experience when allocating resources to the current reproductive event, as females did not increase their parental care when paired with large males during their second mating because large males failed to provide any benefits during the initial breeding. Male quality influences intersexual dynamics, but not intrasexual interactions, suggesting that females may be altering their response to the threat of male desertion. Overall, these results suggest that increased female investment may stabilize the pair-bond between the parents, which ultimately increases female reproductive success.

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The text of this dissertation includes a reprint of the following previously published material:

Chapter 1: Robart, AR. 2012. Effect of mate quality on maternal reproductive effort in the convict cichlid, *Amatitlania siquia*. Current Zoology. **58:** 66-72.

Introduction

Parental care patterns of a species are shaped by both mating dynamics and the degree to which sexual selection influences the evolution of traits in each sex (Trivers 1972; Clutton-Brock 1991). Male quality is a strong driver of both intra- and intersexual interactions (Andersson 1982; Candolin 1999; Jones and Hunter 1999). Numerous theories hypothesize why females should choose more attractive males (Fisher 1930; Zahavi 1975; Hamilton and Zuk 1982), but for female choice to be adaptive, males must provide some type of benefit to either the female or her offspring. Direct benefits to females include access to resources (Howard 1978; Gwynne and Simmons 1990; Pizzari and Tommaso 2003), while indirect benefits include superior genetic quality conferred to the offspring (Petrie et al. 1992; Reynolds and Gross 1992; Sheldon et al. 1997) or increased attractiveness in sons (Wedell and Tregenza 1999). In animals that breed multiple times partner quality will likely vary between breeding events and can influence reproductive trade-offs. Reproductive trade-offs can occur within and between breeding events (Williams 1966; Trivers 1972; Stearns 1992) as organisms attempt to maximize their lifetime reproductive success.

In species with biparental care, parents cooperate to jointly rear the offspring to independence, but conflict can arise over the amount of care provided to the young (Lendvai et al. 2009; Johnstone et al. 2014; Creighton et al. 2015). Conflict can occur if a parent decreases its effort to save resources for future reproduction (Harrison et al. 2009; Morales et al. 2010) or if there are additional mating opportunities (Eggert and Sakaluk 1995). Just as females prefer high quality males, female quality can also influence male mating decisions (Shapiro et al. 1994; Gage and Barnard 1996; Engqvist and Sauer 2002) when female quality influences offspring number and quality. When there are differences in the quality of the two parents, Burley (1986) hypothesized that the less attractive partner could stabilize the pair-bond between the parents by increasing it's own investment, and thereby ensure its partner's continued effort. The Differential Allocation Hypothesis (Burley 1986, 1988) posits that the less attractive parent increases it's own reproductive investment to capitalize on the benefits of obtaining a partner of higher than expected quality. Thus, even though it potentially reduces its future reproductive potential, it maximizes its lifetime reproductive success due to the higher quality partner's effect on offspring fitness. Differential allocation has subsequently been applied to all instances in which individuals, typically females, increase their investment due to mate quality, including adjustments in offspring number (Simmons 1987; Petrie and Williams 1993; Balzer and Williams 1998; Evans et al. 2010) and quality (Cunningham and Russell 2000; Uller et al. 2005; Gilbert et al. 2006).

Investigations of the Differential Allocation Hypothesis (Burley 1986) have had a strong emphasis on avian taxa, likely due to the widespread pattern of biparental care. While our understanding of differential allocation has been greatly expanded as a result of these studies, it limits our understanding of what factors are likely to be influential in other taxa. The need to expand the study of differential allocation was emphasized by Ratikainen and Kokko (2010) as a way to test the generality of hypotheses. While parental care occurs in only 20% of all fish families (Blumer 1982), all of the 1000 currently recognized species of cichlids exhibit either uniparental or biparental care of the offspring (Keenleyside 1991). Burley's (1986) narrower focus on the role of differential allocation in maintaining pair-bonds is applicable to many species of cichlids as two parents are more effective at defending offspring than one (Wisenden 1994a). Additionally, as fish and birds have different types of growth (indeterminate and determinate, respectively), the factors that influence and constrain increased parental allocation are likely to be different for these two taxa. Female size is strongly correlated with fecundity in fish (Gross and Sargent 1985) and this relationship could amplify trade-offs between current and future reproduction. Increased investment during the current breeding would decrease energetic reserves available for somatic growth and maintenance. This would reduce fecundity in subsequent breeding events and suggests that the benefit for increased investment must be very large or the cost very small for altered investment to be adaptive.

Convict cichlids (*Amatitlania siquia*; Schmitter-Soto 2007) are freshwater fish, ranging from Guatemala to Panama (Bussing 1987). Both parents care for the offspring for up to six weeks, after which the pair-bond between the parents is terminated. Larger males are higher quality partners because they obtain preferred spawning territories (Itzkowitz et al. 1998) and are more successful at guarding the young (Keenleyside et al. 1985; Wisenden 1994b; Gagliardi-Seeley and Itzkowitz 2006). Males can breed up to four times per breeding season, whereas females typically only breed once (Wisenden 1995). Selecting a high quality mate is therefore more critical for females since they will need to wait until the following breeding season to improve the quality of their partner. Males will sometimes abandon the brood before the offspring reach independence (Wisenden 1994a), leaving the female to care for the young on her own. However, males have never been observed guarding a brood without their mate, indicating that females will not desert the brood first. In other cichlids, females are less successful at protecting the offspring after male desertion, resulting in reduced reproductive success for the breeding event (Nagoshi 1987; Balshine-Earn 1997; Lehtonen et al. 2011). For my dissertation I investigated whether female convict cichlids increase their reproductive effort when mated to high quality males and whether altered investment levels affect subsequent reproduction. Specifically, I quantified parental effort in a natural population and then manipulated mate size in a laboratory experiment that measured primary and secondary reproductive effort, defined as fecundity and parental care, respectively, within and between breeding events. Since the parents of a breeding pair do not interact with one another in isolation from the rest of the population, I also examined the effect of female intrasexual selection on parental behavior. Incorporating both intersexual and intrasexual dynamics can provide insight into the contexts in which male quality influences female investment patterns.

In Chapter 1, “Effect of mate quality on maternal reproductive effort in the convict cichlid *Amatitlania siquia*,” I examined parental effort in naturally formed breeding pairs in a population in Costa Rica. Previous studies on differential allocation in fish have examined altered female primary reproductive effort, either in the form of increased fecundity (Côte and Hunte 1989; Uusi-Heikkila et al. 2012) or egg size (Kolm 2001; 2003); however, no studies have yet investigated whether females also increase their parental care. Consistent with differential allocation, I found that females increased their defense when paired with larger males and that their partners decreased their defense behavior. The Differential Allocation Hypothesis predicts this trade-off in parental effort (Burley 1988), as it allows the more attractive partner to reduce its effort in response to the increased investment of its partner. I also found that females benefited by mating with larger males, as offspring number was positively correlated with male, but not female, size.

An alternative explanation for the correlation between male size and offspring number found in Chapter 1 is that females increase fecundity for larger males, in addition to their parental effort. This would also be consistent with differential allocation, and I therefore conducted a laboratory breeding experiment to investigate female investment in both primary and secondary reproductive effort. In Chapter 2, "Effect of male size on maternal investment within and between breeding events in the convict cichlid," I manipulated male size in consecutive breeding events to examine female reproductive effort within a single event and to investigate whether altered investment affected subsequent reproduction. Breedings in which the female was initially paired with a larger mate had a greater probability of being successful. Females did not alter egg number in response to male size, but did provide more parental care during the larval stage when paired with large males. There was no benefit from pairing with larger males, as the number of offspring was actually lower compared to females paired with small mates. Investment levels during the initial mating did not affect fecundity during the second breeding and male size had a reduced effect on female parental behavior during the second breeding.

Females that are reproductively receptive court already paired males and therefore represent a threat to parental females. In Chapter 3, “Intrasexual competition alters male and female parental behavior in a monogamous, biparental fish,” I examined the effect of a female intruder’s reproductive status on the behavioral response of parents. Parental females directed more aggression at reproductive versus non-reproductive intruders. Smaller females had higher levels of aggression and also lower reproductive success. Males exposed to reproductive intruders first had lower levels of parental care compared to males initially presented with non-reproductive intruders. Males also spent more time interacting non-aggressively with reproductive intruders and with intruders that were larger than their partner, suggesting that males viewed these females as potential mates.

This dissertation contributes new research to the factors that influence parental investment strategies in fish that must balance primary and secondary reproductive investment. Reproductive strategies are an emergent property of the combined effects of intrasexual competition and intersexual interactions (Alonzo 2010); by investigating both of these effects I found that male size influences intra-pair dynamics by altering female investment patterns, but not female intrasexual competition, as parental female response to reproductive rivals was dependent on female, and not male, size. Future research should investigate the ecological and social conditions that influence female mating tactics, particularly what causes reproductive females to court already paired males when others are available. This would also increase our understanding of the factors that influence male desertion, which likely influences female investment. This will ultimately give insight into whether females that increase their behavioral response for higher quality males are able to maximize their reproductive success through increased stability in the pair-bond with their partner.

Chapter 1. Effect of mate quality on maternal reproductive effort in the convict cichlid, *Amatitlania siquia*

ABSTRACT

The differential allocation hypothesis predicts individuals will increase their reproductive investment when mated to a high quality partner. In many species of fish with biparental care females prefer large males due to the males' greater ability to raise more offspring to independence. I examined the relationship between mate quality, parental care and number of offspring in a natural population of convict cichlids (*Amatitlania siquia*). The frequency of frontal displays by females was positively correlated with male standard length. Additionally, as males increased in length relative to their mate, females increased the frequency of chases towards predators, while males decreased the number of displays towards brood predators. This trade-off in parental effort within a pair due to mate quality is a key prediction of differential allocation. The number of offspring was correlated with male, but not female, standard length. These results support the differential allocation hypothesis in that females offered more parental care to offspring of a larger male, while their mates decreased the amount of care they provided. Additionally, females benefited in terms of number of offspring by pairing with higher quality mates. Increased female investment may provide an incentive to ensure male care and maintain pair bonding, which could lead to greater reproductive success through increased offspring survival.

INTRODUCTION

In species with biparental care, where the quality of a partner influences offspring quality and/or number, either sex may alter its parental investment depending on the quality of its mate. The differential allocation hypothesis (DAH) predicts individuals will increase the amount of care they provide to progeny when mated to a high quality partner (Burley, 1986). It was initially formulated for species exhibiting biparental care where the additional care provided to offspring served as an incentive to maintain pair-bonding (Burley, 1988). It predicts that the less attractive partner will increase its care while its attractive mate will decrease its investment (Burley, 1986). The anticipated quality of future partners and the degree to which mate quality affects offspring survival are factors expected to influence degrees of differential allocation (Sheldon, 2000).

While parental care occurs in only 20% of all fish families (Blumer, 1982), all of the currently recognized species of cichlids (family: Cichlidae) exhibit either uniparental or biparental care (Keenleyside, 1991). The unique feature of ubiquitous care makes cichlids an excellent taxon in which to investigate patterns of differential allocation. Many species of cichlids practice biparental care to combat intense predation of fry (Perrone and Zaret, 1979), making Burley's (1986) focus on the role of differential allocation in maintaining pair bonds applicable.

In many Neotropical cichlids with biparental care large males are preferred mates due to their greater ability to secure preferred spawning sites (Perrone, 1978; Itzkowitz et al., 1998) and protect offspring (Wisenden, 1994b; Gagliardi-Seeley and

Itzkowitz, 2006). However, desertion by males has been reported in several species (*Amatitlania siquia*, Wisenden, 1994a; *Aequidens coeruleopunctatus*, Jennions and Polakow, 2001; *Amphilophus sagittae* and *A. zaliosus*, Lehtonen et al., 2011) with male-deserted broods containing fewer offspring (Wisenden, 1994a) and smaller young (Lehtonen et al., 2011) than non-deserted broods. The direct positive effect of the male's presence on both the number of offspring and growth rate are reasons for females to increase the amount of care they provide if it ensures their mate stays. Hypothetically, females could balance the cost of increased parental investment with the benefit of increased offspring survival if it decreased the likelihood of abandonment of broods by males.

Convict cichlids (*Amatitlania siquia*) range from Guatemala to Panama, inhabiting lakes and streams (Bussing, 1987). They are a sequentially monogamous species exhibiting biparental care. Upon pair formation a male and female will excavate a cave where the eggs are then laid. The offspring become free-swimming fry approximately a week after hatching and emerge from the cave at 4.5-5 mm in standard length (tip of the snout to the posterior end of the caudal peduncle). The offspring become independent after approximately six weeks, at which point the pair bond between the parents is terminated. Despite both sexes preferring larger individuals as mates (Noonan, 1983; Beeching and Hopp, 1999), mutual mate choice (Beeching and Hopp, 1999) results in small males pairing with small females and large males obtaining large females as partners (McKaye, 1986). Males are almost always larger than females within pairs (McKaye, 1986), with females on average

13.2 mm smaller than their mates (Wisenden, 1995). However, there is considerable variation in the pattern of size-assortative mating, with females mating with males 1 mm smaller or up to 31 mm larger than themselves (Wisenden, 1995). A consequence of the assortative size-based pattern is that the attractiveness of an individual is a function of its mate's size. A small female would be less likely to obtain a large male due to the size assortative mating; this would therefore result in a large male being of greater quality to a small female than to a large female. The short-term nature of the pair bond and the variation in size of mate a female obtains make convict cichlids an ideal organism in which to study how mate quality influences the investment decisions in a single reproductive cycle.

The purpose of this study was to investigate patterns of parental investment in a natural population of convict cichlids and to determine if there was a relationship between mate quality and quality of parental care provided by both parents of a breeding pair. I predicted that if a relationship was found females would increase their investment when mated to a high quality male. Due to the direct benefits large males provide to the offspring and the assortative size-based mating pattern, high quality males are large males and males that are substantially larger than their partners. The prediction of altered investment due to mate quality is consistent with the DAH in which individuals increase their parental investment when mated to a more attractive partner.

MATERIALS AND METHODS

The study was conducted in the Río Cabuyo within Lomas de Barbudal Biological Reserve, Guanacaste, Costa Rica (10º30'N, 85º22'W) during February-March 2011. Lomas de Barbudal is located within a tropical dry forest and the study was conducted during the dry season. The site is a series of shallow, connected pools approximately 250 m in total length.

Reproductive pairs were located during snorkeling surveys and uniquely identified using their location within the stream, size of the fry, and distinguishing marks (scars, torn fins, etc) on the parents. Subsequent to each pair and fry sighting, a 10-minute behavioral observation was conducted using a mask and snorkel. A pair of observers simultaneously recorded six discrete behaviors of both parents: 1) chases (rapidly swimming at a predator), 2) biting (making contact with the predator), 3) frontal display (flaring the opercula while facing the predator), 4) fin digging/leaf turning (agitating the substrate or turning leaves over to provide food for offspring), 5) time away from the brood (more than 3 body lengths), and 6) frequency of foraging (feeding without spitting food out that offspring could eat). The frequency of chases has been used in previous field studies of convict cichlids (Wisenden, 1994b; Snekser et al., 2011) and the other behaviors have been utilized in field and laboratory studies of convict cichlids (Lavery and Keenleyside, 1990; Lavery, 1995; Wisenden, 2008). At the end of the observation period the fry were captured using a combination of aquarium hand nets and a 30-ml plastic pipette. A countable number of fry (between 5 and 10) were left with the parents to ensure they did not leave the area.

The captured fry were placed in an 8-liter bucket. The plastic pipette was used to siphon fry into a smaller container for counting and the standard lengths (SL) of the first 10 fry were measured. The fry would typically form a school within the bucket so individual fry were not singled out for measuring. After processing, the fry were placed in a clear container (21.6 cm x 10.2 cm x 9.5 cm). The container was lowered into the water and inverted once it was within approximately 10 cm of the remaining fry. The fry within the container would swim out and the parents would resume defense behavior of the returned fry.

On the next day that the site was surveyed (between one and four days later) previously observed pairs were located. A second 10-minute behavioral observation was conducted using the same behavioral parameters from the first observation. After the observation was completed the parents and offspring were captured. A 6-m seine net with 3.2 cm^2 mesh was used to surround the fish. The male was captured first using a small aquarium net. Next, all the fry were captured using a combination of hand nets and a 30-ml plastic pipette. The female was caught last, with the same method used to capture the male.

Eight-liter buckets were used to separate and temporarily house the parents from the fry. Adults were anesthetized using Aqui-S (Aqui-S New Zealand Ltd.) and marked with a unique combination of visible elastomer implant (Northwest Marine Technologies) along the dorsal area. Adults were weighed and the SL measured. A small portion of the caudal fin was removed for genetic sampling. The adults were then placed in an aerated bucket (Penn-Plax Silent Air® B11) to recover from the anesthetic. While the adults recovered, the fry were processed in an identical manner as on the first observation date. The SL of the first 10 fry siphoned into the smaller container was measured and the remaining fry tallied. After the adults had recovered from the anesthetic, parents and offspring were housed in the same bucket. The bucket was placed within the confines of the net at the original capture site and lowered into the water. The adults would swim out and the fry would follow them out of the bucket and settle on the substrate. After the fish left the bucket the net was removed.

Data were analyzed in JMP 9 (SAS Institute, Cary, NC). Linear regressions were used to analyze the effects of male SL, female SL, intra-pair size difference (male SL-female SL), and all interaction terms on parental behavior for both sexes. Forward inclusion and backward elimination was used to exclude non-significant terms from analysis of each behavior. Once models only included significant terms, repeated measures analysis of variance (ANOVAs) were used with significant model effects as the between-subject variable and observation date as the within-subject treatment. Repeated measures ANOVAs were used in case there were changes in an individual’s behavior between the first and second observation. Linear regression was used to determine the relationship between parental standard lengths and number of observed offspring. The number of offspring at the first observation date was used in case possible handling effects affected the number of offspring at the second observation date. Values are reported as the mean ± standard error (*SE*).

RESULTS

Size of breeding pairs

There was a significant positive size-assortative mating pattern ($F_{1,28}$=18.44, P=0.0002; Fig. 1.1). Males were larger than their partners in all pairs, with a mean intra-pair size difference of 21.5 ± 4.66 mm (Table 1.1). The largest female was smaller in standard length than the smallest male sampled (Table 1.1).

Female parental behavior

The frequency of female bites, fin dig/leaf turn, foraging or time away was not significantly correlated with any of the model effects. Intra-pair size difference was the best predictor of female chase frequency. Frequency of chases by females was positively related to the intra-pair size difference ($F_{1,28}$=9.37, P=0.0048; Fig. 1.2). Male SL was ranked as the best predictor of female frontal display frequency ($F_{1,25}$=0.68, P=0.0004), and female displays were positively related to male SL. The interaction effect of male SL and female SL on frequency of female displays was also significant ($F_{1,25}$=0.60, P=0.0007), indicating that as male SL increased large females increased their frequency of frontal displays.

Male parental behavior

The frequency of male chases, bites, fin dig/leaf turn, foraging or time away was not significantly correlated with any of the model effects. Intra-pair size difference was the best predictor of male frontal display frequency. Males performed significantly fewer frontal displays as the intra-pair size difference increased ($F_{1,28}$=6.88, P=0.014; Fig. 1.3).

Number of offspring

The mean number of offspring at the first observation date was 61.6 ± 6.27, with a range from 17-140 ($n = 30$). The intra-pair size difference was not correlated with the number of offspring at the first observation ($F_{1,28}$=3.02, P=0.093), nor was female SL ($F_{1,28}$=0.854, P=0.363). However, male SL was positively correlated with the number of fry at the first observation ($F_{1,28}$=4.91, P=0.035; Fig. 1.4).

DISCUSSION

Females performed significantly more chases towards potential brood predators as the intra-pair size difference increased. Females also performed more frontal displays when mated to large males. The significant interaction effect of male SL and female SL for female frontal displays could indicate that females also take into consideration their own size when determining the most effective tactic against a potential brood predator. As males increased in size relative to their partner they decreased their parental effort in the form of frontal displays. These results are consistent with the differential allocation hypothesis (DAH, Burley, 1986), which predicts that the less attractive mate will increase its parental effort while its more attractive partner will decrease its effort. It is thought that the increase in effort by the unattractive mate serves as an incentive to maintain the pair bond between the parents. The average chase frequency for all females was 9.7 ± 0.87 and for all males was 6.3 ± 0.71 per 10-minute observation. This is similar to a previous study conducted on a natural population of convict cichlids that found female chase frequency to be 13.84 ± 1.33 and male chase frequency was 7.29 ± 0.93 per 10-

minute observation (Wisenden, 1994b).

The four other observed behaviors (biting, leaf turning/fin digging, foraging, and time spent away from the brood) were not significantly correlated with mate quality. For a parent to bite a potential brood predator the likelihood of injury to the parent itself would be greater than if it chased or displayed from a safe distance. Parents, as well as offspring, were observed feeding on the detritus found on the overturned leaves. The behavior may benefit the parents as much as the offspring and thus should not be correlated with the quality of an individual's mate. The observance of parents feeding on the overturned leaves could also explain why a correlation between foraging and mate quality was not found. The offspring are more vulnerable when a parent spends time away from the brood since only one parent is left guarding. Male SL is positively correlated with the number of offspring at independence (Wisenden, 1994b) and solitary females of a closely related species, *Amphilophus sagittae*, guard significantly smaller territories (Lehtonen et al., 2011). If large males spent more time away, the smaller parent would be left alone to guard which could impact defense effectiveness and the number of offspring that reach independence.

The number of offspring at the first observation date was correlated with male SL. Previous research has observed positive relationships between male size and offspring survival in convict cichlids (Wisenden, 1994a; Gagliardi-Seeley and Itzkowitz, 2006). The benefit of increased offspring survival likely outweighs the costs of increased brood defense by the female, making differential allocation an adaptive strategy.

The parental compensation theory also attempts to explain why differences in parental effort within a pair occurs and predicts that when one parent reduces its parental contribution its partner will increase its effort in an attempt to compensate (Wright and Cuthill, 1989). Compensation by one parent in response to a reduction in care offered by its mate has been observed in both bird and fish species with biparental care (*Sturnus vulgaris*, Wright and Cuthill, 1990; *Eretmodus cyanostictus*, Steinegger and Taborsky, 2007). The positive correlation between female defense behavior and male quality and negative correlation between male defense behavior and intra-pair size difference could indicate that females were compensating for a reduction in their partners' parental effort instead of increasing their effort due to a higher quality mate. However, the parental compensation hypothesis does not predict how the quality of an individual or its partner should influence adjustment of effort in response to a reduction in parental contribution. Parental care is likely to be energetically more expensive for smaller individuals of both sexes since increased defensive behavior reduces energetic reserves (Steinhart et al., 2005). As reproductive potential is tightly correlated with somatic reserves in fish (Gross and Sargent, 1985), increased energetic expenditures to compensate for its partner's reduced effort could impact future breeding success. When considering the impact of reduced future reproductive potential, females would be expected to decrease their effort when mated to large males. This is because small females, those likely to have the largest difference in size with their partners, should conserve energy. Larger males should increase their energetic investment to compensate for reduced efforts by smaller females. Small males should also be expected to exhibit a lower level of care compared to larger males, which would predict a positive relationship between male defense behavior and intra-pair size difference. This prediction for how an individual's size would affect the parental compensation theory is the opposite of the observed pattern in this study in which smaller males and females had the highest level of parental care.

A surprising finding of this study was that male, but not female, SL was positively correlated with the number of offspring. In fish there is a positive correlation between female size and fecundity (Gross and Sargent, 1985), and this pattern has been found during laboratory experiments involving convict cichlids (Galvani and Coleman, 1998). The results of this study indicate that the protective assistance of males may be crucial for offspring survival, and male size may instead be a better predictor of the number of offspring produced for a particular reproductive bout. By mating with larger males females may gain a direct benefit in terms of young produced. Previous field observations in convict cichlids have found evidence for the protective abilities of large males; Gagliardi-Seeley and Itzkowitz (2006) observed fewer intruders near the offspring of large males, while Wisenden (1994b) found that the number of offspring at independence was positively correlated with male SL. An alternative hypothesis for the correlation between male size and the number of offspring is that females increase the number of eggs they produce for a larger mate. This would also support the DAH with females not only increasing their secondary reproductive effort in the form of parental care but also their primary effort. Increased primary reproductive effort either in increased egg number (Côte and Hunte, 1989; Skinner and Watt, 2007; Evans et al., 2010) or size (Kolm, 2001) has been found in fish for females mated to preferred or more attractive males. The pattern of females increasing egg number or egg size for preferred males has only been investigated in fish with either no parental care (Evans et al., 2010) or male-only care (Kolm, 2001). Since female convict cichlids must also maintain enough energetic reserves to provide extended parental care the ability to increase egg number may be more limited.

In summary, this study found a correlation between mate quality and the amount of parental care in breeding pairs of convict cichlids. Females were observed to increase their parental effort while males decreased their investment as male quality increased. This study is the first example of increased parental care in a fish in response to mate quality. This suggests that differential allocation is likely to be utilized by a range of taxa to increase reproductive success when a high quality mate is obtained. The aim of future research should include investigating female fecundity in relation to male quality. This will help clarify how females balance the two components that contribute to parental investment during a reproductive event. If females increase fecundity and also provide a greater proportion of the parental care they may incur greater reductions in future reproductive potential. If the benefit from increased investment for an attractive mate is sufficient to offset a reduction in future reproduction, differential allocation should result in a greater number of offspring produced for a female compared to an individual that does not adjust its investment. Increased female investment may provide an incentive to maintain pair bonding with males, which could increase offspring survival, and ultimately contribute to greater reproductive success.

Acknowledgements

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Tables and Figures

Table 1.1. Standard lengths (mm) of breeding male and female convict cichlids.

	Mean	***SE***	**Min**	**Max**	***n***
Male SL	69.0	1.06	58.5	81.5	30
Female SL	47.5	0.86	38.5	57.5	30
Intra-pair difference (M-F)	21.5	4.66	14	32.5	30

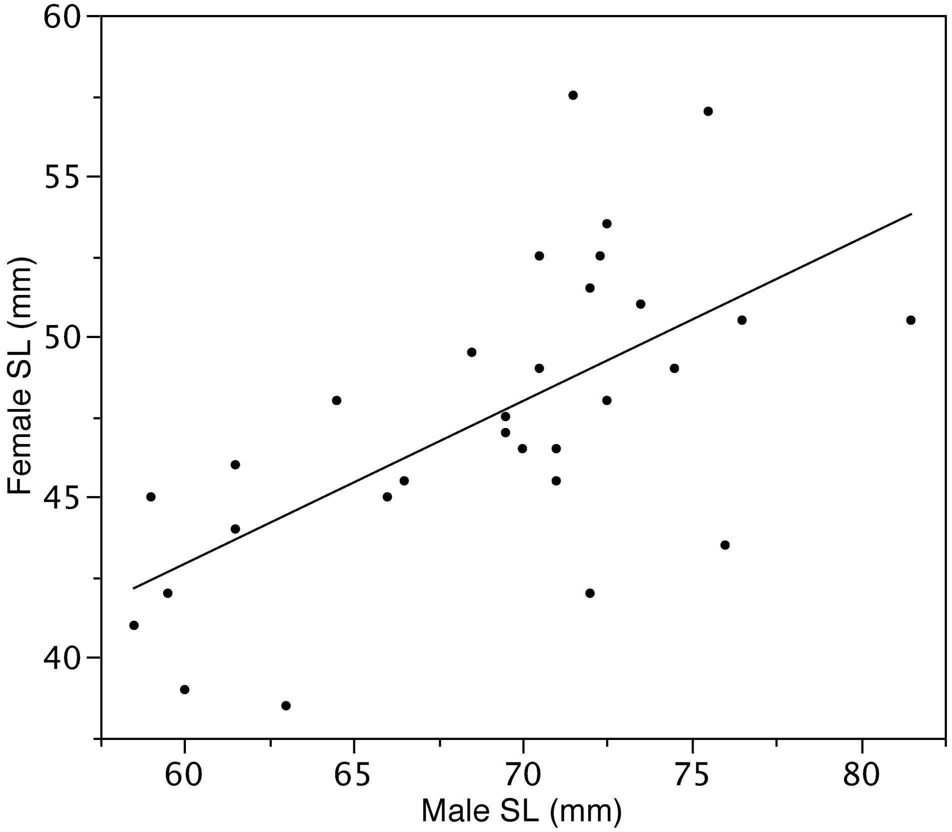

Figure 1.1. Correlation between male standard length and female standard length for breeding pairs (Y=0.51X + 12.56; r^2=0.375).

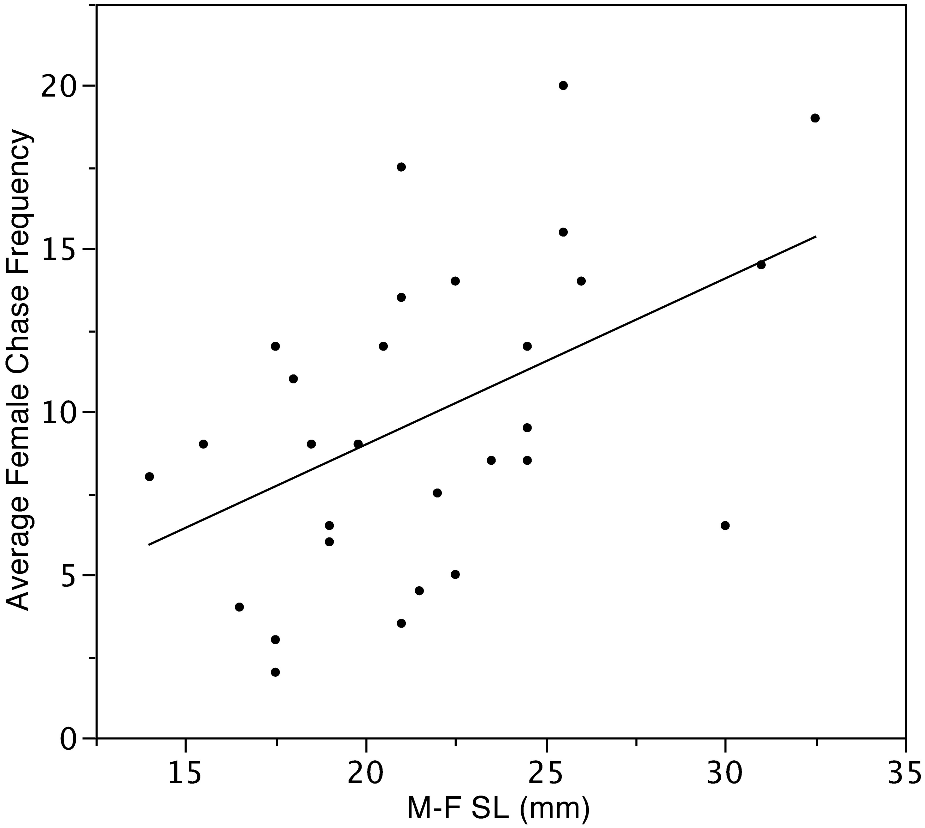

Figure 1.2. Correlation between intra-pair size difference and average female chase frequency per 10-minute observation (Y=0.51X - 1.22; r^2=0.224). An average of the two observations was used since within-subject variation was non-significant ($F_{1,28}$=0.0002, P=0.9389)

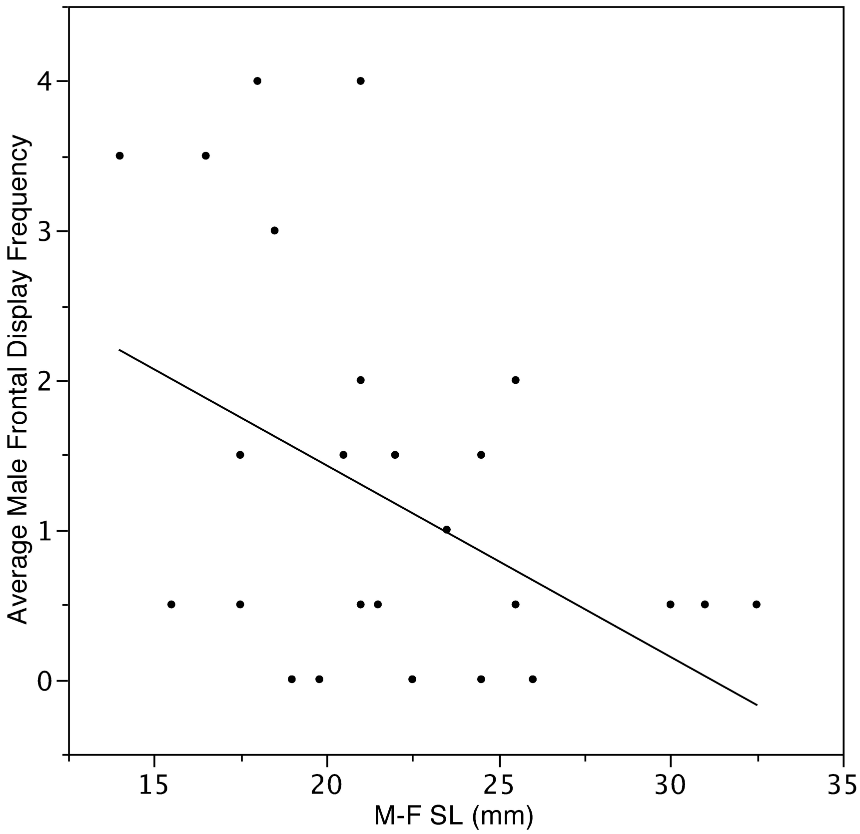

Figure 1.3. Correlation between intra-pair size difference and average male frontal display frequency per 10-minute observation (Y=-0.13X + 3.99; r^2=0.169). An average of the two observations was used since within-subject variation was non-significant ($F_{1,28}$=0.02, P=0.424).

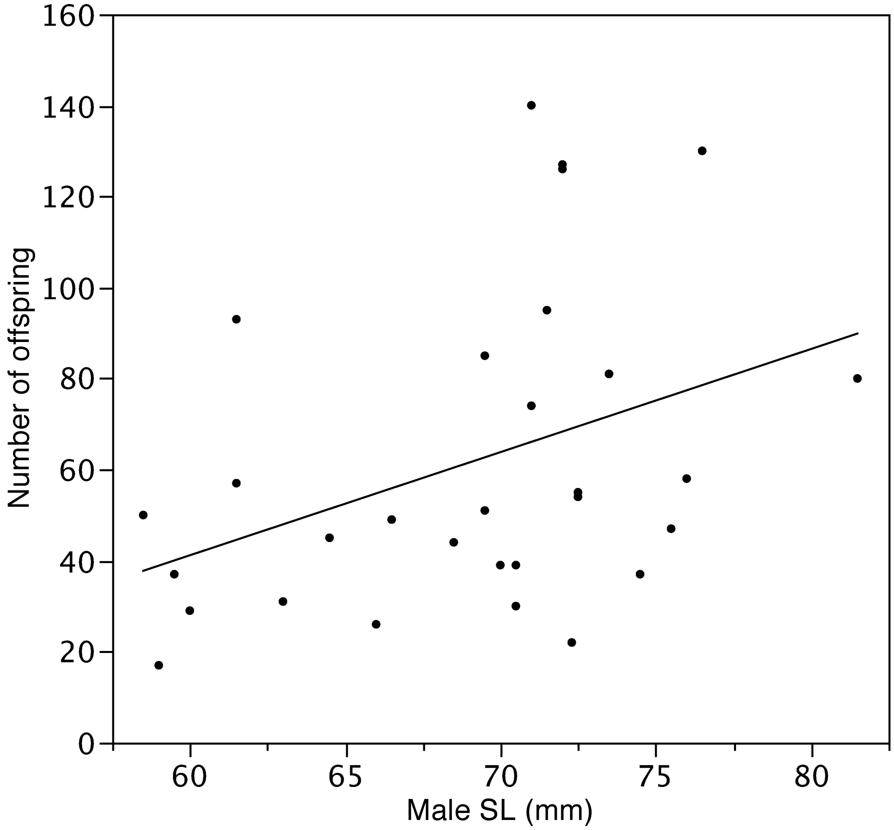

Figure 1.4. Correlation between male standard length and number of offspring at the first observation (*Y*=2.27*X* - 94.76; r^2=0.119).

Chapter 2. Effect of male size on maternal investment within and between breeding events in the convict cichlid

ABSTRACT

When male quality positively influences offspring survival or quality, females are predicted to increase their investment to capitalize on the increased benefits associated with obtaining a higher quality mate. In biparental species, the increased investment is thought to stabilize the pair-bond between the parents, which can lead to an increased number of offspring that survive to independence. Convict cichlids (*Amatitlania siquia*) have biparental care and females have previously been shown to increase their parental care when paired with higher quality (e. g. larger) males. We investigated whether females increase their fecundity, in addition to their parental care when paired with larger males and whether initial maternal effort affected subsequent reproduction by breeding each female twice in a controlled laboratory experiment. We found that the initial breeding had a higher probability of succeeding when females were paired with large males. Females did not increase their fecundity, but did provide more parental care during the larval stage when paired with larger males. Females paired with large males had fewer fry than females partnered with small males, indicating they did not benefit in terms of offspring number. Females provided more parental care to offspring during their second breeding event, but male size had a reduced effect. While increased maternal investment may serve to stabilize the pair-bond in natural populations and prevent male desertion before offspring

independence, the dynamic response in this experiment suggests females consider the effect male quality previously had on reproductive success when deciding current investment levels.

INTRODUCTION

The effect of male phenotype on offspring quality and survival is well documented and multiple hypotheses have been formulated to predict how paternal quality should affect female reproductive investment (Burley 1986, 1988; Sheldon 2000; Gowaty et al. 2007; Gowaty 2008; see Harris and Uller 2009 and Ratikainen and Kokko 2009). The Differential Allocation Hypothesis (Burley 1986) predicts individuals will increase the level of care provided to offspring when paired with high quality partners. Burley (1986, 1988) originally applied differential allocation to biparental species, where the increased effort by the less-attractive partner served as an incentive to maintain the pair-bond between parents. Differential allocation has since been expanded to include any adjustment in investment related to obtaining a high quality partner, including adjustments in offspring number (Simmons 1987; Petrie and Williams 1993; Balzer and Williams 1998; Evans et al. 2010), egg size (Cunningham and Russell 2000; Uller et al. 2005; Gilbert et al. 2006), and even egg contents (Gil et al. 1999). Differential allocation ties the reproductive value of a breeding event to the quality of an individual's partner, with a key assumption being that individuals reduce their future reproductive potential when increasing their current investment to capitalize on the associated benefits of high quality mates

(Sheldon 2000).

Trade-offs in reproductive investment can occur both within and between breeding events (Williams 1966; Trivers 1972; Stearns 1992). Species with parental care must divide their investment within a single breeding event between primary (gametic investment) and secondary (post-hatching care) reproductive effort (Balzer and Williams 1998). Studies that increased the costs of parental care within a breeding event have shown that offspring provisioning and care is reduced (Lavery and Keenleyside 1990b; Heaney and Monaghan 1996), and reproductive success is also affected (Reid et al. 2000). Altered investment within a breeding event can also affect subsequent reproduction and survival (Gustafsson and Sutherland 1988; Jones and Reynolds 1999; Visser and Lessells 2001; Ward et al. 2009; Miller and Zink 2012). Burley (1986) found higher mortality for individuals that increased their investment for high quality partners, while other studies have found effects on female fecundity when mate quality is manipulated in consecutive breedings (Reyer et al. 1999; Skinner and Watt 2007; Evans et al. 2010). Due to their larger investment, females potentially suffer greater reductions to their future reproductive potential compared to males when investment levels are altered. This is especially relevant to fish due to the strong correlation between size and fecundity (Gross and Sargent 1985); females that increase investment in the current breeding reduce their somatic reserves, thereby limiting future growth and reproduction.

Females increase egg number (Côte and Hunte 1989; Uusi-Heikkila et al. 2012) or size (Kolm 2001, 2003) for preferred males in several fish species and the increased investment reduces fecundity in subsequent breedings (Skinner and Watt 2007; Evans et al. 2010). Studies of differential allocation in fish have mainly focused on species without maternal care (Côte and Hunte 1989; Kolm 2001; Skinner and Watt 2007; Evans et al. 2010; Uusi-Heikkila et al. 2012; Rios-Cardenas et al. 2013). The lack of maternal care in these species means females do not need to balance investment between primary and secondary reproductive effort within a breeding event, as any increase due to male quality would only occur at the gametic stage. While one study found that females provide more parental care to the offspring of larger males in a biparental fish (Robart 2012), studies that investigate potential trade-offs between fecundity and parental care within a single breeding event remain rare (Burley 1988; de Lope and Møller 1993).

With the exception of a single species, females provide extended parental care in all Cichlid fish (Goodwin et al. 1998). Obligate parental care makes cichlids an excellent taxon to study whether mate quality alters the balance of investment between fecundity and parental care within a breeding event and whether altered investment affects subsequent reproduction. Research in several Neotropical cichlids shows that large males are higher quality mates due to their ability to secure preferred territories (Perrone 1978; Itzkowitz et al. 1998) and protect the young (Keenleyside et al. 1985; Wisenden 1994b; Gagliardi-Seeley and Itzkowitz 2006). Females benefit from maintaining biparental care, as fewer offspring reach independence when males desert before the young reach independence (Wisenden 1994a). This suggests Burley’s (1986) original application of differential allocation may be particularly relevant to cichlids since pair-bond length has a strong effect on reproductive success.

Convict cichlids (*Amatitlania siquia*; Schmitter-Soto 2007) are sequentially monogamous and both parents care for the young for up to six weeks. They inhabit lakes and streams, ranging from Guatemala to Panama (Bussing 1987). Females lay eggs within a cave excavated in the substrate and the free-swimming offspring (termed fry) emerge after one week. The main form of parental care is protection from predators, including conspecifics. Once the offspring reach independence the pair-bond is terminated, with males often mating with a new female later in the breeding season (Wisenden 1994a). Females prefer larger males (Noonan 1983; Keenleyside et al. 1985) and males in better condition (A. Robart, unpublished data) and provide more parental care when paired with larger males (Robart 2012). Although female size is the strongest predictor of number of eggs spawned (Galvani and Coleman 1998; A. Robart, unpublished data), research on natural populations has found that male size predicts the number of offspring during the larval stage (Wisenden 1994b; Robart 2012). While the relationship between male size and reproductive success could indicate that females gain a direct benefit from obtaining larger mates, an alternative explanation is that females also increase their fecundity in response to pairing with a higher quality male.

In this study we investigated whether female convict cichlids increase not only their parental care, but also their fecundity, when mated to large males. We predicted that females would increase both components of parental effort when paired with larger males. Since energy allocated to reproduction is not available for somatic maintenance (Gross and Sargent 1985), we predicted that females paired with large males would lose more weight during the breeding. We predicted that females paired with larger males should have greater reproductive success, in the form of more offspring, compared to females paired with small males. We investigated the effect of altered investment on subsequent reproduction by breeding each female twice, again manipulating male size in the second breeding. We predicted that the size of the initial male would affect female investment in the second breeding. Specifically, we predicted that females mated to large males in the first breeding would have decreased investment in the subsequent breeding, with a larger decrease observed in females mated to low quality males in the second breeding. For females mated to low quality males in the initial breeding, we predicted that females mated to large males in the second breeding would have greater reproductive effort compared to females that obtained a low quality male again in the second breeding.

MATERIALS AND METHODS

Experimental animals and overview

Fish used in this experiment were lab-reared F1 offspring of wild caught adults originating from Lago Xiloá, Nicaragua. Prior to the experiment, fish were kept in same-sex 208-l aquaria with a 13 L:11 D photoperiod. Water temperature was 26°C ± 1°C and fish were fed daily with commercial cichlid pellets. Females were sexually naïve at the start of the experiment.

We used a full factorial design to investigate the combined effects of mate size (small versus large) and breeding number (1st versus 2nd brood) on female reproductive investment. Male size was randomized across females for both breedings. We used a block design with 12 experimental tanks and a total of 6 blocks. We initially maintained a balanced design; however, 30% of the replicates ($n = 15$) did not successfully breed during the first mating. These replicates were terminated and the females were not used during the second breeding. All replicates during the second breeding were successful.

Mate assessment

For the mate assessment portion of the experiment, we divided 76-l experimental tanks into three compartments (Fig. 2.1). Females were weighed on an electronic balance (Jennings CJ600) and measured with digital calipers (Carrera Precision CP9806-TF) for standard length (tip of the snout to posterior end of caudal peduncle; SL) before being placed in the center compartment of the tank. We allowed females to acclimate for 24 hours before introducing males. We created pairs of males such that larger males were larger for both SL ($\bar{X} \pm SE$: 3.87 ± 0.20 mm) and condition (mass/SL ratio; $\bar{X} \pm SE$: 0.025 ± 0.001 mm) compared to small males. The female was smaller (in SL) than both males. We placed males in the end compartments of the tank, randomizing which end contained the large male. Clear partitions with holes divided the end compartments from the center section containing the female (Fig. 2.1). Opaque partial dividers within the center compartment prevented males from visually interacting with each other (Fig. 2.1). Females had visual and olfactory access to the males for 48 hours before randomly being assigned to mate with the small or large male. We returned the non-selected male to the same-sex stock tank and removed the dividers. We placed half of a terracotta flower pot on the left side of the tank to serve as a spawning cave. Several females ($n = 4$) spawned on the clear divider before the end of the 48-hour assessment period and were not used for the remainder of the experiment.

Parental investment

We checked tanks daily for signs of spawning, beginning 24 hours after the barriers were removed. We photographed the eggs and used the photographs to determine clutch size. After photographing the eggs, we recorded two videos to measure parental care and defensive behaviors. We placed a video camera (Sony DCR-SR68) on a tripod in front of the tank and recorded a 10-minute video that was later used to score parental care behavior. Immediately following the 10-minute parental care video, we measured defensive behavior by introducing a confined female convict cichlid that simulated a potential brood predator. We weighed and measured the SL of a female from the all-female stock tank and placed her inside a clear plastic box (12 cm x 12 cm x 13.5 cm) with holes. We placed the box at the end of the tank opposite of the flower pot. We then recorded a 2-minute video to record defensive behavior of both parents.

Approximately two weeks after spawning ($\bar{X} \pm SE$: 15.4 ± 0.21 days) we measured parental care and defensive behavior at the fry stage, using the same procedure as at the egg stage. We ended the first breeding within 24 hours of the videos conducted during the fry stage. We weighed and measured the SL of the male and returned him to the all-male stock tank. We then siphoned the fry from the tank. We measured the SL of 10 fry to calculate mean fry SL and counted the remaining fry. We euthanized the fry using an overdose of clove oil. The female was weighed and measured for SL and returned to the experimental tank.

We waited approximately four weeks ($\bar{X} \pm SE$: 28.2 ± 0.57 days) after the end of the first breeding before allowing the female to breed a second time. Females were kept in the experimental tanks and the dividers reinserted 24-hours prior to introducing two new males. The mate assessment and parental investment portion were repeated a second time using the same protocol.

Behavioral scoring

A total of three observers scored the behavioral videos; one observer scored all defensive videos, while one observer scored parental care behavior at the egg stage and a separate observer scored parental care during the fry stage. All videos were scored twice, once to measure the female's behavior and a second time to record the male's behavior. Observers were blind to the mate treatment when scoring videos.

We scored five behaviors for the parental care videos recorded during the egg phase. We recorded the frequency of mouthing (nipping gently at eggs), total time spent fanning the eggs (continuously beats fins while within one body length of eggs), time away (more than two body lengths) from the clutch, intra-pair bite (focal parent bites mate) and intra-pair frontal display (focal parent flares its opercula while facing mate). During the larval stage we measured five behaviors for the parental care videos: fry retrieval (parent places fry in its mouth and expels it into the center of the brood), fin dig (beating pectoral fins while in contact with substrate to stir up gravel), time away from the brood, intra-pair bite and intra-pair frontal display. The behaviors scored from the defensive videos were the same for the egg and larval stage. We measured the frequency of ram (swimming rapidly at and making contact with intruder box), ram with frontal display (ram performed in conjunction with frontal display), charge (swimming toward intruder box, but stopping before making contact), charge with frontal display (charge performed with frontal display behavior), frontal display, tail beat (fish presents its lateral side and beats fins, pushing water toward intruder box), latency to attack the intruder, intra-pair bite, and intra-pair frontal display. We also calculated an overall aggression score by summing the frequency of rams, rams with frontal displays, charges, charges with frontal displays, frontal displays and tail beats.

Data analysis

We analyzed behaviors separately for each sex as well as each development stage. In addition to analyzing behaviors individually, we also employed Principal Component Analysis (PCA) to examine overall parental behavior at each development stage. PCA summarizes the included behaviors and can indicate which behaviors most strongly influence general patterns of parental care. We calculated the principal components (PCs) for five separate stages: the egg stage for all replicates for the first breeding (failed and successful); egg stage for successful first breedings; larval stage for successful first breedings; the egg stage for both breedings (1st and 2nd); and the larval stage for both breedings. We saved all PCs with an eigenvalue greater than one (Norman and Streiner 2008). We visually checked the distributions of response variables and used non-parametric tests when distributions did not appear normal. Data were analyzed in JMP® Pro 11.0 (SAS Institute 2013) and R 3.1.0 (R. Core Development Team 2014).

Failed versus successful breedings

To investigate the factors that affected breeding success we used logistic regressions with breeding success or failure as the response variable. We tested the separate effects of number of eggs, female SL, latency to spawn, and behaviors on breeding success. We also tested the effect of mate size on breeding success using chi-square analysis. There was insufficient variation in the frequency of female intra-pair aggression and all male behaviors except time away, and these behaviors were not analyzed.

Successful first breedings

We investigated whether females altered their fecundity for larger males by testing the effects of female SL, mate size, and their interaction on number of eggs spawned. To determine whether females increase their parental care during the egg stage for larger males we tested the effects of number of eggs, mate size, and their interaction on individual behaviors and PC scores. We used the same procedure to test whether females alter their behavior at the larval stage but included number of fry instead of egg number. We used ANCOVAs to analyze PC scores and the individual behaviors that were normally distributed. Most of the individual behaviors were not normally distributed and were analyzed using generalized linear model (GLM) with a

Poisson distribution and log link. We removed non-significant terms in a stepwise manner for all analyses until models only contained significant effects. There was insufficient variation in behavior at the egg stage for all female intra-pair interactions and all male behaviors except time away and these variables were not analyzed. For the fry stage, frequency of female intra-pair bites during defense, male charge and charge with frontal display frequency, male frequency of tail beats, and frequency of male intra-pair bites during defense had insufficient variation and were not analyzed. In order to test for benefits associated with mating with large males, we examined the effect of mate size on mean fry size and the number of fry present at the end of the experiment; we tested the effect of male size on the change in female weight during the experiment to investigate whether there was an energetic cost associated with mating with large males.

Investment differences between first and second breedings

To investigate whether mate size in a female's initial breeding affected her subsequent investment we tested the effects of mate size, breeding number (1st vs. 2nd), and their interaction on individual female behaviors, and female PC scores. In order to test if male size and/or experience influenced reproductive success we examined the effect of mate size, breeding number, and their interaction on the number of fry and mean fry size. In order to determine whether gametic investment in the first breeding affected subsequent fecundity we tested the effects of breeding number, mate size, and their interaction on number of eggs, with female SL added as a covariate. We used linear mixed models for response variables that were normally distributed and the lme4 package (R. Core Development Team 2014) to run generalized linear mixed models with a Poisson distribution and log link for behaviors that did not conform to normality. For all mixed models we included female ID as a random effect. We removed non-significant terms using stepwise–backward elimination until models contained only significant terms. For the egg stage, there was insufficient variation in all intra-pair aggression, except intra-pair bites during the parental observation, and these behaviors were not analyzed. We did not analyze male behavior for differences between breeding events; due to experimental design, female breeding number did not necessarily correspond to the number of times a male had mated and thus did not reflect his actual experience.

RESULTS

Failed versus successful breedings

There was no effect of female SL ($\chi^2 = 0.099$, df = 1, $P = 0.752$), number of eggs ($\chi^2 = 0.890$, df = 1, $P = 0.345$), or latency to spawn ($\chi^2 = 1.963$, df = 1, $P = 0.161$) on breeding success. Females paired with large males had a significantly greater probability of breeding successfully ($\chi^2 = 5.832$, df = 1, $P = 0.016$; Fig. 2.2).

With the exception of latency to attack ($\chi^2 = 5.249$, df = 1, $P = 0.022$; Fig. 2.3) and overall aggression ($\chi^2 = 4.716$, df = 1, $P = 0.030$; Fig. 2.4), none of the individual behaviors significantly predicted breeding success.

The first four PCs explained 66.7% of the total variation in female behavior (Table 2.1). Female PC1 explained 24.2% of the variation and indicated high levels of defensive behaviors, moderate levels of mouthing and low amount of time away from the clutch (Table 2.1). PC2 explained 16.5% of the variation and loaded positively for the defense behaviors that included frontal displays, but negatively for parental care (Table 2.1). PC3 explained 15.5% of the variation and loaded positively for fanning and mouthing and negative for most defensive behaviors (Table 2.1). PC4 explained only 10.6% of the variation; it loaded positively for some behaviors and negative for others, with no clear pattern and was not analyzed (Table 2.1). Neither Female PC1, PC2, nor PC3 predicted breeding success.

Successful first breedings

Female SL positively predicted the number of eggs ($F_{1,31} = 39.04$, $P = 0.0001$; Fig. 2.5). Females spent more time fanning the eggs with increasing clutch size and when mated to small males (Table 2.2). The interaction was also significant, with time spent fanning increasing more rapidly when paired with larger males (Table 2.2). Females performed more rams during the egg stage when paired with small males (Table 2.2). The interaction between number of eggs and mate size was significant for the frequency of rams with frontal displays during the egg stage (Table 2.2). The number of eggs was positively correlated with the frequency of rams with frontal display when paired with large males; however, egg number negatively affected ram with frontal display frequency when paired with small males (Table 2.2). Females performed fewer frontal displays for smaller clutches and this pattern was more pronounced when paired with small males (Table 2.2).

The first four PCs of female behavior at the egg stage explained 68.6% of the total variation in behavior (Table 2.3). Female Egg PC1 explained 22.8% of the variation and indicated low amounts of time spent away from the clutch, low latency to attack the intruder, and high levels of ram with frontal display, frontal display and tail beating (Table 2.3). Female Egg PC2 explained 17.4% of the variation and indicated high levels of parental care, but low levels of defense (Table 2.3). Female Egg PC3 explained 17.2% of the variation and loaded positively for mouthing, frontal displays, and tail beats, but negatively for defensive behaviors that involved swimming rapidly at the intruder (Table 2.3). Female Egg PC4 did not have a clear interpretation, explained only 11.3% of the variation (Table 2.3), and was not analyzed. None of the Female Egg PCs were significantly predicted by mate size or correlated with the number of eggs.

Females performed more fry retrievals as fry number increased and more retrievals when paired with larger males (Table 2.4). Females spent more time away from the brood when mated to large males and when there were more fry (Table 2.4). Females performed more intra-pair frontal displays during the parental care observation, rams with frontal displays, charges with frontal displays and frontal displays when paired with large males (Table 2.4). Mate size, number of fry and their interaction significantly influenced ram frequency, with females performing more rams when paired with small mates and for larger broods (Table 2.4). The rate of increase in ram frequency was greater for females paired with large males (Table 2.4). Females were slower to attack the intruder when paired with small males and when there were fewer fry, although fry number mainly affected latency when paired with smaller males (Table 2.4). There was a significant interaction effect on intra-pair frontal display during the defense observations, with females paired with large males performing more intra-pair frontal displays as fry number increased, with this pattern reversed for females mated to small males (Table 2.4).

Six PCs for female fry behavior had eigenvalues greater than one and explained a total 87.4% of the variation (Table 2.5). Female Fry PC1 explained 23.9% of the variation and indicated high levels of both parental care and defensive behaviors (Table 2.5). The remaining PCs explained only 15.0%, 13.8%, 13.0%, 11.3%, and 10.3%, respectively, of the variation and did not have a clear interpretation (Table 2.5). Therefore, only Female Fry PC1 was analyzed; mate size had a significant effect on Female Fry PC1 ($F_{1,29} = 5.15$, $P = 0.031$; Fig. 2.6).

Male size and the interaction between male size and number of fry significantly influenced fry retrieval by males, with larger males retrieving more fry overall and more fry as fry number increased (Table 2.6). Males spent more time away from the brood as fry number increased and small males spent more time away compared to large males (Table 2.6). There was a significant interaction between mate size and number of fry for the frequency of intra-pair bites performed by males during the parental care observation; for small males, fry number had a positive trend on frequency of intra-pair bites, while large males bit their partner more often when brood size was small (Table 2.6). There was a significant interaction effect on frequency of rams, rams with frontal displays, frontal displays, overall aggression, and intra-pair frontal displays during defense by males (Table 2.6). For these behaviors there was a negative trend between fry number and behavior for small males and a positive trend for large males. Number of fry and the interaction between fry number and male size significantly influenced latency to attack the intruder, with males attacking more quickly for smaller brood sizes (Table 2.6). This effect was more pronounced for small males, with larger males taking longer to attack with increasing number of fry (Table 2.6).

Three PCs for male fry behavior explained 61.1% of the variation (Table 2.7). Male Fry PC1 explained 35.0% of the variation and loaded strongly for behaviors associated with parental care and defense (Table 2.7). Male Fry PC2 and PC3 only explained 13.5% and 12.7%, respectively, of the variation, did not have a clear pattern of explaining overall behavior (Table 2.7), and were not analyzed. The interaction between male size and number of fry had a significant effect on Male Fry PC1 ($F_{1,27} = 7.15$, $P = 0.013$; Fig. 2.7).

Despite egg number not differing between small and large males, male size had a significant effect on the number of fry at the end of the experiment ($F_{1,33} = 5.07$, $P = 0.031$; Fig. 2.8). However, fry size did not differ between the two treatments ($F_{1,25} = 0.0001$, $P = 0.991$). There was no difference in weight loss between females paired with small versus large males ($F_{1,32} = 0.44$, $P = 0.511$).

Investment differences between first and second breedings

Female fecundity was greater in the second breeding ($F_{1,29.2} = 13.86$, $P = 0.0008$; Fig. 2.9) and female SL again had a positive effect on fecundity ($F_{1,34.2} = 548.29$, $P = 0.0001$). Mate size, breeding number, and their interaction significantly influenced the time females spent fanning the eggs (Table 2.8). Females fanned more when paired with small males and during their first breeding; mate size had a greater effect on fanning in the first breeding than the second (Table 2.8). Females mouthed the eggs more during the second breeding and when mated with small males; females mated to large males during the second breeding increased mouthing frequency to a greater degree than females paired with small males (Table 2.8). Females bit their partner during the parental care observation more during the second breeding and when mated to large males, but the interaction between mate quality and breeding number was not significant (Table 2.8). Females performed more rams at the intruder for the egg defense observation during the second breeding and when paired with small males (Table 2.8). The increase in ram frequency between the first and second breedings was greater for females paired with small males (Table 2.8). Females performed more rams with frontal displays during the second breeding, while frontal displays and tail beat frequency was higher during the first breeding (Table 2.8).

Four PCs explained 66.7% of the variation in female behavior at the egg stage for both breedings (Table 2.9). Female Egg PC1 indicated low amounts of time spent away from the eggs, high levels of defensive behaviors, and explained 24.8% of the variation (Table 2.9). Female Egg PC2 loaded strongly for behaviors during the parental care observation and explained 16.3% of the variation (Table 2.9). Female Egg PC3 explained 14.9% of the variation and indicated moderate levels of parental care and defense, but negative for rams and charges (Table 2.9). Female Egg PC4 explained only 10.8% of the variation, did not have a clear pattern of explaining overall behavior, and was not analyzed (Table 2.9). Mate size, breeding number, nor their interaction significantly predicted Female Egg PC1, PC2, or PC3.

Females performed more fry retrievals when paired with larger males; the interaction between mate size and breeding number was also significant, with females paired to smaller males increasing their retrieval frequency more between the first and second breeding compared to females mated to large males (Table 2.10). Breeding number and the interaction between breeding number and mate size significantly influenced the amount of time females spent away from the fry (Table 2.10). Females spent more time away from the fry during the second breeding, with a greater difference between the two breeding events for females paired with small males (Table 2.10). During the fry stage parental observation, the frequency of intra-pair bites was greater during the first breeding, while the frequency of intra-pair frontal displays was greater when females were mated to large males (Table 2.10). Females performed more rams with frontal displays when paired with larger males and the interaction between breeding number and mate size was also significant (Table 2.10). The number of rams with frontal displays decreased between the first and second breeding for large males, but increased for small males (Table 2.10). The frequency of chases with frontal displays was greater in the first breeding and for females that were paired with larger males (Table 2.10). Females performed more frontal displays when paired with large males; the increase in frontal display frequency between the first and second breedings was greater for smaller males than large males (Table 2.10). Females attacked intruders more quickly when mated to large males; however, there only appeared to be an effect of mate size on latency times during the initial breeding (Table 2.10). There was a significant interaction effect on overall aggression levels, with aggression decreasing between breeding events for large males, but increasing for small males (Table 2.11). Females performed more intra-pair frontal displays during the defense observation when mated to large males and also during the first breeding event (Table 2.10). The interaction between mate size and breeding number was also significant, with intra-pair frontal displays decreasing between the breeding events for large males and increasing for small males (Table 2.10).

The first five PCs explained 68.6% of variation in female behavior at the fry stage for both breedings (Table 2.12). Female Fry PC1 explained 17.1% of the variation and indicated moderate levels of parental care and high levels of defensive behaviors that included a frontal display (Table 2.12). Female Fry PC2 explained 15.9% of the variation and loaded positively for fry retrieval and ram frequency and indicated females quickly attacked the intruder (Table 2.12). Female Fry PCs 3-5 explained only 12.6%, 11.7%, and 11.3%, respectively, of the variation; they did not have a clear interpretation and were not analyzed (Table 2.12). Breeding number and the interaction between mate size and breeding number significantly influenced Female Fry PC1 (Table 2.11; Fig. 2.10); Female Fry PC2 was not significantly predicted mate quality or breeding number.

Finally, the number of fry at the end of each breeding was significantly predicted by breeding number ($F_{1,29.5} = 39.99$, $P = 0.0001$; Fig. 2.11). Male size had a marginally significant effect on the number of fry ($F_{1,44.5} = 3.85$, $P = 0.056$), with small males having a greater number of fry at the end of each breeding compared to large males. Neither mate size ($F_{1,50.1} = 0.26$, $P = 0.611$) nor breeding number ($F_{1,29.9} = 3.24$, $P = 0.082$) had a significant effect on mean fry size.

DISCUSSION

While female preference to mate with larger males is well documented in convict cichlids (Noonan 1983; Keenleyside et al. 1985; A. Robart, unpublished data), we did not expect male size to have such a strong effect on overall breeding success (Fig. 2.2). Nearly half (12 out of 27) of the replicates in which females were initially paired with small males failed, and all of the replicates in which eggs were not produced ($n = 5$) were with small males. The main reason eggs were not produced was because the male killed the female before spawning occurred. Conflict over matings frequently occurs between males and females (Le Boeuf and Mesnick 1991; Clutton-Brock and Parker 1995; Bisazza et al. 2001; Parker 2006), and low quality males often have fewer mating opportunities (Andersson 1982; Arak 1983; Milinski and Bakker 1990; Brockmann 2002). Due to external fertilization male convict cichlids are not able to force copulations and the aggressive behavior directed at the female may have been due to the female's refusal to mate with him. Most replicates that failed did successfully spawned, but the offspring disappeared before they reached the fry stage. Given that the young can successfully be reared without the parents in a laboratory setting (Lavery and Keenleyside 1990b), the most likely explanation for the disappearance of the young is that one or both of the parents cannibalized them. Previous studies have found smaller clutches have a higher probability of being cannibalized (Lavery and Keenleyside 1990a,b), but we found no difference in clutch size between successful and failed replicates. Since we didn't directly observe the parents eat the young, we do not know which parent was responsible for the cannibalism. However, Raadik et al. (1990) found that young were cannibalized more often when the male was alone with the eggs than when only the female remained with the young. Females that had higher levels of defense (Figs. 3 and 4) were significantly more likely to have broods succeed. Maternal aggression increases offspring survival in several taxa (lizards: Sinn et al. 2008; birds: Cain and Ketterson 2012; spiders: Gonzaga and Leiner 2013) and in convict cichlids the main form of parental care is protecting offspring from predators. Thus, high levels of aggression even at the egg stage may indicate a female's ability to defend the young throughout the care period.

The similarity in number of eggs spawned for small ($\bar{X} \pm SE$: 161.1 ± 14.2) and large ($\bar{X} \pm SE$: 154.4 ± 12.3) males strongly contradicts our prediction that females would increase their fecundity when paired with larger mates (Fig. 2.5). It is possible the mate assessment period of 48 hours was too short for females to increase egg number in response to mate size, but in a trial experiment females frequently spawned on the divider if the mate assessment period was extended to even 72 hours (A. Robart, unpublished data). Spawning latency also did not differ between the two treatments, indicating females paired with larger males did not delay spawning in an attempt to increase fecundity.

Brood size was significantly correlated with parental care by the female during both the egg and fry stage. This is consistent with other studies that have found parents provide more care to larger broods (Lavery and Keenleyside 1990a,b; Lavery 1995). Larger broods provide a greater reproductive pay-off for the breeding event and parents consider the value of the brood when deciding the level of care provided (Coleman et al. 1985; Gross 2005). Male size only significantly affected two behaviors during the egg stage (fanning and ram frequency), but females actually performed more of these behaviors when paired with smaller males. However, male size influenced more behaviors during the fry stage, with females performing more retrievals and higher levels of defense when paired with larger males. Female Fry PC1 provides a more comprehensive view of female behavior for the fry stage and indicated high levels of investment during the parental care observation and high levels of most defensive behaviors (Table 2.5). Females mated to large males had higher levels of Female Fry PC1 (Fig. 2.6), indicating females did increase their investment in response to obtaining a larger mate. The motivation for increasing parental care may be more consistent with Burley's (1986) focus on the role of differential allocation in pair-bond maintenance, as male desertion occurs typically during the larval stage (Wisenden 1994a). Females have the highest reproductive success with biparental care, so any cost of increased behavior should potentially be offset by the increased number of young that survive, if such behavior is adaptive.

Male parental care typically does not start until after the eggs hatch (Lavery and Keenleyside 1990a) so it is not surprising that males performed so few behaviors during the egg stage. During the fry stage, larger males performed more retrievals and spent more time with the fry compared to small males. The interaction between brood size and male size influenced many of the behaviors at the fry stage, with the number of fry having a positive effect on behaviors of large males and a negative effect on small males. This was also true for Male Fry PC1 (Fig. 2.7). Male Fry PC1 indicated high levels of all parental care and defensive behaviors (Table 2.7), which suggests a remarkable level of consistency in male behavior. Other studies in cichlids have found that the level of male parental care is dependent on brood size (Jennions and Polakow 2001; Wisenden et al. 2008) and that males desert smaller than average broods (Wisenden 1994a; Jennions and Polakow 2001). This suggests that any direct benefits females gain by mating with larger males will depend on the number of offspring remaining sufficiently high so as to be worth the male's continued effort. The differential allocation hypothesis predicts increased investment by the female to increase the fitness pay-off that is associated with higher quality mates (Burley 1986, 1988; Sheldon 2000), but it doesn't predict whether the fitness pay-off could feedback and affect the effort of the more attractive partner. Although Burley (1986) formulated the differential allocation hypothesis for biparental species, it has more recently been applied to species without biparental care (reviewed in Sheldon 2000) and, thus, the potential response of the more attractive partner to its mate's increased investment is often ignored.

For differential allocation to be an adaptive response, there must be a benefit to offset the increased cost of investment. However, we did not find an energetic cost, as weight change was not greater or less for females paired with large males. Nor did we find a benefit, as the number of fry at the end of the first breeding was lower for females paired with large males (Fig. 2.8). It is possible that offspring quality was lower for larger males and this resulted in reduced survivorship, but this seems unlikely given that male size positively affects offspring growth and survival in other species of fish (Perrone 1978; Reynolds and Gross 1992). The other possibility to explain reduced brood size for large males is that one or both of the parents cannibalized the fry during the 7-10 day larval period. Males have been observed to consume their young when in confined spaces (A. Robart, pers. observ.) so it is possible the pattern of reduced reproductive success is a laboratory artifact. Additionally, we observed that females paired with large males directed higher levels of intra-pair aggression during the fry stage at their mate. The aggression could be the result of conflict between the parents due to the male cannibalizing the young. Male convict cichlids have a higher probability of remating within the same season than females (Wisenden 1995), so any reduction in reproductive success for the current breeding event could potentially be compensated for later in the breeding season.

When comparing female primary reproductive investment between the two breedings, female fecundity increased in the second breeding (Fig. 2.9). Female SL increased an average of 1.76 mm (± 0.31) between the first and second breedings so it is not surprising that fecundity also increased, given the size-fecundity relationship in fish (Gross and Sargent 1985; Galvani and Coleman 1998).

When behavior for both breedings was pooled, male size had the opposite effect as predicted on female behavior during the egg stage, with females providing more care when paired with small males. These results are actually more in line with the reproductive compensation hypothesis (Gowaty et al. 2007; Gowaty 2008), which predicts that when individuals are forced to mate with non-preferred individuals, they will increase their investment to make up for the inferior quality of the partner. Harris and Uller (2009) modeled scenarios under which maternal investment patterns should follow differential allocation versus reproductive compensation and found that reproductive compensation was predicted when there was a high probability of offspring survival. In natural populations the eggs are deposited in spawning caves, which have very small entrances; females remain at the entrance and aggressively chase any fish that approach. Therefore, survival during the egg stage is very high, with the majority of offspring mortality occurring during the free-swimming fry period (A. Robart, unpublished data). Thus, the increased effort during the egg stage associated with small males may be the female's response to compensate for his inferior quality, given that it will yield a high return in terms of hatching success.

The behaviors during the first and second fry stages that were significantly affected by mate size (Table 2.10) support differential allocation, with females increasing their behavior when paired with larger males. When behavior during the fry stage was pooled for both breedings, Female Fry PC1 indicated moderate levels of parental care, but generally high for defensive behavior (Table 2.12). Female Fry PC1 was higher during the second breeding compared to the first and the significant interaction effect of mate size and breeding event indicates that male size had a greater influence on overall levels of female behavior during the first breeding (Fig. 2.10). Previous research in convict cichlids (Lavery 1995) has shown that low reproductive success in a previous breeding can reduce parental care in the subsequent breeding and we found a negative, although non-significant, trend for females that had lower fry survival during the first breeding event to also have lower Female Fry PC1 scores during the second breeding.

The increase in the number of fry at the end of the second breeding (Fig. 2.11) is consistent with previous research in convict cichlids that found more experienced parents have higher reproductive success (Colgan and Salmon 1986). It was surprising that the number of fry was greater for small males across both breedings since we predicted females would gain a benefit in the form of number of offspring when paired with large males. However, also consistent across both breedings was the pattern of females showing more aggression toward their mate when paired with large males. The higher aggression and reduced reproductive success may be the result of conflict between the parents due to differential probability of future reproduction. Smaller males may have a lower probability of remating due to female preference for larger males, so they may place a greater value on current versus future reproduction compared to large males.

Overall, the results of this experiment provide mixed support for differential allocation in convict cichlids. Females did not increase their primary reproductive effort when paired with larger males. Changes in gametic investment due to differential allocation primarily take the form of either increased fecundity (Côte and

Hunte 1989; Petrie and Williams 1993; Skinner and Watt 2007; Evans et al. 2010; Uusi-Heikkila et al. 2012;) or egg size (Cunningham and Russell 2000; Kolm 2001, 2003; Uller et al. 2005; Gilbert et al. 2006). While we did not directly measure egg size, larger eggs typically result in larger offspring (Coleman and Galvani 1998; Cunningham and Russell 2000; Christians 2002). Therefore, we would have expected to find differences in mean offspring size if females increased egg size rather than fecundity. However, there was no difference in mean fry size between small and large males. Fecundity was also nearly identical between the two treatments, indicating females do not adjust egg number in response to male size. The studies in fish that found females increase fecundity for high quality males have been in species with either no parental care (Skinner and Watt 2007; Evans et al. 2010; Uusi-Heikkila et al. 2012; Rios-Cardenas et al. 2013) or male-only care (Côte and Hunte 1989). Therefore, the need to provide extended parental care may constrain adjustments in fecundity in species with maternal care.

Females did increase their secondary reproductive effort, in the form of increased behavior during the fry stage, for large males during the first breeding, but the differential allocation hypothesis assumes both a cost and benefit to the increased investment. Females that increased their behavior during the fry stage did not lose more weight (A. Robart, unpublished data), nor did they benefit in terms of number of offspring produced for the breeding event. Previous experience can influence mate preference and reproductive investment (Bakker and Milinksi 1991; Lavery 1995; Pöysä et al. 1996; Brown and Laland 2003), and the decrease in the effect of male size on female behavior during the second breeding suggests behavioral plasticity in response the prior breeding outcome. This dynamic response would prevent females from continuing to allocate more resources when paired with larger males when their experience suggests no reproductive benefit.

The results from studies conducted on natural populations, however, add another layer of complexity when considering the role of differential allocation in convict cichlids, as several studies have in fact found a correlation between male size and the number of offspring (Wisenden 1995; Robart 2012). The results of this study exclude the possibility that this relationship is due to increased fecundity, indicating that females mated to preferred partners gain a direct benefit in the form of more offspring that reach independence, likely due to the greater protective assistance of larger males (Keenleyside et al. 1985; Wisenden 1994b; Gagliardi-Seeley and Itzkowitz 2006). However, the relationship between male size and number of surviving offspring is variable between breeding seasons and females only increase their parental care when male size predicts reproductive success (Robart 2012; A. Robart, unpublished data). This suggests the possibility of a socially mediated cue that signals the male's potential benefits within a season and allows females to increase their investment when it would lead to higher fitness.

In conclusion, we found that female preference for larger males results in increased breeding success when initially paired with preferred mates. Females do not alter their primary reproductive effort in response to mate size, but their secondary reproductive investment suggests a more complex strategy than initially hypothesized. The effect of male size on female behavior indicates females alter their investment during the egg stage in a pattern that is consistent with the reproductive compensation hypothesis and then switch to differential allocation during the larval stage. This suggests females consider the effect of male quality on offspring survival at each stage and utilize the strategy that will maximize reproductive success for each development phase. Sexual conflict between females and large males is likely the result of the current brood being valued differently by each parent with respect to their expected future reproductive opportunities. This resulted in females adjusting their parental care during their second breeding in response to the lowered reproductive success experienced in their initial mating. Research on natural populations should attempt to determine the ecological and social conditions that contribute to male quality impacting offspring survival. This will give a greater understanding of when females should increase investment due to obtaining a higher quality partner. The frequency of male desertion before offspring independence varies throughout the breeding season and it would be interesting to investigate whether females that increase their investment when paired with larger males also have lower abandonment rates. This would indicate that differential allocation plays a role in pair-bond maintenance, which ultimately leads to greater reproductive success for female convict cichlids.

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Tables and Figures

Table 2.1. Loading scores for PC axes 1-4 of female behavior during the egg stage for successful and failed initial breedings.

Behavior	PC1	PC2	PC3	PC4
Fanning (s)	-0.188	-0.318	0.576	0.407
Mouthing	0.387	-0.071	0.700	-0.038
Time Away (s)	-0.501	0.660	-0.152	-0.254
Ram	0.316	-0.599	-0.525	-0.177
Ram with Frontal Display	0.673	0.242	-0.072	0.446
Charge	-0.019	-0.433	-0.291	0.215
Charge with Frontal Display	-0.022	0.559	-0.348	0.334
Frontal Display	0.707	0.426	0.203	0.084
Tail Beat	0.369	0.074	0.271	-0.654
Latency (s)	-0.887	-0.005	0.318	0.099
Eigenvalue	2.418	1.646	1.547	1.063
% Variation Explained	24.18	16.46	15.47	10.63

Table 2.2. Results of generalized linear model on female behavior at the egg stage for successful first breedings. Significant terms shown in bold.

Behavior	Effect	χ^2	*df*	*P*
Fanning (s)	Mate Quality	88.51	1	**0.0001**
	Egg Number	239.98	1	**0.0001**
	Mate*Egg	156.24	1	**0.0001**
Ram	Mate Quality	15.69	1	**0.0001**
Ram with Frontal Display	Mate Quality	2.94	1	0.086
	Egg Number	0.76	1	0.383
	Mate*Egg	18.87	1	**0.0001**
Frontal Display	Mate Quality	0.31	1	0.577
	Egg Number	13.34	1	**0.0003**
	Mate*Egg	5.84	1	**0.016**

Table 2.3. Loading scores for PC axes 1-4 of female behavior during the egg stage for successful first breedings.

Behavior	PC1	PC2	PC3	PC4
Fanning (s)	-0.256	0.602	0.216	0.513
Mouthing	0.321	0.549	0.531	-0.101
Time Away (s)	-0.510	-0.575	0.339	-0.383
Ram	0.295	0.151	-0.768	-0.239
Ram with Frontal Display	0.636	-0.271	0.020	0.556
Charge	-0.080	0.176	-0.502	0.025
Charge with Frontal Display	-0.120	-0.665	0.071	0.277
Frontal Display	0.630	-0.266	0.451	0.075
Tail Beat	0.426	0.237	0.404	-0.488
Latency (s)	-0.870	0.215	0.249	0.137
Eigenvalue	2.276	1.737	1.719	1.126
% Variation Explained	22.76	17.37	17.19	11.26

Table 2.4. Results of generalized linear models on female behavior at the fry stage for successful first breedings. Significant terms shown in bold. (P) and (D) denote intra-pair aggression during the parental care and defense observations, respectively.

Behavior	Effect	χ^2	*df*	*P*
Fry Retrieval	Mate Quality	17.31	1	**0.0001**
	Fry Number	25.94	1	**0.0001**
Time Away (s)	Mate Quality	4.79	1	**0.029**
	Fry Number	63.83	1	**0.0001**
Intra-pair Frontal Display (P)	Mate Quality	28.58	1	**0.0001**
Ram	Mate Quality	7.50	1	**0.006**
	Fry Number	6.05	1	**0.014**
	Mate*Fry	7.23	1	**0.007**
Ram with Frontal Display	Mate Quality	29.08	1	**0.0001**
Chase with Frontal Display	Mate Quality	13.84	1	**0.0002**
Frontal Display	Mate Quality	23.70	1	**0.0001**
Latency (s)	Mate Quality	160.30	1	**0.0001**
	Fry Number	38.20	1	**0.0001**
	Mate*Fry	35.94	1	**0.0001**
Intra-pair Frontal Display (D)	Mate Quality	0.13	1	0.714
	Fry Number	0.06	1	0.810
	Mate*Fry	4.56	1	**0.033**

Table 2.5. Loading scores for PC axes 1-6 of female behavior during the fry stage for successful first breedings.

Behavior	PC1	PC2	PC3	PC4	PC5	PC6
Fry Retrieval	0.710	-0.094	0.255	-0.175	0.267	-0.487
Fin Dig	0.777	0.284	0.189	-0.080	0.282	0.296
Time Away (s)	-0.292	0.157	0.635	-0.874	-0.067	0.436
Ram	-0.279	-0.135	0.673	0.468	0.321	-0.107
Ram with Frontal Display	0.401	-0.422	0.074	0.076	-0.773	-0.077
Charge	-0.019	0.625	-0.443	0.389	0.139	-0.260
Charge with Frontal Display	0.606	0.473	-0.053	0.237	-0.223	0.455
Frontal Display	0.644	-0.435	-0.121	-0.224	0.301	0.124
Tail Beat	-0.196	-0.580	-0.448	0.258	0.328	0.449
Latency (s)	-0.378	0.223	-0.080	-0.843	0.055	0.075
Eigenvalue	2.395	1.500	1.384	1.303	1.127	1.030
% Variation Explained	23.95	15.00	1.384	13.03	11.27	10.30

Table 2.6. Results of generalized linear models on male behavior at the fry stage for successful first breedings. Significant terms shown in bold. (P) and (D) denote intra-pair aggression during the parental care and defense observations, respectively.

Behavior	Effect	χ^2	*df*	*P*
Fry Retrieval	Mate Quality	5.02	1	**0.025**
	Fry Number	0.24	1	0.626
	Mate*Fry	7.14	1	**0.008**
Time Away (s)	Mate Quality	60.62	1	**0.0001**
	Fry Number	7.98	1	**0.0001**
	Mate*Fry	33.69	1	**0.0001**
Intra-pair Bite (P)	Mate Quality	0.04	1	0.834
	Fry Number	0.09	1	0.763
	Mate*Fry	5.82	1	**0.016**
Ram	Mate Quality	1.75	1	0.185
	Fry Number	0.01	1	0.934
	Mate*Fry	4.02	1	**0.045**
Ram with Frontal Display	Mate Quality	2.18	1	0.140
	Fry Number	1.32	1	0.251
	Mate*Fry	33.62	1	**0.0001**
Frontal Display	Mate Quality	0.03	1	0.852
	Fry Number	0.85	1	0.356
	Mate*Fry	32.24	1	**0.0001**
Latency (s)	Mate Quality	2.04	1	0.154
	Fry Number	18.15	1	**0.0001**
	Mate*Fry	341.47	1	**0.0001**
Overall Aggression	Mate Quality	3.01	1	0.083
	Fry Number	1.62	1	0.203
	Mate*Fry	62.55	1	**.0001**
Intra-pair Frontal Display (D)	Mate Quality	0.14	1	0.711
	Fry Number	1.15	1	0.283
	Mate*Fry	11.33	1	**0.0008**

Table 2.7. Loading scores for PC axes 1-3 of male behavior during the fry stage for successful first breedings. No males performed a charge during the defense observation and it was not included in the PCA.

Behavior	PC1	PC2	PC3
Fry Retrieval	0.598	-0.411	0.006
Fin Dig	0.473	-0.435	0.132
Time Away (s)	-0.257	-0.122	0.199
Ram	0.720	-0.048	0.011
Ram with Frontal Display	0.844	-0.042	-0.208
Charge with Frontal Display	0.087	0.517	-0.751
Frontal Display	0.656	0.223	0.333
Tail Beat	0.127	0.684	0.598
Latency (s)	-0.902	-0.234	0.084
Eigenvalue	3.145	1.217	1.141
% Variation Explained	31.45	12.17	11.41

Table 2.8. Results of generalized linear mixed models on female behavior at the egg stage for first and second breedings. Significant terms shown in bold. (P) and (D) denote intra-pair aggression during the parental care and defense observations, respectively.

Behavior	Effect	*z*	*P*
Fanning (s)	Mate Quality	9.05	**0.0001**
	Breeding Number	6.68	**0.0001**
	Mate*Breeding	-9.66	**0.0001**
Mouthing	Mate Quality	92.54	**0.0001**
	Breeding Number	85.23	**0.0001**
	Mate*Breeding	-42.32	**0.0001**
Intra-pair Bite (P)	Mate Quality	-3.52	**0.0004**
	Breeding Number	3.11	**0.002**
Ram	Mate Quality	3.11	**0.002**
	Breeding Number	2.52	**0.012**
	Mate*Breeding	-2.74	**0.006**
Ram with Frontal Display	Breeding Number	2.19	**0.029**
Frontal Display	Breeding Number	-3.01	**0.003**
Tail Beat	Breeding Number	-2.42	**0.015**

Table 2.9. Loading scores for PC axes 1-4 of female behavior during the egg stage for first and second breedings.

Behavior	PC1	PC2	PC3	PC4
Fanning (s)	-0.276	0.632	0.196	-0.481
Mouthing	0.230	0.604	0.235	0.327
Time Away (s)	-0.410	-0.617	0.245	0.418
Ram	0.280	0.015	-0.790	0.074
Ram with Frontal Display	0.739	-0.122	0.086	-0.459
Charge	-0.085	0.086	-0.555	0.138
Charge with Frontal Display	-0.026	-0.599	0.226	-0.337
Frontal Display	0.751	-0.123	0.360	0.021
Tail Beat	0.437	0.239	0.389	0.457
Latency (s)	-0.891	0.170	0.250	-0.078
Eigenvalue	2.478	1.628	1.488	1.076
% Variation Explained	24.78	16.28	14.88	10.76

Table 2.10. Results of generalized linear mixed models on female behavior at the fry stage for first and second breedings. Significant terms shown in bold. (P) and (D) denote intra-pair aggression during the parental care and defense observations, respectively.

Behavior	Effect	*z*	*P*
Fry Retrieval	Mate Quality	-3.26	**0.001**
	Breeding Number	-0.26	0.776
	Mate*Breeding	2.99	**0.003**
Time Away	Mate Quality	-0.60	0.547
	Breeding Number	6.50	**0.0001**
	Mate*Breeding	-4.88	**0.0001**
Intra-pair Bite (P)	Breeding Number	-2.95	**0.003**
Intra-pair Frontal Display (P)	Mate Quality	-5.93	**0.0001**
Ram with Frontal Display	Mate Quality	-3.69	**0.0003**
	Breeding Number	-0.02	0.987
	Mate*Breeding	3.72	**0.0002**
Charge with Frontal Display	Mate Quality	-2.69	**0.007**
	Breeding Number	-2.03	**0.042**
Frontal Display	Mate Quality	-3.45	**0.0006**
	Breeding Number	-0.57	0.567
	Mate*Breeding	3.99	**0.0001**
Latency (s)	Mate Quality	8.54	**0.0001**
	Breeding Number	0.15	0.882
	Mate*Breeding	-7.43	**0.0001**
Intra-pair Frontal Display (D)	Mate Quality	-2.40	**0.017**
	Breeding Number	-2.05	**0.040**
	Mate*Breeding	2.83	**0.005**

Table 2.11. Results of linear mixed models on female behavior at the fry stage for first and second breedings. Significant terms shown in bold.

Behavior	Effect	*F*	*df*	*P*
Aggression	Mate Quality	0.02	1, 53.0	0.886
	Breeding Number	1.84	1, 32.2	0.184
	Mate*Breeding	5.56	1, 52.6	**0.022**
Female Fry PC1	Mate Quality	0.62	1, 52.8	0.435
	Breeding Number	5.28	1, 30.1	**0.029**
	Mate*Breeding	7.99	1, 52.9	**0.007**

Table 2.12. Loading scores for PC axes 1-5 of female behavior during the fry stage for first and second breedings.

Behavior	PC1	PC2	PC3	PC4	PC5
Fry Retrieval	0.259	0.740	-0.140	0.214	0.152
Fin Dig	-0.131	-0.035	-0.048	0.248	0.858
Time Away (s)	-0.356	-0.021	0.585	0.239	-0.299
Ram	-0.371	0.769	-0.111	-0.102	-0.028
Ram with Frontal Display	0.757	-0.141	0.294	0.169	-0.175
Charge	0.084	-0.263	-0.263	-0.818	0.073
Charge with Frontal Display	0.250	0.614	0.614	-0.264	0.474
Frontal Display	0.572	-0.134	-0.306	0.349	0.061
Tail Beat	-0.025	-0.370	-0.505	0.204	-0.067
Latency (s)	-0.627	-0.469	-0.010	0.260	0.114
Eigenvalue	1.711	1.592	1.258	1.174	1.131
% Variation Explained	17.11	15.92	12.58	11.74	11.31

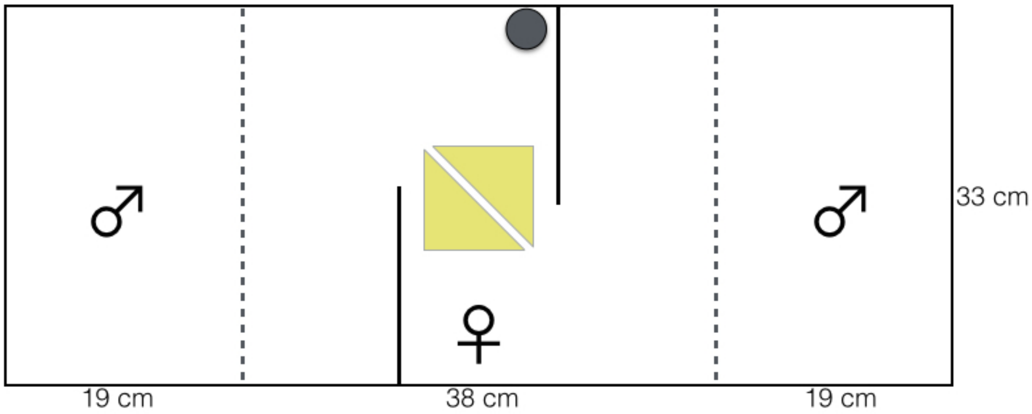

Figure 2.1. Diagram of tank during mate assessment period. Dashed lines indicate transparent barriers that divided males from the female. Solid lines in female compartment represent opaque dividers that prevented males from visually interacting. Two sponge filters were placed in the female compartment (yellow triangles), as well as an aquarium heater (gray circle).

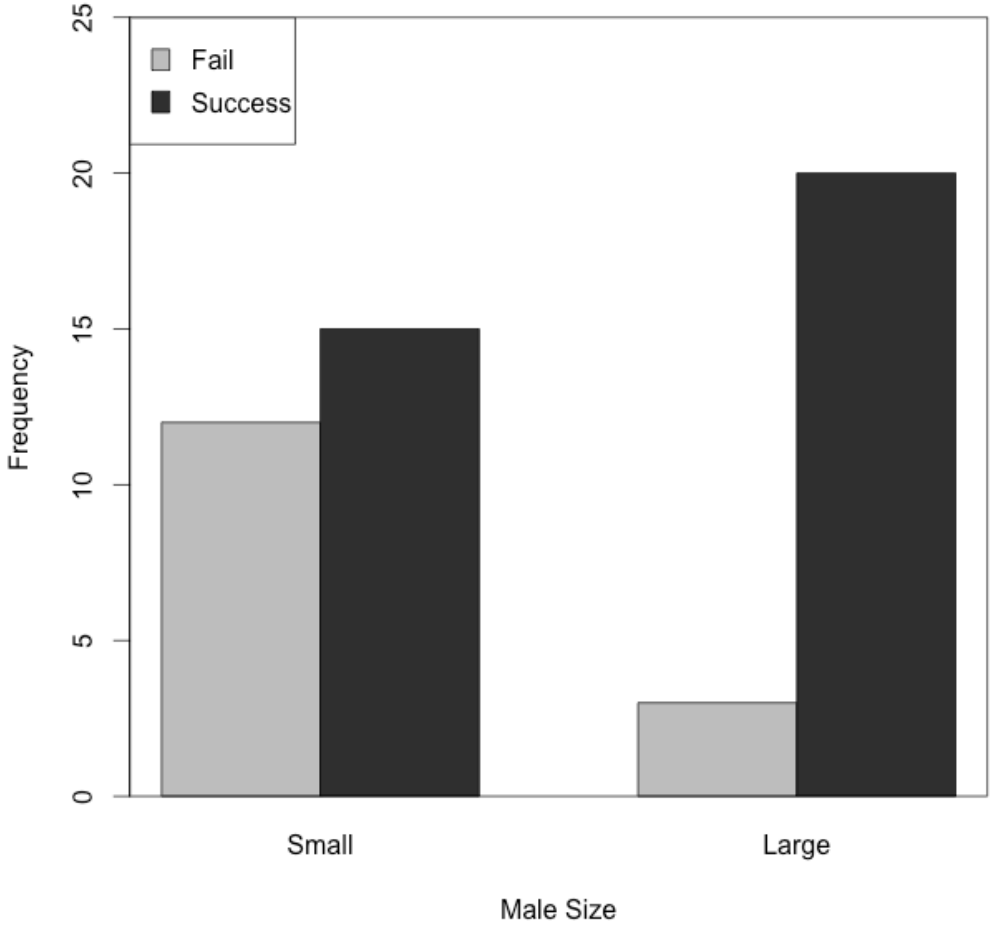

Figure 2.2 Frequency of successful and failed initial breedings by male size. Failed breedings were due to the male killing the female before spawning occurred, a failure to spawn, or respawning after the offspring were consumed.

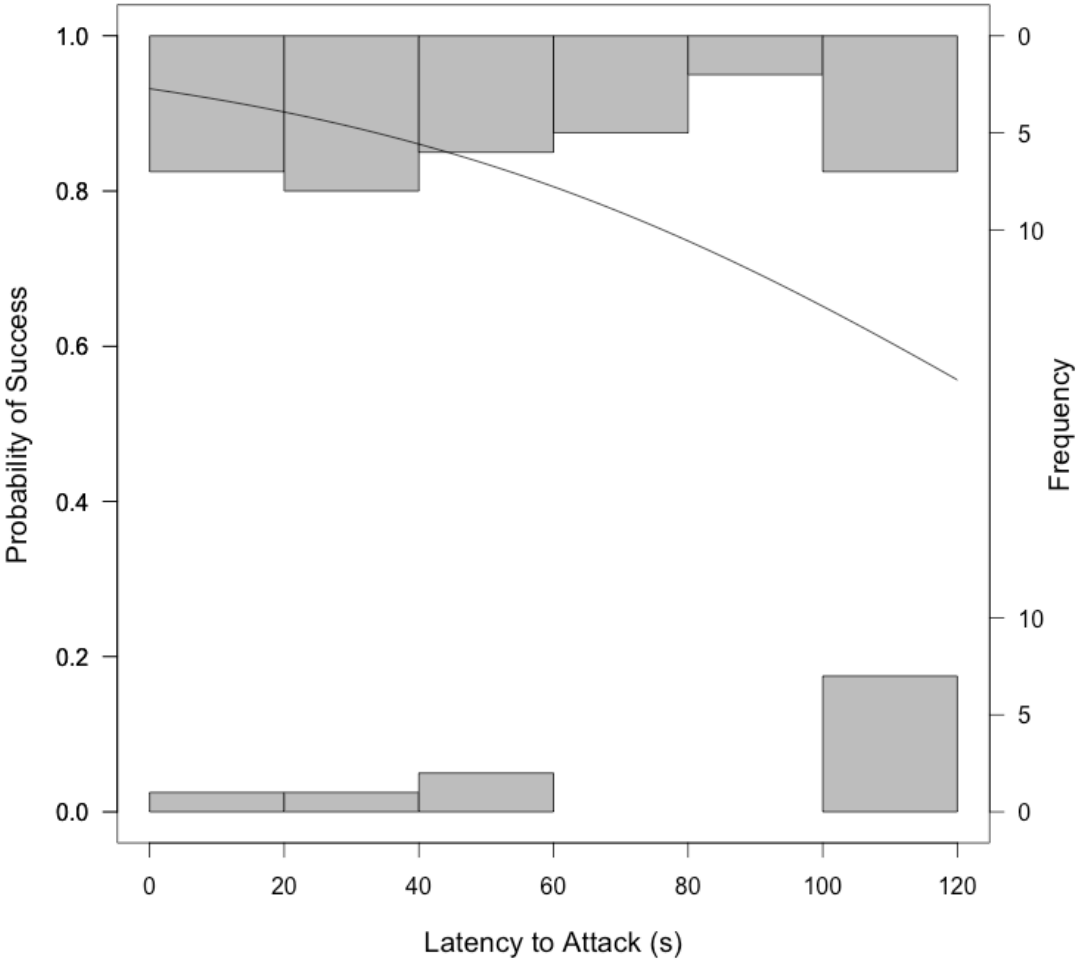

Figure 2.3. Logistic regression of probability of breeding success (0 = no, 1 = yes) and female latency to attack the intruder (s). Histograms show frequency counts of female latency times, while the grey line is the fitted logistic regression equation.

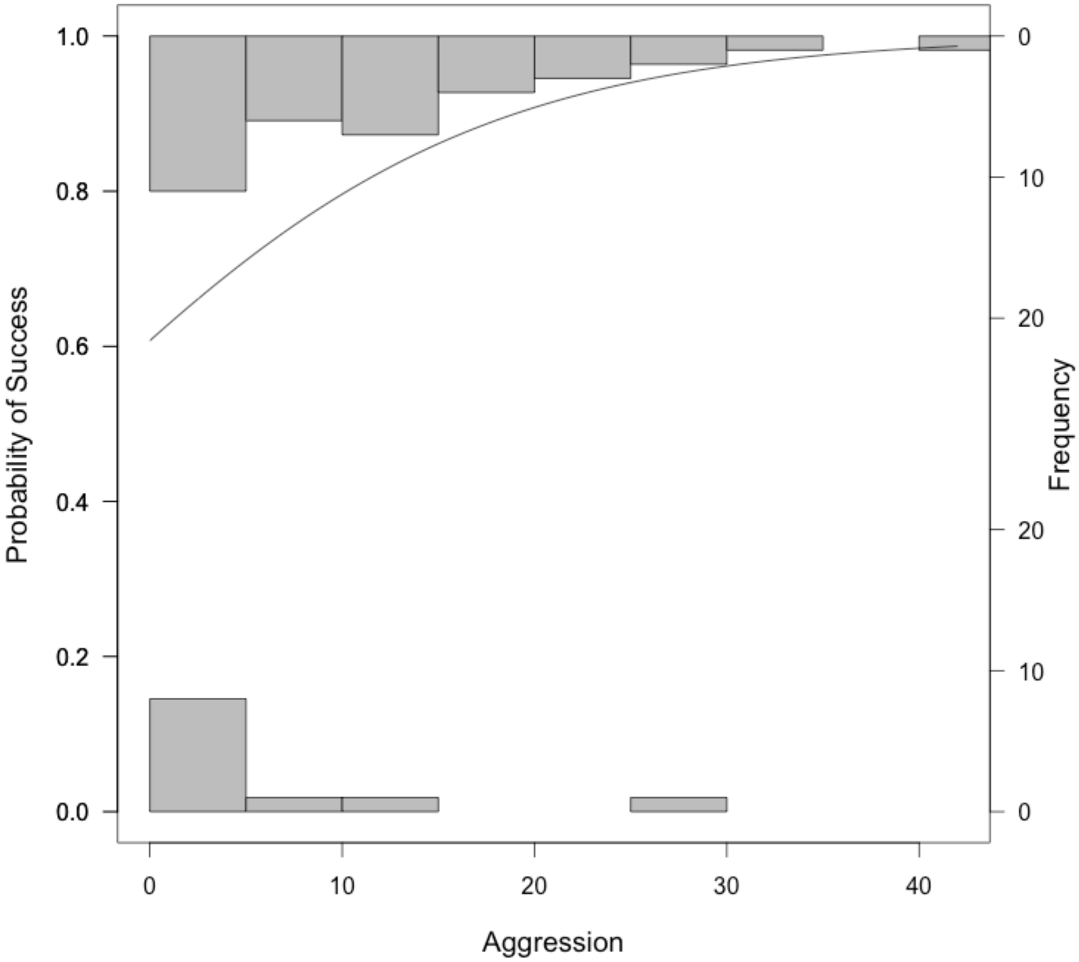

Figure 2.4. Logistic regression of probability of breeding success (0 = no, 1 = yes) and female overall aggression during the defense observation. Histograms show frequency counts of female aggression, while the grey line is the fitted logistic regression equation.

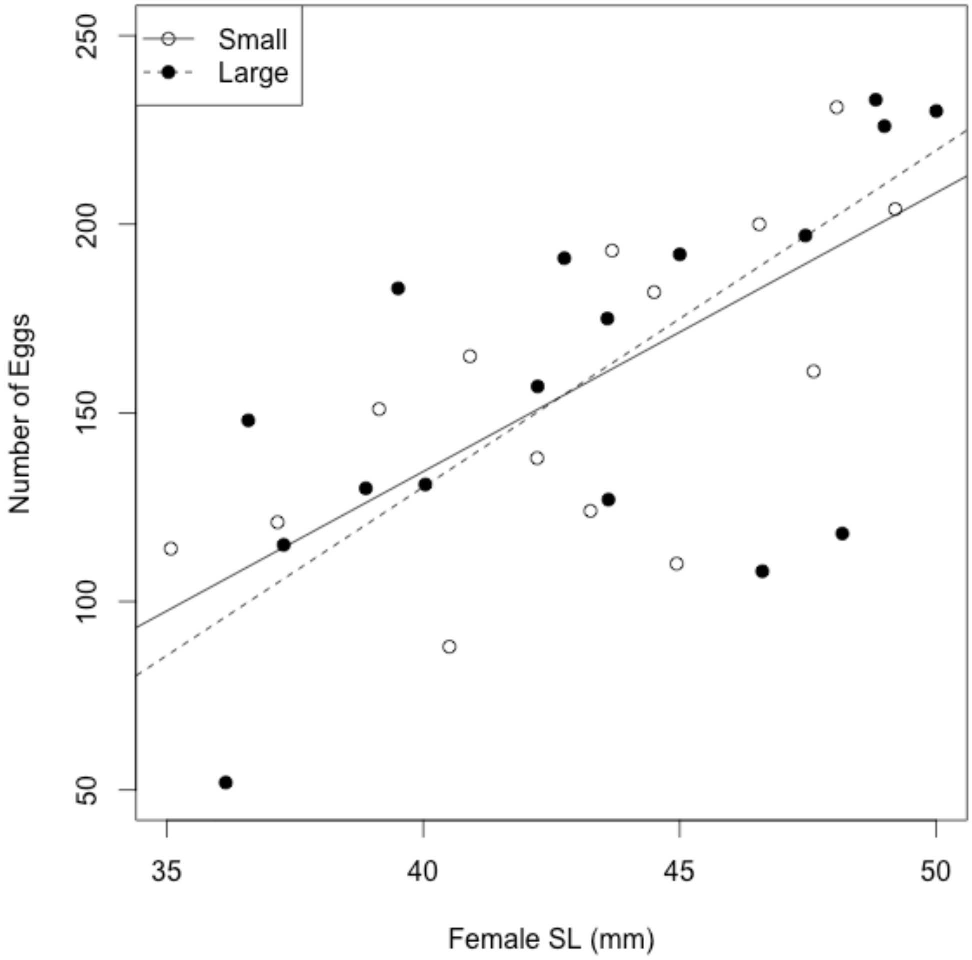

Figure 2.5. The number of eggs was positively correlated with female SL (mm). Mate size (small, large) did not influence egg number (*$F_{1,31}$* = 0.004, *P* = 0.946), nor did the interaction between mate size and female SL (*$F_{1,31}$* = 0.30, *P* = 0.589).

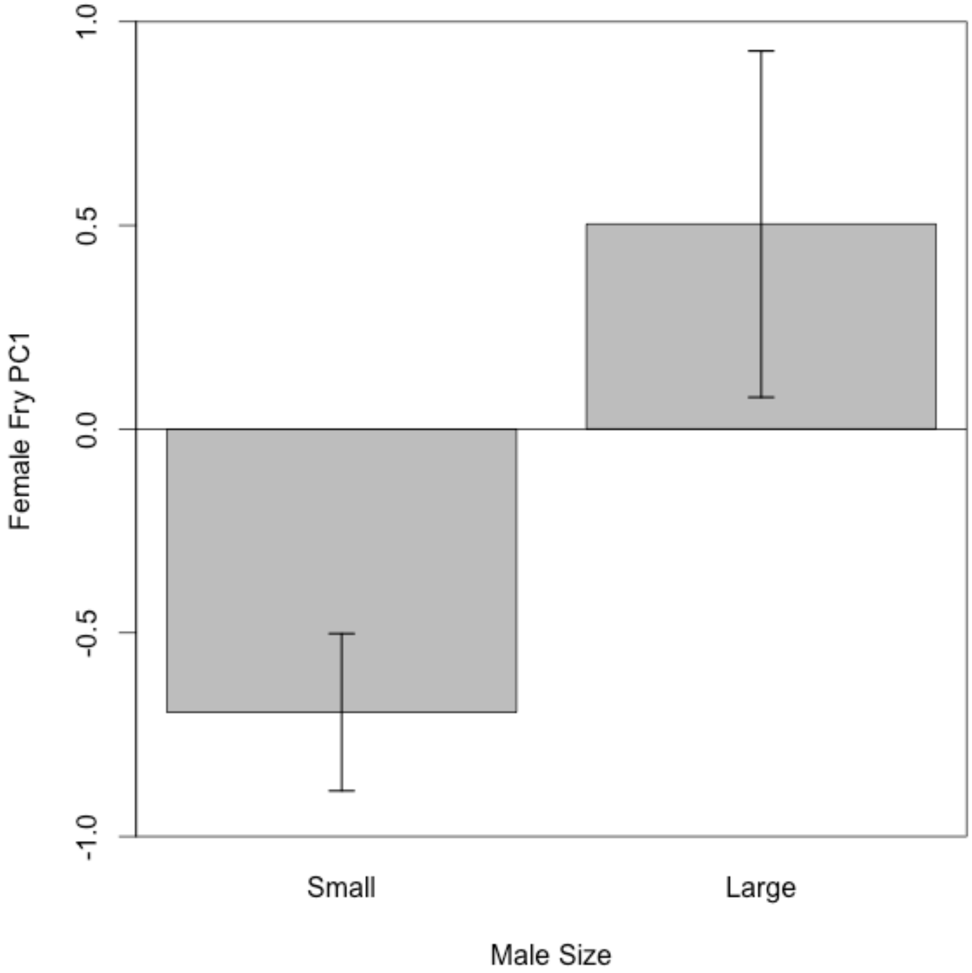

Figure 2.6. Mean ± SE scores for Female Fry PC1 for small and large males. Positive scores represent high levels of parental and defensive behaviors (see Table 2.5 for loading values).

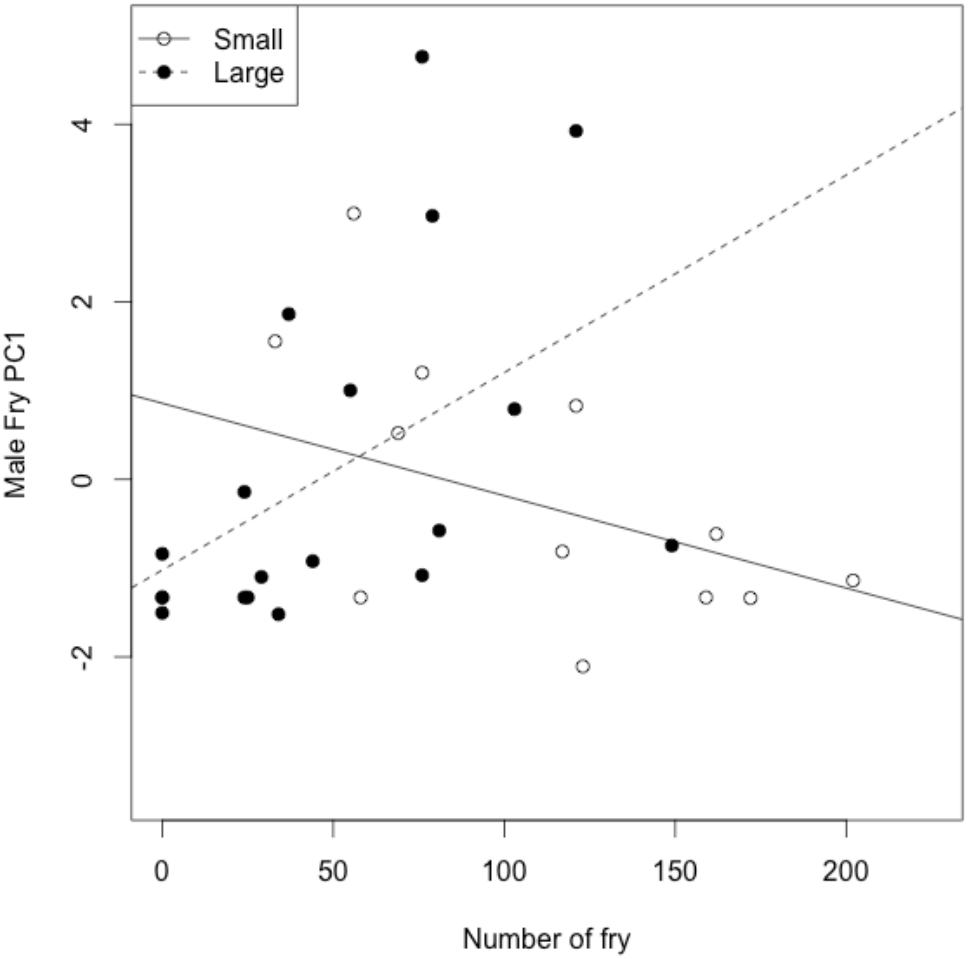

Figure 2.7. Relationship between Male Fry PC1 and number of fry. There was a significant interaction effect of male size on Male Fry PC1, but neither mate size ($F_{1,27}$ = 0.67, P = 0.420) nor number of fry significantly ($F_{1,27}$ = 0.94, P = 0.34) influenced Male Fry PC1. Positive scores represent high levels of parental and defensive behaviors (see Table 2.7 for loading values).

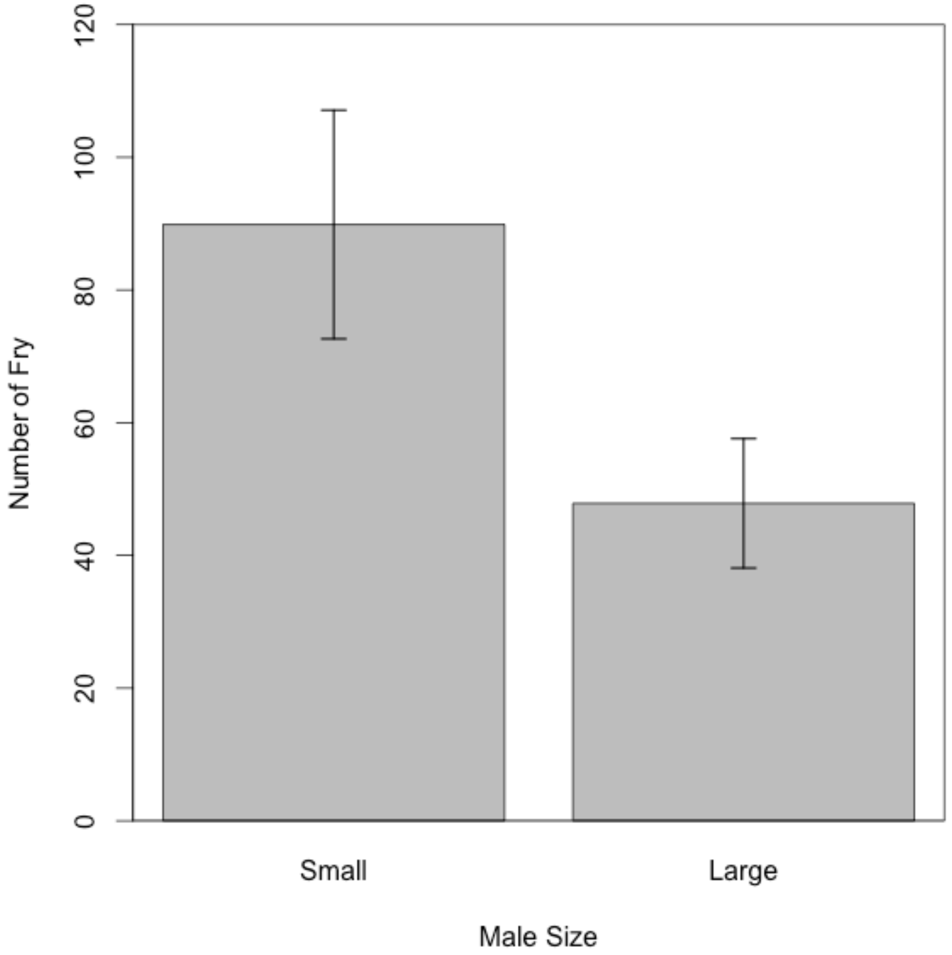

Figure 2.8. Mean ± SE number of fry at the end of the first breeding for small and large males.

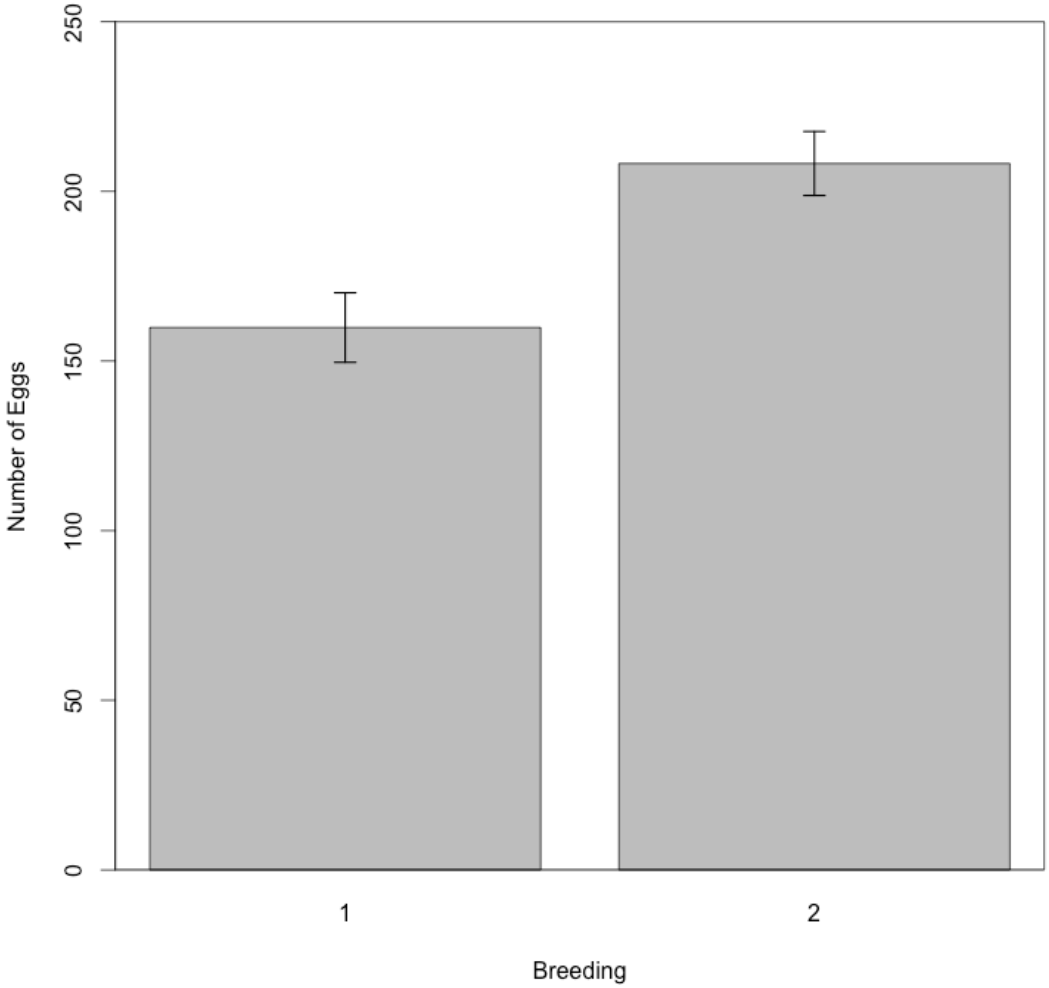

Figure 2.9. Mean ± SE number of eggs for the first and second breedings.

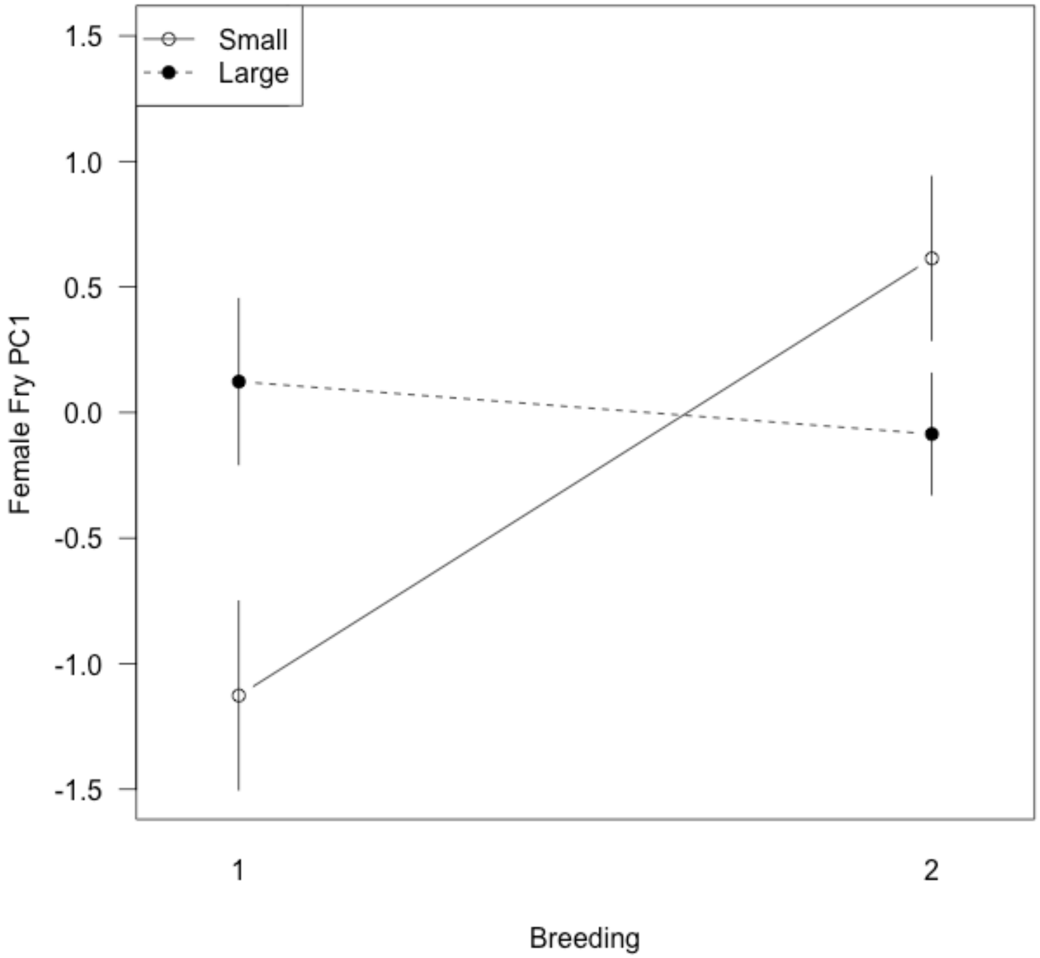

Figure 2.10. Mean ± SE scores for Female Fry PC1 for the first and second breedings. Positive scores represent moderate levels of parental and high levels of defensive behaviors (see Table 2.12 for loading values).

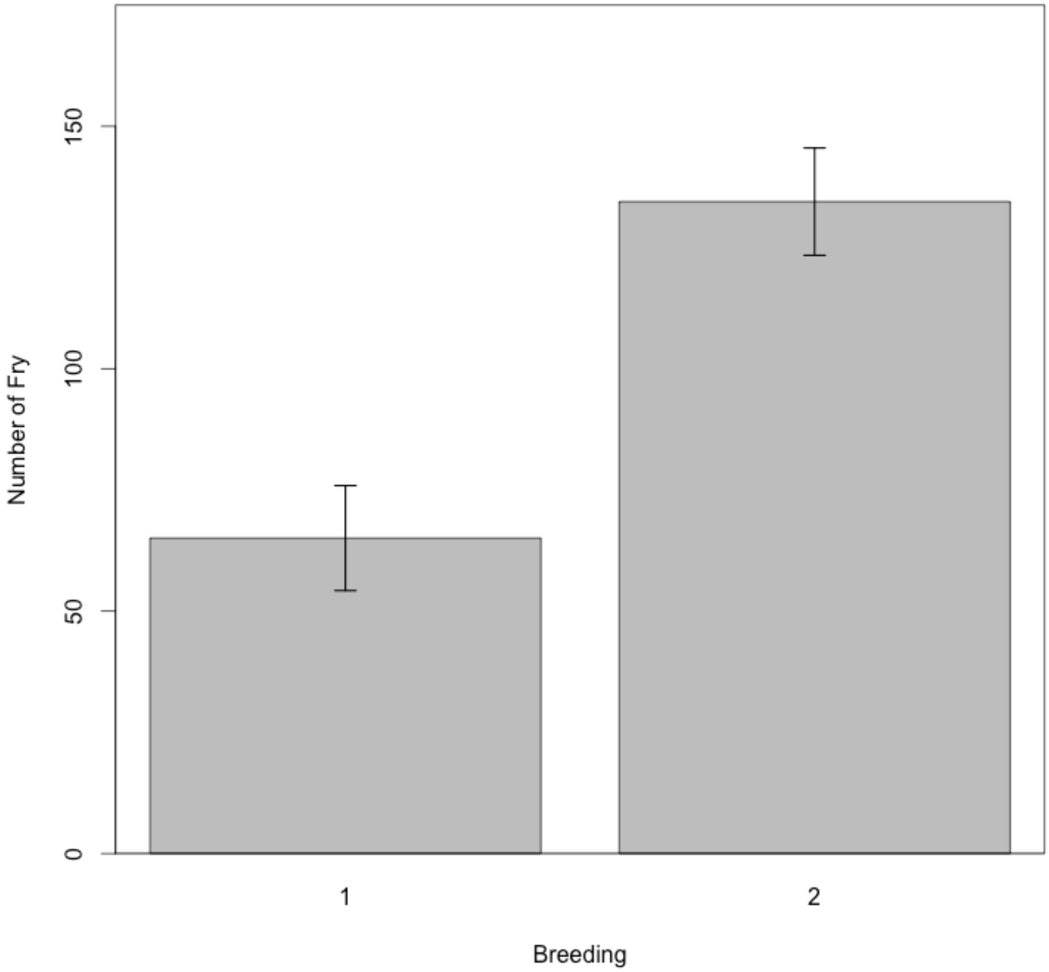

Figure 2.11. Mean ± SE number of fry at the end of the first and second breedings.

Chapter 3. Parental response to reproductive female intruders in a monogamous, biparental fish

ABSTRACT

Female aggression and ornamentation can influence mating dynamics through their role in both intra- and intersexual signaling. In species with facultative polygyny, females can use aggression to deter rivals and maintain their monogamous status. Convict cichlids (*Amatitlania siquia*) are sexually dichromatic, monogamous fish that exhibit biparental care. Females develop gold ventral coloration when reproductively receptive and actively court males. We investigated whether parental response to female conspecific intruders was affected by the intruder's reproductive status. Parental females were more aggressive towards reproductive than non-reproductive intruders and parental female size was negatively correlated with aggression. Males had lower levels of parental care when presented with the reproductive intruder first compared to males initially presented with non-reproductive intruders. Males spent more time associating non-aggressively with reproductive intruders and with intruders that were larger than their mate. Increased aggression by parental females towards reproductive rivals may play an important role in the maintenance of monogamy, which helps females maximize reproductive success for a breeding event.

INTRODUCTION

Female ornamentation and aggression can play an important role in shaping mating dynamics (Kempenaers 1994; Amundsen et al. 1997; Sandell 1998; Kokita and Nakazono 2001; Rosvall 2008; Wong et al. 2008) and these traits can increase female access to males during female-female competition (Owens et al. 1994; Bernet et al. 1998; Baldauf et al. 2011). Females may compete for access to males that provide direct benefits (Gwynne and Simmons 1999) or for access to higher quality males, which are thought to confer indirect benefits via superior genetic quality (Petrie et al. 1992; Saether et al. 2001; Bro-Jørgensen 2002). Temporal shifts in female competitiveness, which are often associated with changes in the operational sex ratio (Kvarnemo et al. 1995; Waights 1996; Forsgren et al. 2004), reinforce the effect dynamic social interactions can have on the strength of mating competition.

Females often compete for access to males that provide care (Summers 1989; Kempenaers 1994; Sandell and Smith 1997; Wong et al. 2008) and when males vary in the quality of care provided to young, females compete for access to higher quality males (Petrie 1983; Owens et al. 1994). Many of the studies that have examined female-female competition over access to male parental care have examined whether monogamous females are able to prevent secondary females from settling in the male's territory (Sandell 1998; Kokita 2002). These studies indicate that males and females often have conflicting interests in terms of mating strategy (Kokita and Nakazono 2001; Smith and Sandell 2005) and that females gain a fitness benefit when they prevent additional females from mating with their partner (Kempenaers

1994; Brandtmann et al. 1999; Kokita and Nakazono 2001). While females can respond to the threat of polygyny by soliciting more copulations from their mate (Eens and Pinxten 1996), the predominant mechanism females use to maintain their monogamous status is aggressive, sometimes lethal (Morales et al. 2014), behavior directed towards rival females (Yasukawa and Searcy 1982; Slagsvold 1993; Liker and Szekely 1997; Kokita 2002).

While female aggression is typically confined to intrasexual interactions, female ornamentation may serve as either an intrasexual (Beeching et al. 1998; Bernet et al. 1998; Baldauf et al. 2011) or intersexual signal (Amundsen et al. 1997; Amundsen and Forsgren 2001; Cornwallis and Birkhead 2007; Baldauf et al. 2011). Females may increase their aggressive behavior towards more ornamented females (Beeching et al. 1998), or conversely, females may decrease courtship activity when in the presence of more ornamented rivals (Berglund and Rosenqvist 2009). Males prefer more ornamented females in a variety of taxa (birds: *Luscinia s. svecica*, Amundsen et al. 1997; fish: *Gobiusculus flavescens*, Amundsen and Forsgren 2001, *Pelvicachromis taeniatus*, Baldauf et al. 2011; lizards: *Crotophytus collaris*, Baird 2007), and ornamentation often signals female quality (Weiss 2006; Cornallis and Birkhead 2007; Doutrelant et al. 2008). Female ornamentation can also serve simultaneously as an inter- and intrasexual signal (Bernet et al. 1998; Baldauf et al. 2011). In the biparental African cichlid *Pelvicachromis taeniatus* males prefer females with a larger area of ventral coloration, as it indicates readiness to spawn, fecundity, and maternal quality (Baldauf et al. 2011). More brightly colored females are more aggressive and more likely to win fights compared to less ornamented females, indicating an intrasexual role of ventral coloration as well (Balduaf et al. 2011).

Convict cichlids (*Amatitlania siquia*; Schmitter-Soto 2007) are freshwater fish, ranging from Guatemala to Panama (Bussing 1987). They are sexually dichromatic (Beeching et al. 1998), with females exhibiting three distinct color phases. Non-breeding females are pale tan and brown, with muted vertical bars. Although the timing and cue remains unclear, prior to mating, females develop gold coloration on the ventral area, with dark grey and black pigmentation partially obscuring the bars. The yellow-orange ventral coloration is reduced, but still present after mating and during the egg-guarding phase (approximately 48 hours after spawning; A. Robart pers. obs.). Females transition to the parental care color phase by the time the fry become free-swimming (approximately 7-10 days after spawning; Anderson et al. 2014; A. Robart pers. obs.). This coloration is characterized by strongly contrasting black bars against a white background color. Females retain this coloration for the duration of the parental care phase, which lasts up to six weeks.

The yellow-orange ventral coloration that female convict cichlids develop prior to mating is carotenoid-based (Brown et al. 2013; Brown et al. 2014; Sefc et al. 2014) and carotenoid signals are used in both intrasexual competition and intersexual mate attraction (Svensson and Wong 2011). Since they cannot be metabolized directly and must be ingested, they are honest signals of the overall health and quality of an individual (Lozano 1994; but see Candolin 1999). When carotenoids are limited, organisms must trade-off allocation between different physiological functions (Svensson and Wong 2011), such as resistance to oxidative stress and reproduction (Bertrand et al. 2006). Female convict cichlids with the gold ventral coloration have a higher ovary mass compared to non-breeding and breeding females (Wisenden 1995), indicating an elevated level of reproductive investment associated with ornamentation. Anderson et al. (2014) tracked ventral coloration of female convict cichlids through a breeding event and hypothesized that the decline in ornamentation intensity between spawning and subsequent parental care was due to females reallocating carotenoids to eggs or the female's reduced foraging ability during parental care.

Courtship and breeding in convict cichlids is characterized by females following a male and chasing away other females in his vicinity (Mackereth and Keenleyside 1993). Ornamented females actively court males, including those that are already guarding young with a female partner (Wisenden 1995; A. Robart pers. obs.). Spawning territories are not established until the day of spawning (Mackereth and Keenleyside 1993), indicating that the timing of breeding is strongly female-dependent. Both parents care for the young, with protection from both conspecific and heterospecific predators the main form of parental care. They typically exhibit sequential monogamy, but if brood size is smaller than expected males will sometimes abandon the brood, leaving the female to guard the young (Wisenden 1994a). Females are less successful at caring for the young on their own in other cichlids (Nagoshi 1987; Balshine-Earn 1997; Lehtonen et al. 2011), suggesting that female reproductive success is reduced even further when males terminate the pair-bond before offspring independence. Males can mate up to four times per breeding season, whereas females rarely breed more than once (Wisenden 1995). Females become receptive throughout the six-month breeding season, which results in a continual supply of potential mates for males, and thus potential rivals for already paired females. Laboratory experiments have found that when new partners are available, divorce in convict cichlids is more likely to be influenced by female, rather than male, intrasexual competition (Triefenbach and Itzkowitz 1998).

The purpose of this study was to investigate male and female response during the parental care phase to female conspecific intruders that differ in their reproductive status. Specifically, we predicted that parental females would behave more aggressively to reproductive intruders than non-reproductive intruders. Male quality can influence female response to intruders in other monogamous species of fish (Whiteman and Côte 2003) and female convict cichlids increase their parental care behavior when paired with higher quality mates (Robart 2012). We therefore predicted higher levels of aggression directed at intruders when females were paired with high quality mates. Fry development stage and brood size affect the likelihood of male desertion (Wisenden 1994a), so we predicted females would respond more aggressively when brood size was smaller than expected and fry were closer to independence. Finally, since non-reproductive females are not a potential new mate for males, and thus pose only a threat to the offspring, we predicted that males would be more aggressive towards non-reproductive female intruders.

MATERIALS AND METHODS

We conducted this experiment in Lomas de Barbudal Biological Reserve, Guanacaste, Costa Rica (10°30’N, 85°22’W), from January to March 2013. The breeding season of convict cichlids is from January-June, which coincides with the long dry season when water levels are stable. We chose four pools to use as study sites within the río Cabuyo, spanning approximately one kilometer of stream length. All sampling and behavioral observations were conducted using snorkeling.

We captured reproductive and non-reproductive female convict cichlids to use as conspecific intruders (Fig. 3.1). Fish were captured with aquarium hand nets and came from the same pool where focal breeding pairs were located. Breeding pairs are typically found in the shallower parts of pools and defend only the immediate area surrounding their brood. Non-breeding individuals forage throughout the pool and are often found in the deeper areas, which have a greater concentration of leaf litter and detritus for adults to feed on (A. Robart, pers. observ.). We therefore believed it unlikely that dear-enemy effects (Leiser and Itzkowitz 1999; Frostman and Sherman 2004; Olendorf et al. 2004) would influence the behavioral response of parents to intruders from the same pool.

Reproductive females were identified based on the presence of gold coloration on their ventral area, whereas non-reproductive females were light brown on their dorsal with a pale grey ventral area (Wisenden 1995). We attempted to size match intruders as closely as possible for standard length (tip of snout to posterior end of caudal peduncle; SL); however, reproductive females were slightly larger than non-reproductive females (Reproductive – non-reproductive SL ($\bar{X} \pm SE$): 3.03 ± 0.47 mm; paired t-test: $t = -6.57$, $df = 86$, $P = 0.0001$). After capture, intruders were measured for SL, weighed on an electronic balance (Jennings CJ600), and photographed. The intruders were held in a live well at all times except for when they were presented to breeding pairs. The live well was constructed from shade cloth (Cooleroo™, 70-80% cover) and heavy gauge wire, with a diameter of 60 cm. The live well was placed in the stream with several rocks in the bottom; depth was dependent on stream depth and ranged from approximately 60-90 cm. Occasionally we conducted experiments in the same pool on consecutive days and fish were kept overnight in the live well for use the following day. We checked intruders at the beginning of the next day to ensure appearance and behavior had not changed. Intruders were never used for more than two consecutive days.

After breeding pairs with free-swimming fry were located, we conducted an initial 10-minute baseline behavioral observation for a separate study, with a pair of observers recording behavior for both parents. For all observations we scored the following behaviors: chases (swimming rapidly at approaching fish), frontal displays (flaring opercula while facing another fish), time away from the brood (3 or more body lengths away), intra-pair bite (focal parent bites partner), and intra-pair frontal display (focal parent directs frontal display at mate); males also perform a lower intensity display (low level displays: swimming directly, but slowly, at approaching fish) that was recorded. As the main form of parental care is protection from predators, we considered aggressive displays and time spent in close proximity to the brood to be indicative of high levels of parental investment.

After the baseline observation we conducted two additional 10-minute observations to measure parental response to the intruders. Intruders were presented in a clear, plastic box (12 cm x 12 cm x 13.5 cm) with holes to allow for potential olfactory cues. We placed the confined intruder on the substrate, approximately 40 cm from the parents and fry. We discriminated between chases, frontal displays, and low level displays based on whether they were directed at the confined intruder or other fish in the general vicinity of the brood. Approximately 2-3 weeks after beginning the experiment we noticed that the parents (typically the male) would occasionally attempt to interact with the intruder in a non-aggressive manner. We therefore added time spent with the intruder (focal parental within 10 cm of box, facing intruder with no observed aggressive behavior) to the behaviors recorded during all subsequent observations.

Each breeding pair was presented with both intruder types, with the order of presentation randomized. The first intruder was typically presented immediately following the conclusion of the baseline observation. However, one parent (usually the male) would occasionally leave the vicinity of the brood during the observation and be gone through the end. In these instances, we waited until both parents were actively guarding the brood before presenting an intruder.

Immediately after the final intruder observation, we captured both parents and the fry. A cylindrical net (1 m diameter x 1.5 m height) was constructed from shade cloth (Cooleroo™, 70-80% cover) and several heavy gauge wire rings. The net was constructed with a skirted bottom that extended approximately 75 cm in all directions from the base, with leaded weights along the perimeter. Several empty plastic bottles (~250-475 ml) were attached to the top of the net for buoyancy. Both parents typically stayed within very close proximity to the brood and this allowed us to lower the net directly over the parents and brood. Once the breeding pair and fry were encircled, we used hand nets to capture the male. After the male was caught, we captured the fry using a combination of hand nets and a 30-ml plastic pipette. The female was caught once all the fry had been captured. The parents were kept together in an aerated (Penn Plax Silent Air® B11) 8-liter bucket, with the fry in a separate 8-liter bucket. We used visible elastomer implant (Northwest Marine Technologies) to uniquely mark parents along the dorsal area. We weighed and measured adults for SL and removed a small portion of the caudal fin as a genetic sample. We counted the fry and measured a subset of the brood (*n* =10) to calculate mean fry SL.

After the parents and fry were processed, we returned them to the cylindrical net. The female was placed in the bucket with the fry and the bucket was lowered into the net. Once the female and fry swam out we released the male, also within the confines of the net. We removed the net after at least one parent resumed guarding the brood.

Data analysis

Data were analyzed using JMP® Pro 11.0 (SAS Institute 2013) and R 3.1.0 (R. Core Development Team 2014). We used principal component analysis (PCA) to summarize female and male behavior. PCA can highlight if particular suites of behaviors are used in conjunction with one another and contribute to a general pattern of behavior. Time spent with the intruder was not recorded for all observations and was analyzed separately. We saved all principal components (PCs) with an eigenvalue greater than one (Norman and Streiner 2008), resulting in three PCs each for female and male behavior.

Males are more likely to desert the brood when fry are 8 mm or larger and when the number of fry is below average (Wisenden 1994a). We therefore converted mean fry SL into a discrete variable (relative fry size) with two categories: small (< 8 mm) and large (>8 mm). To determine if a brood contained fewer fry than expected we regressed mean fry SL onto number of fry to determine the expected number of fry for a given size. This was done as fry number decreases during the six-week parental care period (Wisenden 1994b; Robart, unpublished data). We then used the normalized number of fry to convert fry number into a discrete variable (expected number of fry) with breeding pairs having either “more” or “fewer” fry than expected.

In addition to controlling for attrition during the fry stage, normalizing the number of fry indicates how successful a breeding pair is at guarding their offspring compared to other pairs in the population. To investigate the parental factors that influence breeding success we tested the effects of male SL, female SL, and all PC scores on the normalized number of fry. We used linear regression and removed non-significant terms using stepwise-backward elimination.

We used linear mixed models to examine the effect of intruder type, intruder SL, the interaction between intruder type and intruder SL, female SL, intra-pair size difference (M-F SL), presentation order, relative fry size, expected number of fry, and the interaction between relative fry size and expected number of fry on PC scores, with pair ID included as a random effect. We removed non-significant terms using stepwise-backward elimination until models contained only significant terms.

Time spent with the intruder was non-normally distributed and we used the glmer function of the lme4 package (R. Core Development Team 2014) to perform generalized linear mixed models with a Poisson distribution. As time spent with the intruder was added several weeks after observations began, the sample size was smaller (*n* = 120 vs. *n* = 174, respectively); this prevented us from adding more than one continuous fixed effect, as the models became over-parameterized. Since we hypothesized that males would exhibit greater interest in reproductive intruders that were larger than their current mate, we removed intruder SL and female SL from the initial model and instead added the discrete effect of which female (parental vs. intruder) had a larger SL. Thus, full models included intruder type, parental vs. intruder size category, the interaction between intruder type and parental vs. intruder size category, intra-pair size difference, presentation order, relative fry size, expected number of fry, and the interaction between relative fry size and expected number of fry. Stepwise-backward elimination was used until models only contained significant terms.

RESULTS

There was a high degree of similarity in the loading scores for the female and male PCs. For each sex, the first PC loaded strongly for aggressive behavior directed at fish in the general vicinity of the brood and low levels of time spent away from the young (Tables 3.1 and 3.2). Since these behaviors are indicative of increased investment in the offspring, we assigned Female PC1 and Male PC1 the labels of “Female Parental Care” and “Male Parental Care”, respectively. The second PC for female and male behavior loaded positively for aggression directed specifically at the confined intruder and thus were labeled “Female Intruder Response” and “Male Intruder Response”, respectively (Tables 3.1 and 3.2). The final PCs indicated conflict between the parents, characterized by increased levels of intra-pair aggression, and were labeled “Female Intra-pair Aggression” and “Male Intra-pair Aggression” (Tables 3.1 and 3.2).

Intruder type, intruder SL, female SL, intra-pair size difference, presentation order, relative fry size, expected number of fry, nor any interactions significantly influenced the PCs representing Female Parental Care, Female Intra-pair Aggression, Male Intruder Response, or Male Intra-pair Aggression.

Both intruder type ($F_{1,\ 80.0} = 15.160$, $P = 0.0002$) and female SL ($F_{1,\ 79.0} = 13.651$, $P = 0.0004$) significantly predicted Female Intruder Response (Fig. 3.2). In addition, the breeding success of pairs was significantly predicted by female SL ($F_{1,79} = 15.486$, $P = 0.0002$; Fig. 3.3). Females spent more time with non-reproductive intruders ($z = -3.213$, $P = 0.001$) and there was a significant interaction effect between intruder type and parental vs. intruder size category ($z = 3.422$, $P = 0.0006$) on the amount of time females spent associating with intruders (Fig. 3.4).

Presentation order of the intruders significantly influenced Male Parental Care ($F_{1,\,85.0} = 5.980$, $P = 0.0165$; Fig. 3.5). We therefore tested the interaction between intruder type and presentation order to determine if presentation order altered Male Parental Care for both observations, or only for the first intruder observation. The interaction between intruder type and presentation order was not significant ($F_{1,\,85.0} = 0.278$, $P = 0.5993$), indicating that the level of parental care observed in males that were initially presented the reproductive intruder persisted during the second observation with the non-reproductive intruder. Males spent more time with the intruder when it was larger than his partner ($z = 4.112$, $P < 0.0001$) and when presented with the reproductive intruder ($z = 7.061$, $P < 0.0001$). There was also a significant interaction effect between intruder type and parental vs. intruder size ($z = -2.946$, $P = 0.003$; Fig. 3.6).

DISCUSSION

The results of this study indicate that both parents of a breeding pair alter their behavior to the presence of reproductive intruders. Parental care was affected in males, but not females. Males had lower levels of parental care when first presented with the reproductive intruder compared to males initially presented with the non-reproductive intruder. The lower level of Male Parental Care was observed for both observations, indicating that presenting the reproductive intruder first altered the male’s subsequent behavior. This may have been due to presenting the second intruder often immediately after the first intruder, as behavioral changes can last up to 72 hours in response to social interactions in cichlids (Maruska and Fernald 2010). Breeding pairs and their fry can move up to 14 m within a single day (Wisenden 1995) and we did not stagger the intruder observations out of concern that we would not be able to locate them at a later time. Males may have lowered their parental care because it allowed them to stay in the vicinity of the brood and observe the interaction between their mate and the intruder. The outcome of competitive interactions can influence mate preferences in the opposite sex (Candolin 1999; Doutrelant and McGregor 2000) and pair-bond stability (Triefenback and Itzkowitz 1998). Males therefore may have been attempting to “eavesdrop” on the interaction between his mate and the intruder. We observed a male abandon his current brood after a reproductive female engaged his current mate in a sustained aggressive interaction in which the females chased, displayed, and bit one another for more than one hour. During this interaction, the male foraged in the leaf litter between the two females and performed very few behaviors, either at the rival female or other fish in the vicinity of the brood. His mate was unable to drive off the other female and the male abandoned his offspring and paired with the new female by the end of the day.

We did not expect the parents to approach the intruders and interact with them in a non-aggressive manner; however, the results suggest that each sex associated with an intruder when doing so would potentially benefit the parent. Males have been found to increase their attractiveness to females by associating with less attractive rivals (Dugatkin and Sargent 1994; Bateson and Healy 2005; Gasparini et al. 2013). Here we found that females spent more time with intruders that were not a threat to their mating status. Perhaps by spending more time with non-reproductive intruders, females similarly highlight that the rival cannot provide a benefit to the male due to her non-reproductive status. Males, meanwhile, spent more time with reproductive intruders and intruders that were larger than his current mate. Male convict cichlids prefer larger females (Nuttall and Keenleyside 1993; Triefenbach and Itzkowitz 1998; Beeching and Hopp 1999), and more ornamented females are more fecund in several species of fish (Amundsen and Forsgren 2001; Svensson et al. 2006; Baldauf et al. 2011). In this study males may be preferentially biasing their mate attraction towards females that would give them the greatest reproductive benefit (Gross and Sargent 1985; Wisenden 1995; Galvani and Coleman 1998; A. Robart, unpublished data) by associating with larger and more ornamented intruders.

Females responded more aggressively to reproductive than non-reproductive intruders, which suggests females are increasing their aggression for intruders that pose a threat not only to their offspring, but also to their mating status. In addition to loading positively for aggression directed at intruders, Female Intruder Response loaded positively for aggression directed at her mate. This suggests higher levels of sexual conflict between the parents when presented with reproductive intruders. Conflict between parents can occur when males have the option to increase their reproductive success through securing an additional mate (Smith and Sandell 2005). Males must divide their parental effort between two broods (Kempenaers 1994), and this often reduces female fitness (Kokita and Nakazono 2001). This conflict between competing reproductive interests could explain why we observed higher intra-pair aggression in the presence of reproductive intruders compared to non-reproductive intruders.

We found a significant effect of female size on both Female Intruder Response and the normalized number of fry. Smaller females responded more aggressively to intruders, regardless of the intruder's reproductive status. Smaller females were less successful at guarding their brood, resulting in fewer fry than expected for a given size. The combined effects of male preference for larger females (Nuttall and Keenleyside 1993; Triefenbach and Itzkowitz 1998; Beeching and Hopp 1999) and desertion by males when broods contain fewer fry than expected (Wisenden 1994a) may act synergistically to increase aggression in smaller females. The reduced reproductive success would elevate the risk of male desertion and any reproductive females that the male encountered would likely be larger his current mate. Small females may therefore have higher levels of aggression due to their increased need to prevent interactions between their mate and rival females.

Male size is positively correlated with offspring number in convict cichlids (Wisenden 1994b; Robart 2012) and females increase their parental care when paired with larger males (Robart 2012). However, we found that male quality did not influence female intrasexual dynamics in this study. Unlike previous studies that examined whether females were able to maintain their monogamous status through aggressive behavior (Sandell 1998; Kokita 2002), convict cichlids have sequential monogamy (Keenleyside et al. 1990; Wisenden 1994a), rather than simultaneous polygyny. The termination of the pair-bond in monogamous species results in lower reproductive success for the individual replaced by a sexual rival (Fernandez-Duque and Huck 2013) and male-deserted broods have lower reproductive success than those with biparental care (Nagoshi 1987; Balshine-Earn 1997; Lehtonen et al. 2011). If females are unable to maintain their monogamous status it doesn't result in a reduction in male parental effort, but rather a total absence of it. Hence, a potential explanation for no effect of male size on female response may be because when faced with male desertion, simply the presence or absence of the male may be more important to reproductive success than male quality.

Secondary sexual traits with both intra- and intersexual functions are hypothesized to evolve first via intrasexual competition and are subsequently used for intersexual mate attraction (Berglund et al. 1996; Watson and Simmons 2010). The results of this study suggest that the gold ventral coloration in female convict cichlids serves as both an intra- and intersexual signal. Carotenoid-based signals influence intrasexual dynamics in other cichlids (Evans and Norris 1996), and the presence of intrasexual rivals can increase both signal intensity and androgen levels (Dijksta et al. 2007). Increases in androgens (11-ketotestosterone and testosterone) are also associated with higher levels of aggression (Desjardins et al. 2005; Taves et al. 2009), which would increase the success of reproductive females during intrasexual competition (Rosvall 2008). Male preference for female ornamentation is predicted to evolve when males are selective and when their potential reproductive rate is limited due to large investments (Svensson et al. 2006). When carotenoid-based signals are used for mate attraction, the honesty of the signal is reinforced when it indicates readiness to mate (Svensson and Wong 2011). The combined effects of reproductive females having a higher ovary mass than non-reproductive or breeding females (Wisenden 1995) and male investment in parental care predicts male convict cichlids should use female ventral coloration when making mating decisions. Although Beeching et al. (1998) did not find a difference in male preference for females with and without the ventral coloration, signals are effective if they in some way alter the behavior of another individual (Maynard Smith and Harper 2003). Males preferentially associated with and decreased their parental care when in the presence of reproductive intruders, indicating that female ornamentation does indeed alter male behavior.

While there has been increased debate in recent years over how to classify female intrasexual competition (Rosvall 2011; Lyon and Montgomerie 2012; Tobias et al. 2012; Clutton-Brock and Huchard 2013), parental and reproductive female convict cichlids are potentially competing over different resources. Parental females are behaving aggressively to retain their monogamous status and for continued paternal care, which will maximize their reproductive success. Reproductive females, however, may be competing for immediate access to a male to fertilize her eggs, in addition to his future parental effort. Convict cichlids have been observed to spawn eggs in the laboratory when housed only with other females (A. Robart, pers. obs.), possibly indicating that females are unable to reabsorb eggs once they develop. As females typically only breed once per season (Wisenden 1995), if a female is not able to secure a mate by the time she is forced to spawn then she may need to wait until the following year to reproduce. This difference in the immediate resource that females are competing for highlights the complexities of female intrasexual competition.

In conclusion, we found that females directed higher levels of aggression at reproductive than non-reproductive intruders. Males lowered their parental behavior when exposed to the reproductive intruder first compared to males initially presented with the non-reproductive intruder and they spent more time associating in a non-aggressive manner with reproductive intruders. Smaller females may need to defend their mating status more aggressively compared to large females due to their lowered reproductive success and the likelihood their mate would encounter larger rival females. While we observed a male desert his current mate in order to mate with a reproductive female, more research is needed to assess the prevalence of such male desertion behavior and the conditions under which reproductive females target already mated males when unpaired males are also available. This will give insight into the social interactions parental females face when rearing a brood to independence and the selective pressures that influence reproductive success.

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Tables and Figures

Table 3.1. Loading scores for PC axes 1-3 for female behavior.

Behavior	Female Parental Care	Female Intruder Response	Female Intra-pair Aggression
Chases	0.707	-0.254	-0.325
Frontal Displays	0.647	0.377	0.183
Time Away from Brood (s)	-0.375	-0.306	0.382
Chases at Intruder	-0.432	0.555	-0.229
Frontal Displays at Intruder	-0.043	0.677	-0.327
Intra-Pair Bites	-0.388	0.108	0.267
Intra-Pair Frontal Displays	0.338	0.391	0.727
Eigenvalue	1.513	1.231	1.044
% Variation Explained	21.613	17.589	14.915

Table 3.2. Loading scores for PC axes 1-3 for male behavior.

Behavior	Male Parental Care	Male Intruder Response	Male Intra-pair Aggression
Chases	0.618	0.014	0.338
Frontal Displays	0.465	0.167	0.058
Low Level Displays	0.622	-0.245	0.055
Time Away from Brood (s)	-0.699	-0.149	0.144
Chases at Intruder	-0.148	0.707	-0.103
Frontal Displays at Intruder	0.152	0.583	-0.150
Low Level Displays at Intruder	-0.006	0.702	0.103
Intra-Pair Bites	-0.205	0.106	0.772
Intra-Pair Frontal Displays	-0.005	0.037	0.708
Eigenvalue	1.561	1.457	1.283
% Variation Explained	17.344	16.187	14.251

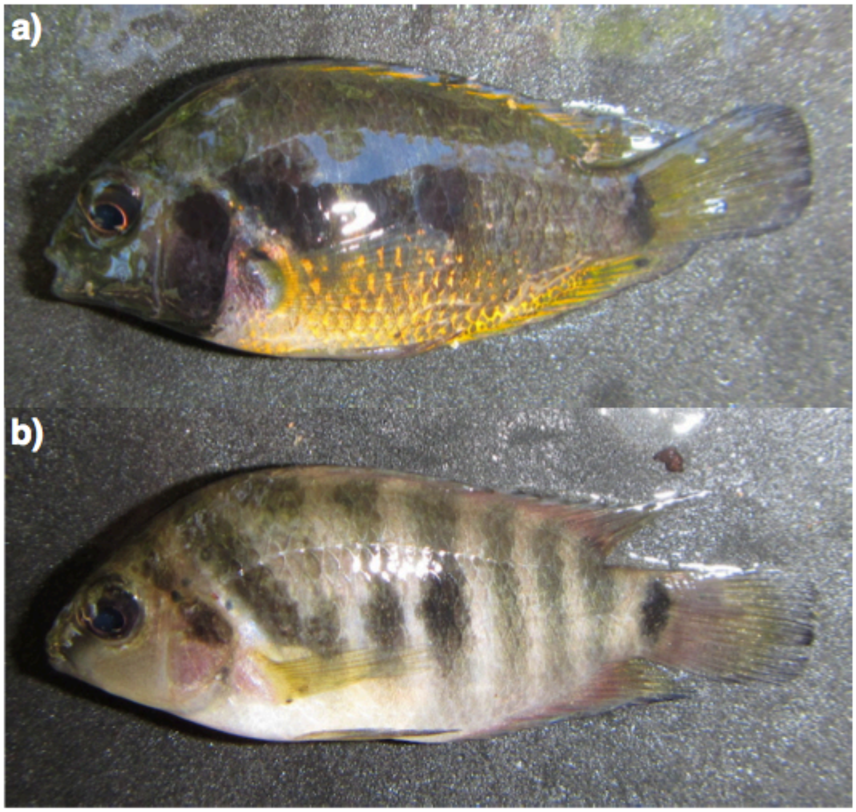

Figure 3.1. Example of reproductive (a) and non-reproductive (b) intruders. Reproductive intruders were identified based on gold ventral coloration, whereas non-reproductive intruders were olive colored.

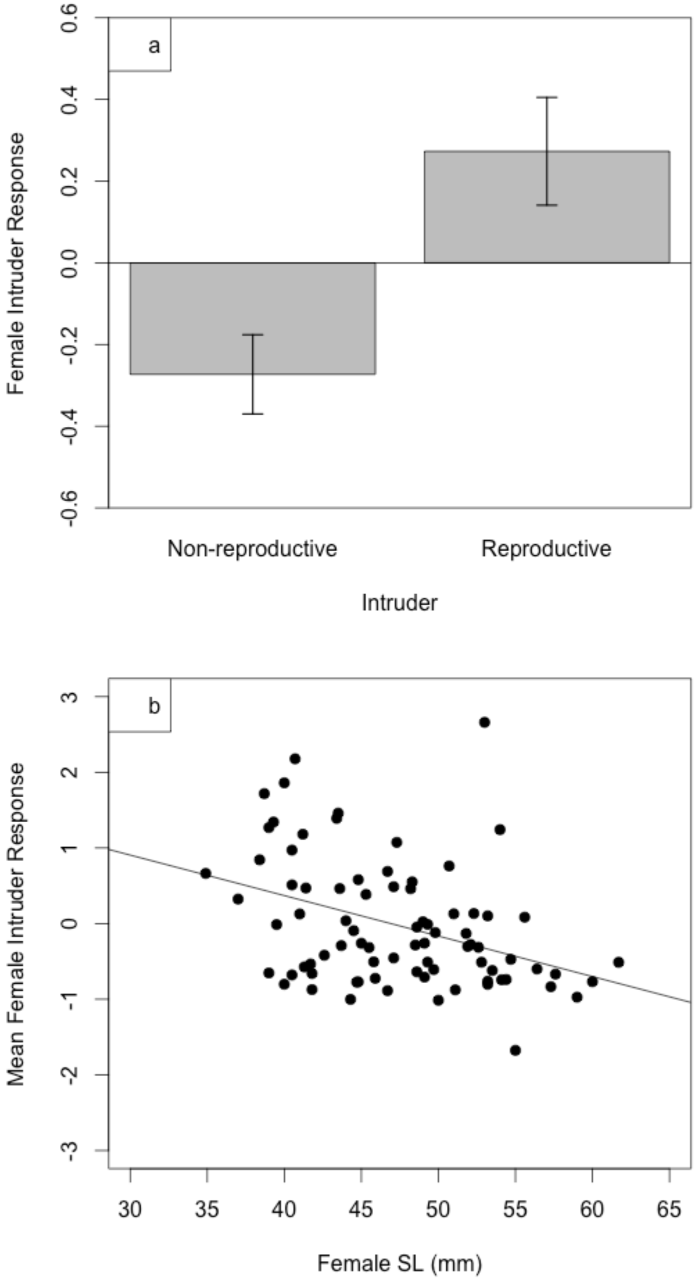

Figure 3.2. Effect of intruder type (a) on Female Intruder Response. Female SL (mm) was negatively correlated with Female Intruder Response (b). The mean response of an individual female was used to reflect the number of females actually sampled. Large Female Intruder Response values indicate high levels of aggression directed at intruders (see Table 3.1 for PC loading values).

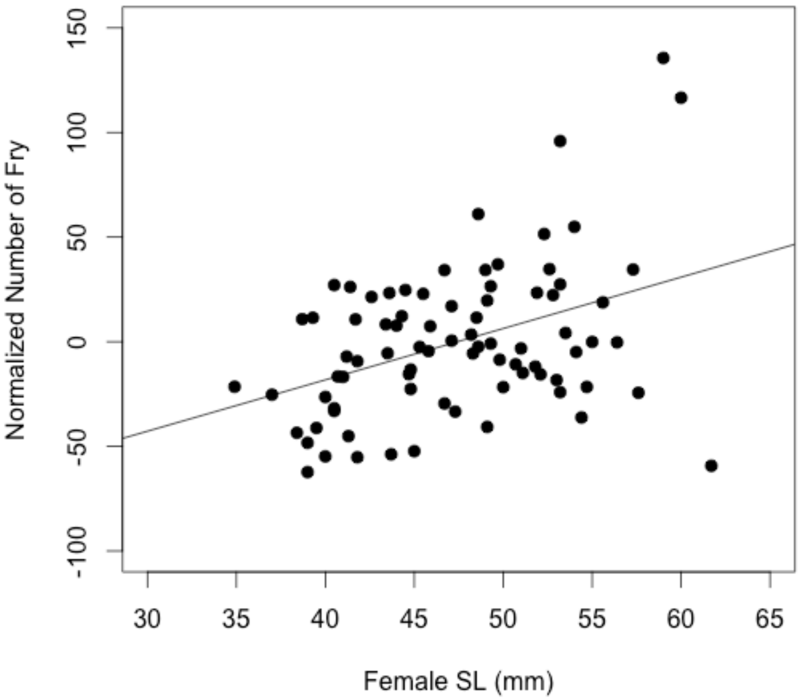

Figure 3.3. Correlation between Female SL and normalized number of fry.

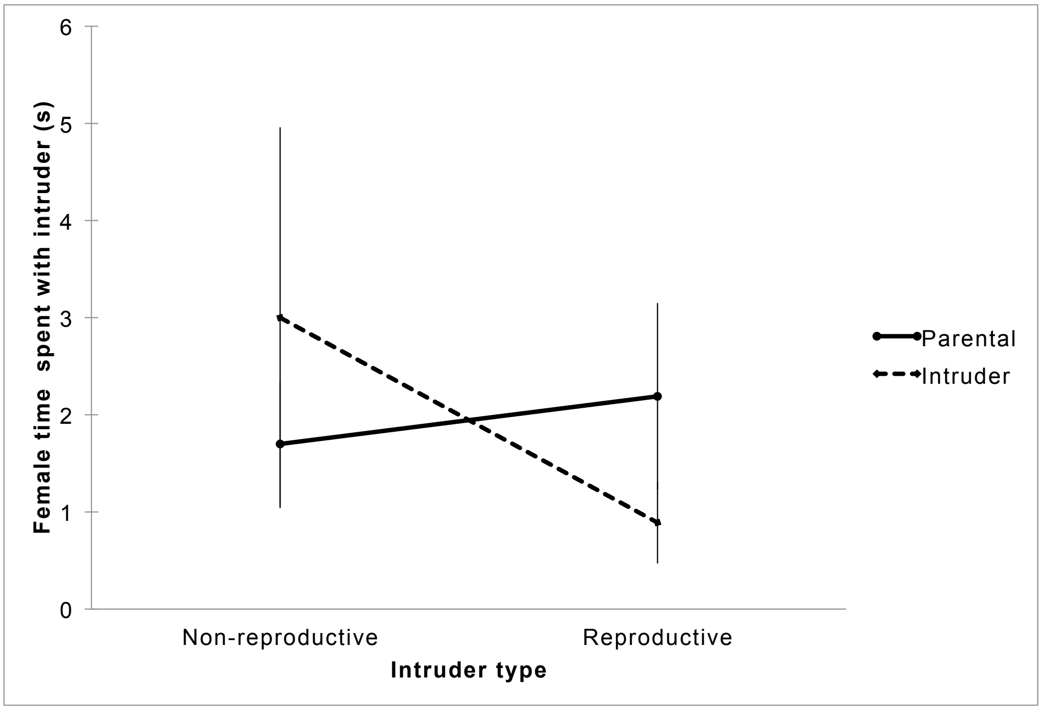

Figure 3.4. Amount of time females spent associating non-aggressively when presented with non-reproductive and reproductive intruders. Females were either larger (Parental) or smaller (Intruder) than the intruder female.

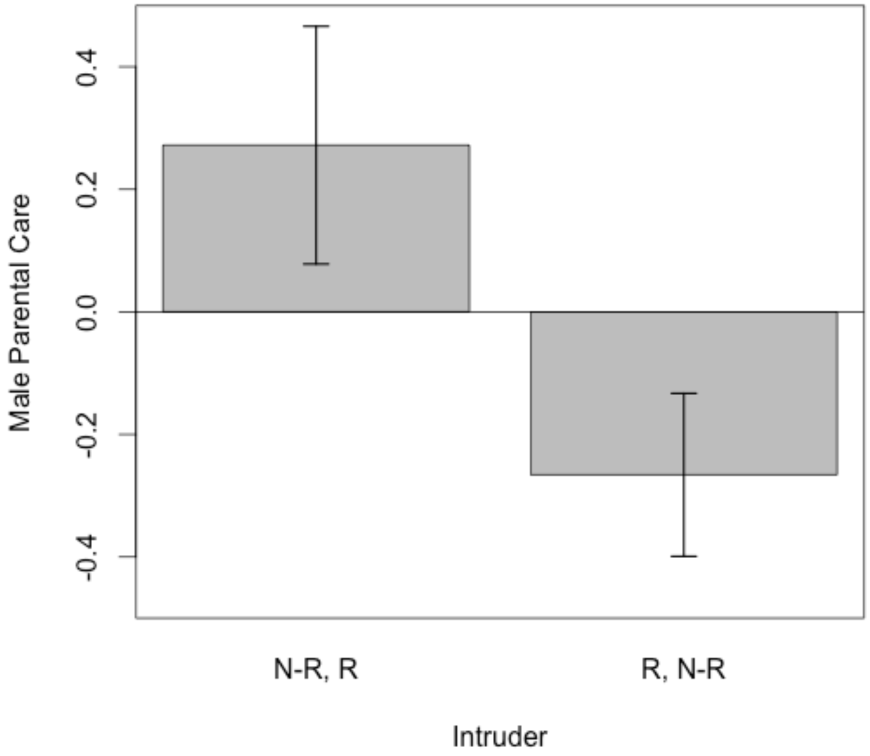

Figure 3.5. Effect of intruder presentation order on Male Parental Care. N-R, R males were initially presented with the non-reproductive intruder followed by the reproductive intruder, with the order reversed for R, N-R males. Regardless of presentation order, Male Parental Care did not significantly change between the first and second intruder presentations ($F_{1, 85.0} = 0.278$, $P = 0.5993$), nor did intruder type significantly predict Male Parental Care ($F_{1, 85.0} = 3.122$, $P = 0.0808$). Large Male Parental Care values indicate high levels of aggression directed at fish in the vicinity of the brood and low amount of time spent away from the brood (see Table 2 for PC loading values).

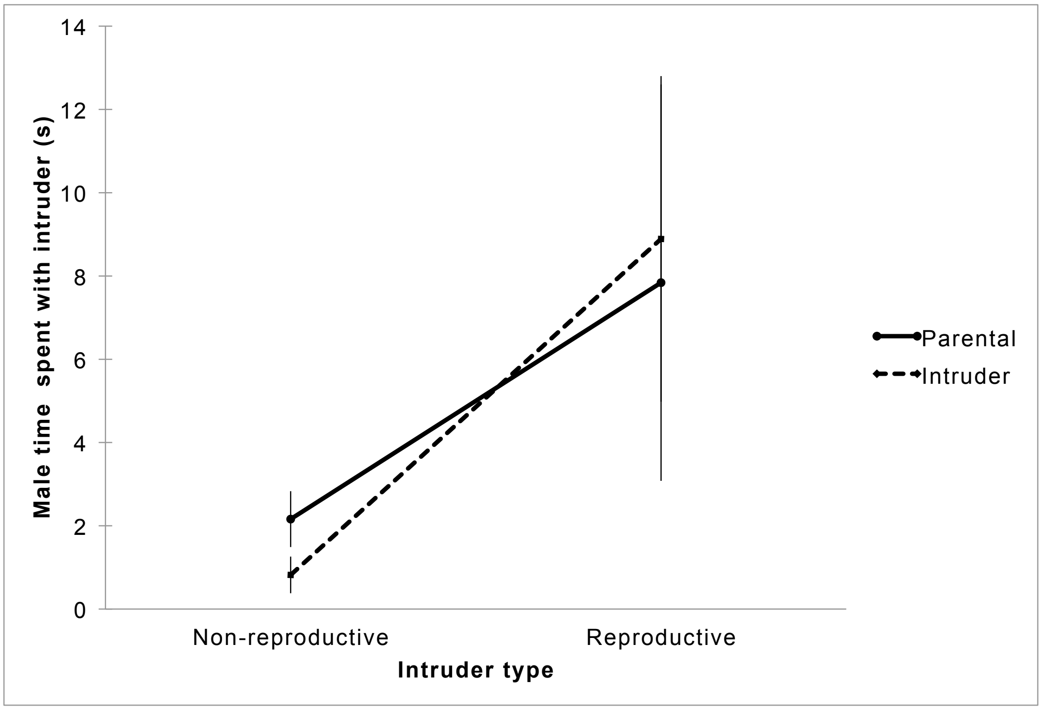

Figure 3.6. Amount of time males spent associating non-aggressively when presented with non-reproductive and reproductive intruders. The male's partner was either larger (Parental) or smaller (Intruder) than the intruder female.

Conclusion

Intersexual and intrasexual interactions have typically been investigated in isolation from one another, but their combined effects influence the social dynamics that affect mating and parental investment strategies (Alonzo 2010). The results of this dissertation show that male quality influences intersexual interactions, but not intrasexual female competition. Chapters 1 and 2 demonstrate that females increase their parental care for larger males, but do not increase their gametic investment. While females did not benefit from larger males in the form of more offspring in Chapter 2, the results of Chapter 1 show that in natural populations male size is correlated with reproductive success. This highlights some of the challenges of extrapolating laboratory results to the dynamics of natural populations. Female size, rather than male size, influenced parental female response to intruders in Chapter 3. The absolute effect of male presence versus the relative effect of male quality may therefore be more important to female reproductive success. Overall, the dynamic effect male size has on female behavior indicates that mate quality may be more influential to parental investment patterns, specifically the behavioral response during the larval stage, than to mating tactics.

This study is the first to investigate the effects of male quality on both fecundity and parental care in a single breeding event in a non-avian taxa. The majority of studies that have investigated differential allocation examine female investment at only a single stage (Petrie and Williams 1993; Gil et al. 1999; Cunningham and Russell 2000); however, in species with maternal care females must balance investment between the two stages of reproductive effort (gametic and parental care). The studies on differential allocation in fish have shown that females adjust their gametic investment in response to higher quality males (Kolm 2001, Skinner and Watt 2007; Evans et al. 2010), which is in contrast to the results of Chapter 2. Since females need to maintain sufficient energetic reserves to provide parental care, convict cichlids may be more limited in their ability to increase fecundity. Increased investment at the larval stage may also have a greater effect on reproductive success than increased investment in fecundity. Females can spawn over 360 eggs, but the largest free-swimming brood observed only contained 225 young (A. Robart, unpublished data). Therefore, there may be an upper limit to the number of offspring parents can successfully defend and increasing fecundity would not actually result in increased reproductive success. The reduced effect of male size in the second breeding of Chapter 2 suggests females are able to adjust their current reproductive effort in response to the outcome of prior breeding events. This dynamic response would allow females to adaptively adjust their effort in response to the expected costs and benefits of a particular reproductive event.

The focus of studies investigating differential allocation has predominantly been on female gametic investment (Sheldon 2000). However, the results of this dissertation suggest that Burley's (1986) original application of differential allocation in stabilizing the pair-bond between parents is more likely to be applicable to convict cichlids. A previous study determined the factors most likely to influence male desertion before offspring independence (Wisenden 1994a) and I found that these factors also influenced female investment. In Chapters 1 and 2, I found that females increased their behavior only during the free-swimming larval stage, which is when male desertion is more likely. Males will also abandon broods that are smaller than average, and in Chapter 3 I found that smaller females were more aggressive, but also had fewer offspring than expected. Together, these results suggest females are altering their behavior in response to the likelihood of male desertion. Increasing their effort when the risk of desertion is highest would help females maximize their reproductive success if it's in fact able to stabilize the pair-bond.

Overall, the results of this dissertation indicate that females respond to a number of cues during the course of a breeding event and alter their behavior in response to the perceived threat to their breeding status. Future research should investigate the cues responsible for egg development since females may not be able to reabsorb them once they've developed. This may force females to pair with either a low quality male or compete for access to high quality males that are already paired with a female. Offspring survival and male desertion vary with predator regimes in natural populations (Wisenden 1994a, 1994b) and research should examine female investment in high and low predation habitats as the female's response will likely vary in relation to the need for biparental care. Finally, these results illustrate the need to test theories in a variety of taxa and in species that differ in their life history strategies. This will help uncover whether a pattern applies to a diverse range of organisms or if it's application is more limited in scope.

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