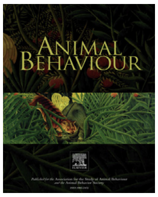
Animal Behaviour 104 (2015) 31–37

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Female breeding experience affects parental care strategies of both parents in a monogamous cichlid fish

Nicholas Santangelo*

Department of Biology, Hofstra University, Hempstead, NY, U.S.A.

A R T I C L E I N F O

Article history:
Received 9 October 2014
Initial acceptance 20 November 2014
Final acceptance 4 February 2015
Available online 9 April 2015
MS. number: A14-00802R2

Keywords:
Archocentrus nigrofasciatus
biparental
convict cichlid
division of labour
naïve female
virgin female

Previous breeding experience affects parental care, yet in biparental species it is unclear how the inexperience of only one parent influences parental dynamics and division of labour. Using the biparental convict cichlid, *Amatitlania siquia*, I assessed how female breeding experience affects male and female parental behaviour. Females that either had bred (experienced) or were virgins (inexperienced) were paired with experienced males. Inexperienced females were less likely to form pairs and took longer to spawn. Female experience also affected parental division of labour between direct offspring care and territory defence. Female behaviour was compared in the presence and absence of their male partners. When males were present, all females divided their time similarly: more time was spent in direct care. When male mates were removed, experienced females divided their time equally between territory defence and direct care, while inexperienced females continued to spend more time in direct care. Males paired to inexperienced females divided their time equally between territory defence and direct care, while males paired to experienced females spent more time in defence. Males were also more aggressive towards experienced females. Overall, experienced females tended to adopt the male-typical role of defence, which probably caused the increased intrapair conflict in these pairs. This aggression helps explain why both experienced and inexperienced females showed similar role choices in the presence of their male partner and supports previous claims that male aggression helps maintain the division of labour in this species. Female inexperience potentially presents a trade-off for males: males paired to inexperienced females engaged in less intrapair conflict, but showed less division of labour between parental roles than is typical and were less likely to pair and spawn. The effect of female experience on division of labour, parental dynamics and pair bonding success probably influences other factors such as mate choice, effectiveness of parental care and overall fitness.

The amount of reproductive experience individuals have can affect their reproductive success. Experience is known to affect an individual's reproductive investment and ultimate reproductive success in various mammalian (e.g. Broussard, Dobson, & Murie, 2008; Cameron, Linklater, Stafford, & Minot, 2000; Green, 1990; Lunn, Boyd, & Croxall, 1994; Sydeman, Huber, Emslie, Ribic, & Nur, 1991) and avian systems (e.g. Nol & Smith, 1987; Pyle, Spear, Sydeman, & Ainley, 1991; Sanz-Aguilar, Tavecchia, Pradel, Mínguez, & Oro, 2008; reveiwed in Snowden, 1996). Typically, these studies show that more experienced individuals enjoy higher reproductive success. Some studies have not only shown changes in reproductive success due to experience level, but have linked levels of experience to specific behaviours as the mechanisms of increased or decreased reproductive success. For example, in birds, breeding experience affects the feeding and ultimate growth rate of offspring (e.g. Coulson & Porter, 1985; Daunt, Wanless, Harris, Money, & Monaghan, 2007; Limmer & Becker, 2009; Woodard & Murphy, 1999). Pup retrieval and adoption can be affected by experience in mammals (Carlier & Noirot, 1965; Moltz & Wiener, 1966). Parental aggression has also been linked to breeding experience in mammals (Poindron & Le Neindre, 1980) and fish (Bandoli, 2002). Even physiological changes occur based on experience, such as levels of parental hormones (e.g. Angelier, Weimerskirch, Dano, & Chastel, 2007; Nunes, Fite, & French, 2000; Nunes, Fite, Patera, & French, 2001; Riechert, Chastel, & Becker, 2012), responsiveness to hormones (Wang & Buntin, 1999), neuronal phenotypes (Numan, 2006) and epigenetic effects (Stolzenberg, Stevens, & Rissman, 2012). All of these examples are direct effects from the experience level of an individual to the parental performance of that individual.

---

* Correspondence: N. Santangelo, Department of Biology, 114 Hofstra University, Hempstead, NY 11550, U.S.A.
E-mail address: Nicholas.santangelo@hofstra.edu.

http://dx.doi.org/10.1016/j.anbehav.2015.03.004
0003-3472/

However, in biparental systems, less is known about how the experience of one partner influences the other partner as well as itself.

Biparental pair bonds made up of individuals with different levels of breeding experience are not uncommon. This happens most commonly in serially monogamous species where individuals raise multiple broods with different partners over multiple breeding seasons (Wickler & Seibt, 1983). However, even in lifetime monogamous species, situations arise that cause breeding partners to find new mates, such as differential survival between breeding seasons, or in species where divorce rates are high (e.g. Black, 1996; Olsson, 1998). The effect of this varying level of experience among parents has the potential to influence the parental care provided by these individuals.

Pairs in biparental systems coordinate their duties in raising offspring, and this coordination is sometimes based on one's ability (e.g. Bartlett, Mock, Schwagmeyer, & Murphy, 2005; Itzkowitz, Santangelo, & Richter, 2002, 2003; Itzkowitz, Santangelo, Cleveland, Bockelman, & Richter, 2005; Schwagmeyer, Mock, & Parker, 2002; Schwagmeyer, Schwabl, & Mock, 2005; Wright & Cuthill, 1989; Wright & Cuthill, 1990; reviewed in Gowaty, 1996). Thus, if experience affects the parental care ability of a mate, then the partner of that mate should alter its level of care to compensate. Similarly, the presence of an experienced mate might mitigate the effects of a lack experience on the other mate. For example, in western gulls, *Larus occidentalis*, experienced males enjoy better forging success, but only experienced females enjoy higher reproductive success due to larger clutch sizes and shorter incubation times (Pyle et al., 1991). So, males paired to these females enjoy a higher reproductive success as well. In eastern kingbirds, *Tyrannus tyrannus*, having at least one experienced partner raises a pair's reproductive success, but this is based on different effects of experience in each sex (Woodard & Murphy, 1999). While some studies, such as these bird studies, have explored sex-specific effects of experience, few studies (if any) to date have addressed how males and females might coordinate their duties differently based on varying levels of experience between pair members.

Here, I explore whether experience influences the parental care strategy of individuals and that of their mates. The convict cichlid, *Amatitlania siquia* (Schmitter-Soto, 2007), is an ideal species in which to explore this question as it is a serially monogamous biparental fish that breeds readily in the laboratory, enabling control over an individual's experience. In this system, both males and females are heavily involved in the rearing of offspring. Females are typically invested in direct care of eggs and larvae (which includes fanning, cleaning and feeding) while males typically are invested in territorial defence (Itzkowitz, Santangelo, & Richter, 2001; Keenleyside, Bailey, & Young, 1990). Although the differences in experience between pairs of cichlids has not been assessed in the wild, it is likely that males often have more experience than their mates due to the increased reproductive potential of males in this system. Within a single breeding season, males and females both attempt to raise additional broods, if possible, with males typically being more successful than females (Wisenden, 1995). Males raise one to four broods, whereas females raise one to two broods, with two broods being somewhat rare for females (Wisenden, 1995). Therefore, given that males are more successful in raising additional broods, and they almost always mate with a new partner (Wisenden, 1995), it is likely that males pair with a female having more limited experience. The combined experience of a convict cichlid pair is known to affect parenting strategies. Lavery (1995) showed that pairs of equally inexperienced mates were less aggressive in defending their offspring, spent less time away from their brood in the presence of a predator and performed less feeding behaviours (i.e. fin digging) than did pairs where the mates had raised previous broods. In addition, experienced males fanned offspring larvae more than did inexperienced males. Lavery's (1995) study controlled for experience level between mates, so it remains unclear whether these differences between pairs existed because of both parents' experience level or whether the presence of at least one inexperienced parent would show similar results.

Here, I paired experienced males to either inexperienced or experienced females and tested whether parental care strategies between these pair types differed. I also tested whether parental care differed between the experienced and inexperienced females in the absence of their mate (i.e. the male was removed). Previous studies of mate removal in this species have shown that females who are deserted by their mate will attempt to care for and raise their offspring alone (Itzkowitz et al., 2002; Keenleyside et al., 1990; Wisenden, 1994; for a comparative discussion relative to other species, see Itzkowitz et al., 2001). I chose to vary female experience mainly for convenience (laboratory breeding produces a highly female-biased sex ratio). However, the higher reproductive potential of males per season in the wild combined with female-biased sex ratios (Cleveland, 2003; Wisenden, 1995) would likely cause more pairs of inexperienced females with experienced males than the reverse (i.e. experienced females paired with inexperienced males). Thus, I specifically tested whether female experience level affects the parental care strategies that females use as well as the parental care strategies of their mates. Individuals within pairs are known to assess each other's abilities when coordinating their parental care duties (Itzkowitz, Santangelo, & Richter, 2003), and based on the effects of experience on pairs in Lavery's (1995) study, I hypothesized that experienced females are more aggressive and thus are less inclined to engage in direct care than inexperienced females. Therefore, I predicted that coordination of parental roles would differ between pairs with experienced versus inexperienced females. The presence or absence of the male partner should have no effect on the degree to which the female invests in her parental role regardless of her level of experience.

METHODS

Study Animal

The convict cichlid is a monogamous biparental substrate spawner (Lavery, 1995). Offspring develop through three defined stages: egg, larval and free-swimming fry. Eggs usually hatch within 2–4 days. Once the eggs hatch, the offspring enter the larval stage, termed the wriggler stage, which lasts 5–6 days. During this time, parental behaviour is known to change as offspring get older (Keenleyside et al., 1990). After this time, the young become free-swimming fry. Fish used in this study were bred from wild stock and raised in the laboratory. All fish were maintained in sex-specific stock tanks (473-litre). All experimental procedures were approved under Institutional Animal Care and Use Committee protocols from Eastern Kentucky University (03-2009) and Hofstra University (13/14-1).

Experimental Subjects

Male and female fish were selected for the experiment based on size compatibility. The mean ± SE size difference within each pair was 1 ± 0.2 cm. Every male used in this study had previous breeding experience, while the females to which they were paired either had breeding experience ($N = 25$) or were first-time breeders ($N = 30$). Males and females were placed together in experimental tanks (151-litre). In addition to the male and female pair, a male ‘intruder’ fish of similar size to the paired male was placed behind a clear partition in the tank (i.e. the intruder compartment) to facilitate pair formation. That is, males and females are more likely to form pair bonds if there are other individuals present, which can be the focus of the forming pair's aggression (Itzkowitz & Draud, 1992). Each tank contained a clay flowerpot for spawning and a clear plastic partition to separate the intruder fish. At the end of a replicate, the fish were placed back into separate stock tanks to ensure they were not used again.

Experiment Design

In each experimental tank, a nest site (i.e. a clay flowerpot) was placed in the back corner at one end of the tank. A clear plastic partition was placed across the width of the tank 15 cm from the other end, thereby creating an intruder compartment separate from the nesting compartment. Tape markings placed along the outside bottom of the tank divided the nesting compartment into three areas; the intruder area (15 cm from the intruder partition), the neutral area (50 cm in between the intruder and offspring area) and the offspring area (20 cm from the end of the tank including the flowerpot nest).

Using these experimental tanks, I tested all 55 pairs (25 with an experienced female and 30 with an inexperienced female), recorded number of days to spawn, and which pairs failed to spawn. To assess parental behaviour, I videotaped a subset of these 55 pairs ($N = 12$ inexperienced, $N = 11$ experienced). Each female was tested with her male partner and alone, which provided four groups: (1) experienced female with partner, where both the male and the female had previously raised a brood; (2) inexperienced female with partner, where the male had previously raised a brood, but the female had not; (3) experienced female without partner (i.e. the females from group 1 without their experienced male partners present) (4) inexperienced female without partner (i.e. the females from group 2 without their experienced male partners present). The males from groups 1 and 2 were then compared to test for the effect of female experience on male parental care behaviour. The females from groups 1 and 2 were compared to test for the effect of female experience on female parental care behaviour in the presence of their partners. The females from groups 3 and 4 were compared to test for the effect of female experience on female parental care behaviour when their partners were absent.

To collect data for these comparisons, I used the following procedure. Once pairs spawned, I removed the intruder fish that was used to stimulate pair formation. On day 1 of the wriggler stage, I replaced the intruder fish and videotaped the pair for 10 min. After videotaping, I removed both males (mate and intruder) and placed them in separate holding tanks. On the second day, I replaced the intruder and videotaped the female for 10 min. After videotaping, I replaced the female's mate in the experimental tank and removed the intruder. On the third day no testing took place. The procedures on days 1 and 2 were repeated on days 4 and 5, respectively. Therefore, data for males and females with their mates present were recorded on days 1 and 4 of the wriggler stage, and data for females without their mates present were recorded on days 2 and 5. All videos were later scored with a computer event recorder (The Observer®, Noldus Information Technology, Wageningen, The Netherlands).

Within biparental cichlid studies, particularly convict cichlid studies, the time spent with offspring (direct care) versus the time spent away from offspring (territorial defence) is a typical proxy for establishing an individual's division of labour (e.g. Fitzgerald & Keenleyside, 1978; Itzkowitz, 1985; Itzkowitz et al., 2005, 2001, 2002, 2003; Keenleyside et al., 1990; Lavery, 1995; Lavery & Colgan, 1991; Lavery & Keenleyside, 1990a; Richter, Santangelo, & Itzkowitz, 2005; reviewed in Barlow, 1991, 2002). Therefore, I used the same strategy here, and I recorded the following data: (1) amount of time each parent spent in each of the three sections of the experimental tank, to assess investment in direct care and parental defensive roles; (2) number of bites each parent directed towards the intruder, to assess the level of aggression towards intruders; (3) the number of bites directed at one's partner, to assess the level of intrapair conflict. The data were quantified by observers blind to the experience level of the pairs and whether the females were tested with versus without their mates present.

Data Analysis

For males and for females tested with and without their partners, there were no significant differences in any behaviour across testing days; therefore, days were averaged for each behaviour and the means were analysed. Parametric tests were used where possible. Where parametric assumptions were violated, transformation did not redistribute the data to meet parametric assumptions; therefore, nonparametric tests were used. All analyses were two-tailed tests, and the specific analyses were as follows. I used independent *t* tests to compare the number of days to spawn between experienced and inexperienced females, and a chi-square test to compare the percentage of individuals that bred successfully in pairs with experienced versus inexperienced females. I used a 2 × 2 ANOVA between–within subject design to analyse the distribution of time (i.e. time near offspring versus time near intruder) for experienced and inexperienced females when their partners were present, and Wilcoxon signed-ranks tests to analyse the females' distributions of time when their mates were absent. I used a between–within subject 2 × 2 ANOVA to analyse female aggression towards the intruder, with experience as a between-subject factor (inexperienced versus experienced) and female status (partner present versus partner absent) as a within-subject factor. I used Mann–Whitney *U* tests to test for an effect of experience on aggression between male and female mates across experience levels.

RESULTS

Breeding Success

Inexperienced females were significantly less likely to form successful pairs than experienced females (failure to spawn: 30% inexperienced; 8% experienced; chi-square test: $\chi^2_1 = 4.125$, $N = 55$, $P = 0.042$). Inexperienced females also took significantly longer to spawn (mean = 9.25 days) than experienced females (mean = 5.55 days) (independent *t* test: $t_{42} = 2.145$, $P = 0.038$; Fig. 1).

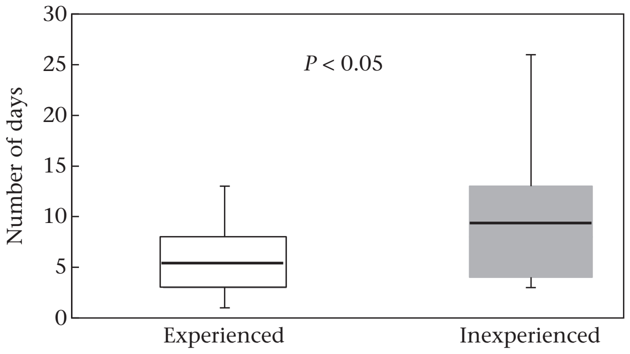


Figure 1. Number of days to spawn by pairs of convict cichlids when the female member of the pair was experienced or inexperienced. Boxes indicates first and third quartiles, whiskers indicate ranges and lines within boxes indicate means.

Parental Behaviour

Experience level did affect how females distributed their time during parental defence when their partner was absent, but not when their partner was present. In the 2 × 2 ANOVA for females with their mate present, there was no main effect of experience on where females spent their time ($F_{1,21} = 0.058$, $P = 0.81$; Fig. 2a), but there was a significant main effect of location on where females spent their time ($F_{1,21} = 34.996$, $P < 0.001$), with all females spending more time with the offspring than with the intruder. There was no significant interaction between female experience and location of time spent ($F_{1,21} = 0.003$, $P = 0.96$). In the absence of their male partner, inexperienced females spent significantly more time with the offspring (Wilcoxon signed-ranks test: $T = 2.295$, $N = 12$, $P = 0.028$; Fig. 2b) while experienced females did not differ significantly in their distribution of time between tending offspring and defending against the intruder ($T = 1.42$, $N = 11$, $P = 0.286$). Despite the increase in inexperienced females' time with offspring in the absence of their mates, experienced and inexperienced females did not differ significantly in their time spent with the offspring (Mann–Whitney *U* test: $U = 57$, $N_1 = 11$, $N_2 = 12$, $P = 0.58$) or with the intruder ($U = 38$, $P = 0.09$). Overall, an effect of experience was seen only in females when their experienced male partner did not participate in caregiving duties (i.e. was absent).

Female experience also influenced how males distributed their time during nest defence. Males paired with experienced females spent more time defending against the intruder than at the nest with the offspring (Wilcoxon signed-ranks test: $T = -7.36$, $N = 11$, $P = 0.004$; Fig. 2c). However, males paired with inexperienced females did not differ significantly in where they spent time during parental defence ($T = -1.28$, $N = 12$, $P = 0.24$). Thus, males paired to inexperienced females tended to show a more equal distribution of their time between defending and caring for offspring compared to males paired to experienced females. Despite the difference in time distribution for males paired to experienced versus inexperienced females, males did not differ significantly with regard to how much time they spent at the nest with the offspring (Mann–Whitney *U* test: $U = 42$, $N_1 = 11$, $N_2 = 12$, $P = 0.14$) or near the intruder ($U = 59$, $P = 0.667$).

There was a main effect of experience on female aggression (i.e. numbers of bites per seconds in intruder area), with experienced females being more aggressive than inexperienced females (ANOVA: $F_{1,21} = 5.417$, $P = 0.03$; Fig. 3a). There was also a significant effect of mate's presence on aggression, with females being more aggressive when their partner was absent than when their partner was present ($F_{1,21} = 6.901$, $P = 0.016$). However, there was no significant interaction of aggression between experience level and presence of mate ($F_{1,21} = 0.423$, $P = 0.522$). The bite rate of the males paired to these females was not significantly affected by their female's experience level (Mann–Whitney *U* test: $U = 56$, $N_1 = 11$, $N_2 = 12$, $P = 0.57$). Experience level did affect the amount of the intrapair aggression. Males partnered with experienced females were significantly more aggressive towards their mates than males

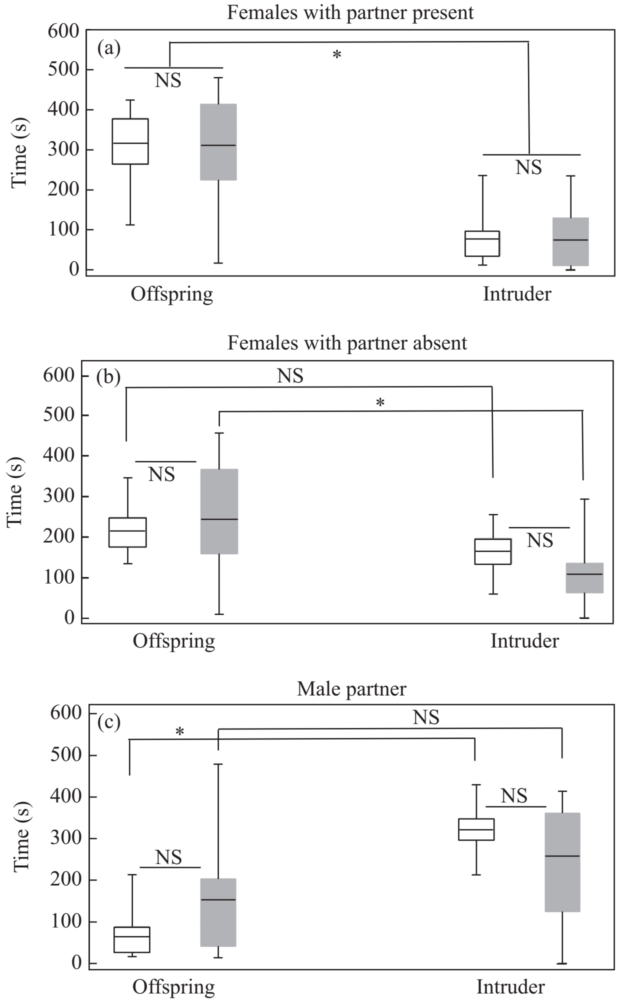


Figure 2. Time spent by convict cichlids in each parental role (with offspring or defending against an intruder) for (a) females with their male partner present, (b) females with their male partners removed and (c) male partners. Boxes indicates first and third quartiles, whiskers indicate ranges and lines within boxes indicate means. White boxes indicate pairs with experienced females, and grey boxes indicate pairs with inexperienced females. Connected lines indicate statistical comparisons: $^*P < 0.05$.

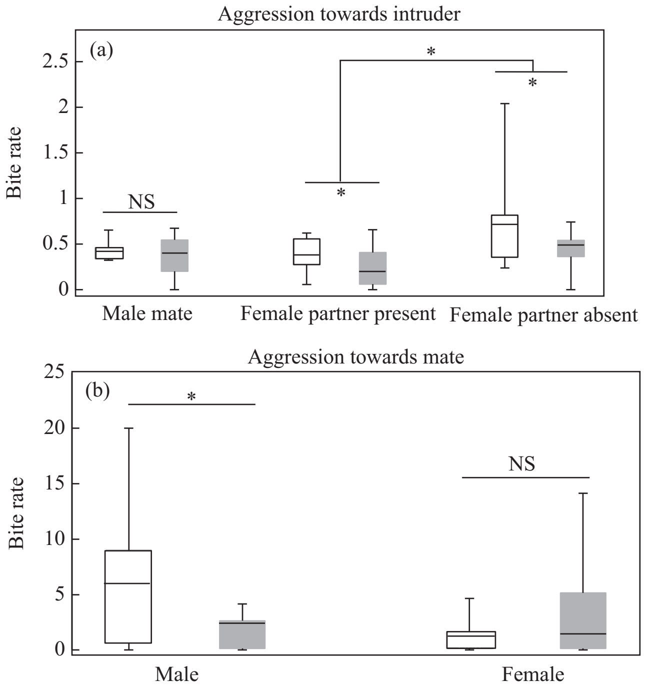


Figure 3. (a) Aggression (number of bites) towards intruders by males in the presence of their female partner and by females when their male partner was present or absent. (b) Aggression by males and females towards their partners. White boxes indicate pairs with experienced females, and grey boxes indicate pairs with inexperienced females. Connected lines indicate statistical comparisons: $^*P < 0.05$.

partnered with inexperienced females ($U = 28$, $P = 0.02$; Fig. 3b). Experience, however, did not significantly affect the level of aggression of females towards their male mates ($U = 57.5$, $P = 0.59$).

DISCUSSION

Female experience influenced pairs in a variety of ways. Inexperienced females were less likely to form pairs and took longer to spawn once paired than experienced females. Experience also affected how females cared for their offspring. The prediction that the experience level of the female would alter how both parents coordinate their care strategies was supported, but in a surprising way. Both female types divided their time similarly between attacking the intruder and tending the nest when their male partners were present, but males differed in this regard even though all males were experienced. In addition, opposite of what was predicted, when male mates were removed, the two female types used different strategies: inexperienced females continued to spend more time at the nest with offspring while experienced females spent relatively equal time at the nest and defending against an intruder. This result supports the prediction that experienced females do tend towards a more aggressive role. Thus, female parental behaviour differs based on the female's experience, but the presence of an experienced male mate appears to ‘normalize’ this behaviour.

The increase in aggression shown by experienced females in the absence of their mate follows from what has been shown previously in convict cichlids. Lavery (1995) compared experienced pairs to inexperienced pairs and showed that experienced pairs were more aggressive. Itzkowitz et al. (2001) showed that when females are left to defend offspring alone, they take on more of the male's defensive role. Here, both female types increased their aggression when alone, but experienced females did so to a greater extent. Females with experience not only approached intruders more when alone, but were also more overtly aggressive (i.e. physical attacks such as biting) to the intruder.

The effect of experience on females also had consequences for male parental behaviour. The similarity in female behaviour for both experience types when their mates were present indicates that a male's response has a regulatory effect on female parental behaviour. This effect may in part be female choice, but males did actively engage in aggressive interactions with their mates, being more aggressive towards the experienced females than towards the inexperienced females. This suggests that experienced females place an added strain on pair bonds and perhaps males engage in more intrapair aggression to manage the division of labour. For example, convict cichlid pairs show a great deal of coordination while raising offspring, and although this coordination differs among various pairs, all pairs obtain a very consistent level of coordination throughout the raising of a brood (Itzkowitz et al., 2002). The mechanism for obtaining this coordination is unknown. It has been suggested that both parents are involved in the process, with male aggression in part responsible for the observed division of labour (Itzkowitz et al., 2003). The difference between females when they were alone indicates that experienced females are much more geared to adopting the male-typical defensive role. Therefore, a male's increased aggression towards his experienced female partner might be due to her tendency to undertake more of the male-typical role of defence. This overlap in performing the male-typical role when both parents are present would cause more conflict, and ultimately more attacks from the male. Thus, males that have an experienced partner encounter more intrapair conflict, perhaps in order to maintain the division of labour, and is likely the reason why inexperienced and experienced females behaved similarly in the presence of their male mates.

Although inexperienced females may not have elicited as many attacks from their mates, these males could still have engaged the intruder to the same degree as males paired to experienced females, but chose not to. Rather, males paired with inexperienced females showed a great deal more variation in the time they spent in each area of the test tank (nest area and intruder area) than their male counterparts paired with experienced females. This variation is likely the reason for the atypical result of no significant difference in the amount of time that males spent at the nest and at the intruder location. The reason for this is unclear. It is possible that males are simply ‘attracted’ to the location of their female mates, as has been suggested previously regarding pair coordination of offspring defence (Itzkowitz et al., 2003). Thus, if a female is staying at the nest, her male is more likely to be there with her. Alternatively, variation in the males' time distribution could be related to the pairing process and the ‘type’ of coordination that develops between the parents. Although not much is known about how parental coordination develops, each pair is unique in how it organizes itself to carry out coordinated parental activities (Itzkowitz et al., 2002). The presence of an inexperienced individual potentially makes this coordination less stable, leading to more variable behaviour from the experienced mate. Related to this possibility, inexperienced convict cichlid females may simply require more help from their mates. Inexperienced parents are known to be less efficient at parental care (Clutton-Brock, 1991; Gross & Sargent, 1985). In fact, a recent study of biparental blue-footed boobies, *Sula nebouxii*, found that more experienced biparental partners have less overlap in offspring-rearing duties, suggesting a greater efficiency (Sanchez-Macouzet, personal communication). Here, convict cichlid males may be providing more aid to inexperienced female mates, which would cause more overlap in time spent at the nest and potentially result in less efficient parental care overall. It is tempting to accept this explanation since convict cichlid parental duties are typically divided such that males defend offspring and patrol the territory while females engage more in direct care of offspring (Itzkowitz et al., 2001; Keenleyside et al., 1990; Lavery & Keenleyside, 1990b). However, overlap in convict cichlid parental duties is common, and future work exploring the successful rearing of offspring among pairs of various experience levels while measuring individual reproductive success over a breeding season will be needed in order to address the question of efficiency and its importance.

Conclusions and Future Directions

The effect of experience on females presents males with a potential dilemma when choosing a mate. Inexperienced females appear more geared to care for offspring (at least in terms of spending time at the nest) and cause less intrapair conflict. The reduced intrapair conflict might be an attractive option for males, yet these males would probably experience lower overall reproductive success, because inexperienced females in the present study were less likely to form pairs and required more time to reproduce. Although inexperienced females took, on average, only 4 days longer to spawn than experienced females, this could be significant for males who attempt to produce two to four broods in one breeding season (Wisenden, 1995). A male that mates with an experienced female does not have these reproductive constraints, but there will be more conflict over the division of roles. However, many of these possibilities are based on the assumption that males can assess experience and realize what it means for the future of the pair bond. It would be interesting to test how males view this trade-off by testing which females are more attractive to males. It is possible that the lower success of forming a pair bond with inexperienced females is a male mate choice issue and not the result of a ‘decreased ability’ of inexperienced females to form a pair. I predict that despite the increase in conflict over parental roles, males would still prefer the increased pairing ability and speed of reproduction afforded by experienced females.

Overall, the effect of female inexperience on parental care dynamics clearly has behavioural implications, but it is not clear whether these alterations in behaviour affect fitness. Testing an individual's natural lifetime reproductive success was outside the scope of this study, but an assessment of this for males based on their mate's experience level would address this. For example, a male's ability to defend the territory seems compromised when he is paired with an inexperienced female, but it is unclear whether this compromised ability actually results in loss of offspring. Such a study could help further address the consequences of mating with an experienced or inexperienced female. Additionally, it is possible that the increase in intrapair aggression in pairs with experienced females could be costly in terms of reproductive success. Increased aggression within a pair that has already reproduced is known to lead to pair bond instability (Lamprecht & Rebhan, 1997), so tracking pairs long term may help us to understand the true costs associated with different levels of experience of one's mate. Another obvious avenue to pursue is whether changes in male experience level have as much an effect on how females choose to conduct themselves during parental care as female experience was shown to have on males in the current study. Ultimately, the level of breeding experience of individuals can have significant effects on the interaction of parents and the strategies used to raise offspring in biparental species, and more emphasis on what this means for individuals in terms of fitness should be addressed.

Acknowledgments

I thank Audrey Wilkerson and Chris Snyder, two undergraduates who contributed greatly to collection of this data set. I also thank Eastern Kentucky University for use of their resources in finishing this project, Brian Wisenden for supplying the wild types that led to the stock used for this project, and Molly Morris and two anonymous referees for their insightful comments on previous drafts of this manuscript.

References

Angelier, F., Weimerskirch, H., Dano, S., & Chastel, O. (2007). Age, experience and reproductive performance in a long-lived bird: a hormonal perspective. *Behavioral Ecology and Sociobiology, 61*, 611–621.

Bandoli, J. H. (2002). Brood defense and filial cannibalism in the spottail darter (*Etheostoma squamiceps*): the effects of parental status and prior experience. *Behavioral Ecology and Sociobiology, 51*, 222–226.

Barlow, G. (1991). Mating systems among cichlid fishes. In M. H. Keenleyside (Ed.), *Cichlid fishes: Behaviour, ecology and evolution* (pp. 173–190). London, U.K.: Chapman & Hall.

Barlow, G. W. (2002). *The cichlid fishes: Nature's grand experiment in evolution*. New York, NY: Basic Books.

Bartlett, T. L., Mock, D. W., Schwagmeyer, P., & Murphy, M., Jr. (2005). Division of labor: incubation and biparental care in house sparrows (*Passer domesticus*). *Auk, 122*, 835–842.

Black, J. M. (1996). Introduction: pair bonds and partnerships. In J. M. Black (Ed.), *Partnerships in birds: The study of monogamy* (pp. 3–20). Oxford, U.K.: Oxford University Press.

Broussard, D. R., Dobson, S. F., & Murie, J. (2008). Previous experience and reproductive investment of female Columbian ground squirrels. *Journal of Mammology, 89*, 145–152.

Cameron, E. Z., Linklater, W. L., Stafford, K. J., & Minot, E. O. (2000). Aging and improving reproductive success in horses: declining residual reproductive value or just older and wiser? *Behavioral Ecology and Sociobiology, 47*, 243–249.

Carlier, C., & Noirot, E. (1965). Effects of previous experience on maternal retrieving by rats. *Animal Behaviour, 13*, 423–426.

Cleveland, A. L. (2003). *Courtship to divorce: the effect of sex ratio on the prespawning behavior of a serially monogamous fish (*Archocentrus nigrofasciatus*)* (Doctoral dissertation). Bethlehem, PA: Lehigh University.

Clutton-Brock, T. H. (1991). *The evolution of parental care*. Princeton, NJ: Princeton University Press.

Coulson, J., & Porter, J. (1985). Reproductive success of the kittiwake *Rissa tridactyla*: the roles of clutch size, chick growth rates and parental quality. *Ibis, 127*, 450–466.

Daunt, F., Wanless, S., Harris, M., Money, L., & Monaghan, P. (2007). Older and wiser: improvements in breeding success are linked to better foraging performance in European shags. *Functional Ecology, 21*, 561–567.

Fitzgerald, G. J., & Keenleyside, M. H. A. (1978). Effects of numerical density of adult fish on reproduction and parental behavior in convict cichlid fish *Cichlasoma nigrofasciatum* (Gunther). *Canadian Journal of Zoology-Revue Canadienne de Zoologie, 56*, 1367–1371.

Gowaty, P. A. (1996). Field studies of parental care in birds. *Advances in the Study of Behavior, 25*, 477–531.

Green, W. C. (1990). Reproductive effort and associated costs in bison (*Bison bison*): do older mothers try harder? *Behavioral Ecology, 1*, 148–160.

Gross, M. R., & Sargent, R. C. (1985). The evolution of male and female parental care in fishes. *American Zoologist, 25*, 807–822.

Itzkowitz, M. (1985). Sexual differences in offspring defense in a monogamous cichlid fish. *Zeitschrift für Tierpsychologie, 70*, 247–255.

Itzkowitz, M., & Draud, M. J. (1992). Conspecific intruders influence pair formation in a monogamous fish. *Behavioural Processes, 28*, 59–64.

Itzkowitz, M., Santangelo, N., Cleveland, A., Bockelman, A., & Richter, M. (2005). Is the selection of sex-typical parental roles based on an assessment process? A test in the monogamous convict cichlid fish. *Animal Behaviour, 69*, 95–105.

Itzkowitz, M., Santangelo, N., & Richter, M. (2001). Parental division of labour and the shift from minimal to maximal role specializations: an examination using a biparental fish. *Animal Behaviour, 61*, 1237–1245.

Itzkowitz, M., Santangelo, N., & Richter, M. (2002). How similar is the coordination of parental roles among different pairs? An examination of a monogamous fish. *Ethology, 108*, 727–738.

Itzkowitz, M., Santangelo, N., & Richter, M. (2003). How does a parent respond when its mate emphasizes the wrong role? A test using a monogamous fish. *Animal Behaviour, 66*, 863–869.

Keenleyside, M. H. A., Bailey, R. C., & Young, V. H. (1990). Variation in the mating system and associated parental behavior of captive and free-living *Cichlasoma nigrofasciatum* (Pisces, Cichlidae). *Behaviour, 112*, 202–221.

Lamprecht, J., & Rebhan, T. (1997). Factors influencing pairbond stability in convict cichlids (*Cichlasoma nigrofasciatum*). *Behavioural Processes, 39*, 161–176.

Lavery, R. J. (1995). Past reproductive effort affects parental behaviour in a cichlid fish, *Cichlasoma nigrofasciatum*: a comparison of inexperienced and experienced breeders with normal and experimentally reduced broods. *Behavioral Ecology and Sociobiology, 36*, 193–199.

Lavery, R. J., & Colgan, P. W. (1991). Brood age and parental defence in the covict cichlid, *Cichlasoma nigrofasciatum* (Pisces: Cichlidae). *Animal Behaviour, 41*, 945–951.

Lavery, R. J., & Keenleyside, M. H. (1990a). Parental investment of a biparental cichlid fish, *Cichlasoma nigrofasciatum*, in relation to brood size and past investment. *Animal Behaviour, 40*, 1128–1137.

Lavery, R. J., & Keenleyside, M. H. (1990b). Filial cannibalism in the biparental fish *Cichlasoma nigrofasciatum* (Pisces: Cichlidae) in response to early brood reductions. *Ethology, 86*, 326–338.

Limmer, B., & Becker, P. H. (2009). Improvement in chick provisioning with parental experience in a seabird. *Animal Behaviour, 77*, 1095–1101.

Lunn, N., Boyd, I., & Croxall, J. (1994). Reproductive performance of female Antarctic fur seals: the influence of age, breeding experience, environmental variation and individual quality. *Journal of Animal Ecology, 63*, 827–840.

Moltz, H., & Wiener, E. (1966). Effects of ovariectomy on maternal behavior of primiparous and multiparous rats. *Journal of Comparative Physiology, 62*, 382–387.

Nol, E., & Smith, J. N. (1987). Effects of age and breeding experience on seasonal reproductive success in the song sparrow. *Journal of Animal Ecology, 56*, 301–313.

Numan, M. (2006). Hypothalamic neural circuits regulating maternal responsiveness toward infants. *Behavioral and Cognitive Neuroscience Reviews, 5*, 163–190.

Nunes, S., Fite, J. E., & French, J. A. (2000). Variation in steroid hormones associated with infant care behaviour and experience in male marmosets (*Callithrix kuhlii*). *Animal Behaviour, 60*, 857–865.

Nunes, S., Fite, J. E., Patera, K. J., & French, J. A. (2001). Interactions among paternal behavior, steroid hormones, and parental experience in male marmosets (*Callithrix kuhlii*). *Hormones and Behavior, 39*, 70–82.

Olsson, O. (1998). Divorce in king penguins: asynchrony, expensive fat storing and ideal free mate choice. *Oikos, 83*, 574–581.

Poindron, P., & Le Neindre, P. (1980). Endocrine and sensory regulation of maternal behavior in the ewe. *Advances in the Study of Behavior, 11*, 75–119.

Pyle, P., Spear, L. B., Sydeman, W. J., & Ainley, D. G. (1991). The effects of experience and age on the breeding peformance of western gulls. *Auk*, 25–33.

Richter, M., Santangelo, N., & Itzkowitz, M. (2005). Biparental division of roles in the convict cichlid fish: influence of intruder numbers and locations. *Ethology, Ecology and Evolution, 17*, 1–15.

Riechert, J., Chastel, O., & Becker, P. H. (2012). Why do experienced birds reproduce better? Possible endocrine mechanisms in a long-lived seabird, the common tern. *General and Comparative Endocrinology, 178*, 391–399.

Sanz-Aguilar, A., Tavecchia, G., Pradel, R., Mínguez, E., & Oro, D. (2008). The cost of reproduction and experience-dependent vital rates in a small petrel. *Ecology, 89*, 3195–3203.

Schmitter-Soto, J. J. (2007). A systematic revision of the genus *Archocentrus* (Perciformes: Cichlidae), with the description of two new genera and six new species. *Zootaxa, 1603*, 1–78.

Schwagmeyer, P., Mock, D. W., & Parker, G. A. (2002). Biparental care in house sparrows: negotiation or sealed bid? *Behavioral Ecology, 13*, 713–721.

Schwagmeyer, P., Schwabl, H. G., & Mock, D. W. (2005). Dynamics of biparental care in house sparrows: hormonal manipulations of paternal contributions. *Animal Behaviour, 69*, 481–488.

Snowden, C. (1996). Infant care in cooperatively breeding species. In J. S. Rosenblatt (Ed.), *Vol. 25. Parental care: Evolution, mechanisms, and adaptive significance* (pp. 643–689). San Diego, CA: Academic Press.

Stolzenberg, D. S., Stevens, J. S., & Rissman, E. F. (2012). Experience-facilitated improvements in pup retrieval; evidence for an epigenetic effect. *Hormones and Behavior, 62*, 128–135.

Sydeman, W. J., Huber, H. R., Emslie, S. D., Ribic, C. A., & Nur, N. (1991). Age-specific weaning success of northern elephant seals in relation to previous breeding experience. *Ecology, 72*, 2204–2217.

Wang, Q., & Buntin, J. D. (1999). The roles of stimuli from young, previous breeding experience, and prolactin in regulating parental behavior in ring doves (*Streptopelia risoria*). *Hormones and Behavior, 35*, 241–253.

Wickler, W., & Seibt, U. (1983). Monogamy: an ambiguous concept. In P. Bateson (Ed.), *Mate choice* (pp. 33–50). Cambridge, U.K.: Cambridge University Press.

Wisenden, B. D. (1994). Factors affecting mate desertion by males in free-ranging convict cichlids (*Cichlasoma nigrofasciatum*). *Behavioral Ecology, 5*, 439–447.

Wisenden, B. D. (1995). Reproductive behavior of free-ranging convict cichlids, *Cichlasoma nigrofasciatum*. *Environmental Biology of Fishes, 43*, 121–134.

Woodard, J. D., & Murphy, M. T. (1999). Sex roles, parental experience and reproductive success of eastern kingbirds, *Tyrannus tyrannus*. *Animal Behaviour, 57*, 105–115.

Wright, J., & Cuthill, I. (1989). Manipulation of sex differences in parental care. *Behavioral Ecology and Sociobiology, 25*, 171–181.

Wright, J., & Cuthill, I. (1990). Biparental care: short-term manipulation of partner contribution and brood size in the starling, *Sturnus vulgaris*. *Behavioral Ecology, 1*, 116–124.