



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



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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.

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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, Minguéz, & Oro, 2008; reviewed 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.

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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 foraging 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  $\pm$  SE size difference within each pair was  $1 \pm 0.2$  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

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