



Odour tracking by young convict cichlids and a mechanism for alloparental brood amalgamation



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ARTICLE INFO

Article history:

Received 31 December 2013
Initial acceptance 19 February 2014
Final acceptance 21 March 2014
Available online 10 June 2014
MS. number: A14-00003

Keywords:

alloparental care
Amatitlania siquia
chemical orientation
convict cichlid
offspring protection

Alloparental care can be maladaptive if foster parents invest in unrelated young. Alternatively, adopted young may benefit foster parents if the presence of adopted young reduces predation on genetically related young. Convict cichlids, *Amatitlania siquia*, form monogamous pair bonds and provide biparental care for their eggs and free-swimming young for up to 6 weeks. Alloparental care is widespread in this species. Parents accrue fitness benefits from adopting unrelated young (1) by dilution of predation risk for their own young and (2) by selectively adopting relatively small young to be the preferred targets of brood predators. The mechanisms by which unrelated young enter foster care are poorly understood. Here, we examined whether displaced young use chemical cues to orient to parental protection and whether they discriminate between odour cues of their biological parents versus those of unrelated parental-phase adults. Young convict cichlids were more attracted to the odour of their parents and to the odour of a maternal female that was not their biological mother (allomaternal) than they were to a blank water control, and they showed no overall preference between the odour of their biological mother and the odour of an unrelated maternal female of aged-matched young. Small young were biased towards biological maternal cues whereas large young were biased towards allomaternal cues. Taken together, these results indicate that displaced young can rely solely on chemical cues to seek out caregiving adults and do not express preference on the basis of biological relatedness. Alloparenting in fishes, altricial birds and other systems with self-feeding young is driven in part by generic attraction of young to any parental conspecific.

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Parental care is any investment in offspring that enhances offspring survival and indirectly provides a fitness benefit to the parent providing the care (Clutton-Brock, 1991). To the degree that care contributes to offspring survival, genes for care behaviour are promoted in the population over time. Alloparental care (allo = other) is parental care behaviour directed at unrelated offspring. In cases of mistaken identity or brood parasitism, alloparental care is maladaptive for foster parents (Lyon & Eadie, 2008). Foster parents may accrue fitness benefits if the adopted offspring are kin, if there is reciprocity of care within a stable social group, or if the presence of adopted offspring reduces predation on the foster parent's own young (Hatchwell, 2009; Wisenden, 1999). In this study, we tested potential mechanisms of adoption in convict cichlids, *Amatitlania siquia*.

Convict cichlids are endemic to Central America (Bussing, 2002; Schmitter-Soto, 2007) and provide biparental care of their eggs and

free-swimming young (Wisenden, 1995). This species has received more attention than many other cichlid species because of the ease with which it can be studied both in the laboratory and in the field. This species commonly engages in alloparental care of conspecific young (Lee-Jenkins, Densmore, Godin, & Smith, 2011; Wisenden, 1999; Wisenden & Keenleyside, 1992, 1994). Young added to an existing family in the field are immediately adopted if they are similar in size to the young related to the caregiving adults (Wisenden & Keenleyside, 1992, 1994, 1995), and microsatellite analysis shows that 78% of broods in the Río Cabuyo, Costa Rica, contain adopted young (Lee-Jenkins et al., 2011). Alloparental care is not a case of misdirected care because experimental introductions of young larger than those of the young in the host family are immediately attacked and chased from the brood (Wisenden & Keenleyside, 1992). Alloparental care in convict cichlids is maintained by fitness benefits to foster parents because the presence of adopted young statistically dilutes the risk of predation on the foster parents' own young (Wisenden & Keenleyside, 1994). In addition, foster parents preferentially adopt young that are smaller and less developed than their own young (Wisenden & Keenleyside, 1992). The size differential is important because

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swimming performance of the young improves markedly over the period of parental protection (Wisenden & Keenleyside, 1992; Wisenden et al., *in press*). By selectively adopting young that are smaller than their own young, adoptive parents set up unrelated adopted young as targets for predators and deflect predation pressure away from their biologically related young (Wisenden & Keenleyside, 1992, 1994). These fitness benefits far outweigh costs of providing care for unrelated offspring because the brood area that requires defending increases only very slowly with the addition of adopted young (Wisenden et al., *in press*).

The conditions that create the opportunity for young to be adopted into other families are less clear (Wisenden, 1999). This is an interesting question because adopted young are sometimes disadvantaged in their adoptive family. One mechanism for transfer of young between families is active kidnapping of young by parents to gain the fitness benefits described above (McKaye & McKaye, 1977). A second possibility is 'farming out', where parents actively deposit their offspring into the care of another family to avoid the costs of parental care (Wisenden, 1994a; Yanagisawa, 1985). A third possibility is brood abandonment. Male convict cichlids in Costa Rican streams occasionally desert their mate and brood before the typical time of brood independence, leaving the female to defend the brood on her own (Wisenden, 1994a). Young from broods from which the male had experimentally been removed (simulating male mate desertion) were significantly more likely than random to appear in the broods of neighbouring families, but the precise mechanism of how young became incorporated into other families was not clear (Wisenden, 1994a). A fourth mechanism for transfer of young between broods is the displacement of young in the aftermath of territorial skirmishes between neighbouring pairs (B. D. Wisenden, personal observation) or catastrophic brood predation events, in which parental defences are overwhelmed and young are scattered as they flee danger (Barnett, 1977; Wisenden, 1994b, personal observation). When the predation event is finished, parents actively search and defend a large area of the substrate and sequester young that may have strayed from the brood area (Wisenden, Snekser, Stumbo, & Leese, 2008). Because mean interbrood distance in Costa Rican streams (Río Cabuyo and Quebrada Amores) is 3.41 ± 0.1 m ($N = 742$; Wisenden et al., *in press*), it is quite plausible that young displaced from their brood either by abandonment or by predation events could find their way into a neighbouring brood.

Wisenden and Dye (2009) tested whether displaced young can use chemosensory information to orient towards their family. In that study, young actively approached tank water from their natal aquarium, which included odours of their parents, their siblings and themselves and the general 'habitat-specific' odours of the gravel substratum. This preference was demonstrated using a dichotomous Y-maze, where one arm of the maze received home tank water while the other arm of the maze received either blank water control cue or tank water from another family. Lee-Jenkins, Jeswiet, and Godin (2014) tested young convict cichlids for preference of association in a four-way maze based on a 2×2 design of kinship and familiarity and found that young larger than 7.5 mm preferred to associate with familiar kin, and secondly, with non-familiar nonkin. Young smaller than 7.5 mm showed no preferences for association with conspecifics based upon kinship or familiarity. Overall, results from Lee-Jenkins and Godin (2013) indicate that decisions of association by young convict cichlids occur only for older young and inconsistently with respect to kinship and familiarity. From an ecological perspective, one might argue that displaced young should respond most strongly to the odour of any conspecific parents, regardless of kinship, because parents are the ones that provide protection from predators. Experimental removal

of parents in the field shows that survival without parental protection can be measured in minutes (Alonzo, McKaye, & van den Berghe, 2001). Lee-Jenkins, Jeswiet, & Godin (2014) experimentally displaced young from their family (parents + siblings) in the laboratory and in the field and recorded the rates at which the young successfully rejoined their family as a function of displacement distance. In the field, success rate was never higher than 50%, even at a displacement distance of only 20 cm, and fell to zero for displacement distances greater than 60 cm. Instead, 62% of displaced young sought refuge in the substratum and did not return to their family during the 5 min observation period (Lee-Jenkins et al., 2014). Left unanswered by these findings is the ultimate fate of young hiding in the substrate and the mechanisms by which they find their way into the protective custody of a family unit, including adoption by unrelated parent fish.

In this study, we refined the methods of Wisenden and Dye (2009) to isolate the odour of the parents from the odour of the young (siblings and themselves) and the habitat odour of the home aquarium. We then compared the orientation responses of young towards odours of maternal females that were either their biological mother or a nonbiological mother (potential foster mother).

METHODS

We used a laboratory stock of F₃ convict cichlids derived from wild-caught fish from Quebrada Amores and Río Potrero located in Guanacaste Province, Costa Rica. Fish were bred in 75-litre aquaria using terra-cotta pots as spawning sites. Breeding tanks were maintained at 26–28 °C, a 12:12 h light:dark cycle and fish were fed a diet of commercial flake food. When the young began exogenous feeding, we supplemented their diet with small amounts of Fry Feed Kyowa (grade 250, Kyowa Hakko USA, New York, NY, U.S.A.).

The dichotomous Y-maze was the same one used by Wisenden and Dye (2009). The maze was constructed with white polyvinyl chloride (PVC) tubing cut in half lengthwise to create a trough (internal diameter = 7.5 cm, total length = 96 cm, maximum depth in the centre = 1.8 cm, surface width = 6.5 cm). The stem forked at an angle of 30° to the left and right at 45 cm from the base and extended another 45 cm to the top of each arm.

Two airline tubing hoses siphoned water from a single elevated 37-litre header aquarium each at a rate of about 7 ± 0.03 ml/s ($N = 10$) into two separate stimulus collection chambers (15.5 cm long, 12 cm wide at the top, 8 cm wide at the base, 6.5 cm high) constructed from PVC eaves-troughing material. These chambers were large enough to hold adult convict cichlids. Each chamber was fitted with a stand-pipe (3.5 cm high) so that water entering from the header tank overflowed and drained into one arm of the Y-maze. Thus, blank water from the header tank passed briefly over the adult fish in the small stimulus collection chambers before entering the arms of the maze below. Another stand-pipe (1.8 cm) at the base of the stem of the Y-maze maintained water depth in the maze and allowed water to exit the maze (Fig. 1).

Experimental Protocol

Room lights were dimmed during all testing to reduce stress on the fish. We conducted three experiments. In the first experiment, we placed a mated pair (female + male) in one stimulus collection chamber and started the siphons from the header tank through the stimulus collection chambers so that odour of parental fish entered one arm of the maze. The second stimulus collection chamber leading to the second arm contained no fish (blank water control). Groups of five young genetically related to the parents in the stimulus collection chamber were removed from their natal tank,

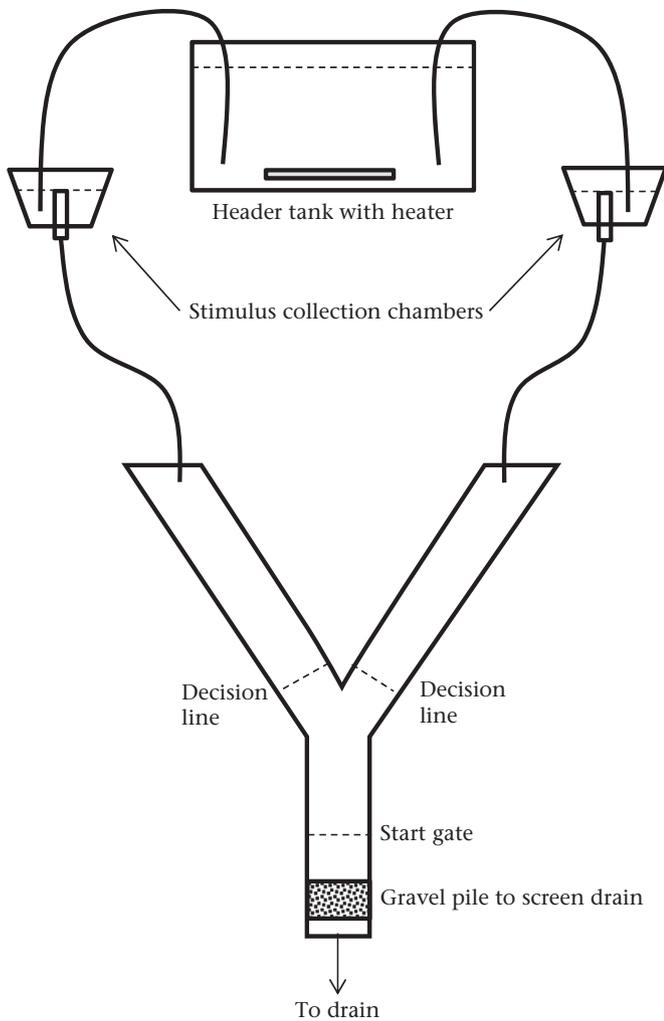


Figure 1. Apparatus for testing odour preference by displaced convict cichlid young.

placed in the stem of the maze and allowed 5 min to acclimate. A small round mesh start gate fitted to the curvature of the maze trough prevented fish from swimming up the maze until the 5 min acclimation period was over. When the gate was removed, fish advanced up the stem to the confluence area and then proceeded up one arm or the other. The position of each of the five young was recorded at 15 s intervals for 5 min. Fish were scored as being either undecided (remained in the stem or confluence area) or present in one arm or the other. We then returned the fish to the starting area, replaced the gate and switched the hoses draining each stimulus collection chamber to the opposite arm of the maze to test for the potential of side bias. We waited at least 15 min for cue gradients to re-establish themselves before removing the gate and repeating another 5 min of observations. We ran 12 trials using young from three different breeding pairs. We measured the length of the young by placing them on a taut piece of fine mesh made transparent by the addition of water. Gradations on a standard ruler could be easily viewed through the wet mesh to determine fish length to the nearest 0.5 mm. Size of young tested ranged from 5.5 to 8.0 mm (mean \pm SE = 6.82 ± 0.11 , $N = 55$). Individual young were used only once (i.e. tested once then retested with arm cues reversed) and then moved to a grow-out tank after testing. To test for side preference, we used a paired t test to compare the number of young observed in each arm totalled over all the observations within each trial.

In the second experiment we placed a female in one collection chamber and left the other chamber blank. We used females only for the latter experiments because females show greater attachment to brood care, particularly in the context of mate desertion (Wisenden, 1994a) or following catastrophic predation events (Wisenden et al., 2008). In this experiment, we used five young from another unrelated family as test subjects to test whether displaced young would orient towards the odour of a maternal female that was not their biological mother. Females used as the cue source had young that were approximately the same length as that of the test subjects. Experimental protocol was identical to the procedure described for the first experiment except that we did not conduct reverse runs. We conducted 15 trials using four different females testing sibling young unrelated to the female from nine families. Length of young ranged from 5.5 to 7.6 mm in standard length, SL (mean \pm SE = 6.91 ± 0.15 mm). We measured the length of young after each trial, allowing us to test the effect of fish size on strength of cue preference directly.

In the third experiment we placed the biological mother in one stimulus collection chamber and another maternal female in the second collection chamber. Females were selected so that their respective young were approximately size-matched. We ran 20 trials using six families (i.e. three pairs of families), alternating sibling groups of five young related to one of the two test females. Size of young ranged from 5.0 to 9.0 mm (mean \pm SE = 6.87 ± 0.27 mm SL). Again, we measured the length of young after each trial, allowing us to test the effect of fish size on strength of cue preference directly.

Ethical Note

All methods used in the collection of these data were pre-approved by the Minnesota State University Moorhead Institutional Animal Care and Use Committee (protocols 10-R/T-Bio-018-N-Y-C and 13-R/T-Bio-018-N-Y-C).

RESULTS

Convict cichlid young strongly preferred to enter the arm receiving cues from their parents over the arm receiving blank water (paired t test: $t_{11} = 8.71$, $P < 0.001$; Fig. 2a). When the same fish were run again with the source cues on reversed sides, we observed the same attraction to parental cues (paired t test: $t_{11} = 3.15$, $P = 0.009$; Fig. 2a).

When convict cichlid young were given a choice between the odour of a maternal female that was not their biological parent (allomaternal cues) and a blank water control cue, the young were strongly attracted to the allomaternal cues (paired t test: $t_{14} = 3.07$, $P = 0.008$; Fig. 2b). We found no effect of size of young on the strength of preference for the maternal cue or willingness to run the maze ($F_{1,13} = 1.72$, $P = 0.213$).

When young were tested for a choice between the odour of their biological mother versus a maternal unrelated female of age-matched young, no overall preference was observed (paired t test: $t_{19} = 0.61$, $P = 0.551$; Fig. 2c). However, strength of preference varied with the size (age) of the young. Overall, there was no effect of fish length on strength of preference for the cue from the biological mother (least squares regression: $F_{1,18} = 0.88$, $P = 0.359$; Fig. 3a), but preference (or lack of aversion) for the allomaternal cue increased with fish length ($F_{1,18} = 11.60$, $P = 0.003$; Fig. 3b), creating an overall increasing preference for allomaternal cues over biological maternal cues as the young increased in size ($F_{1,18} = 6.56$, $P = 0.020$; Fig. 3c).

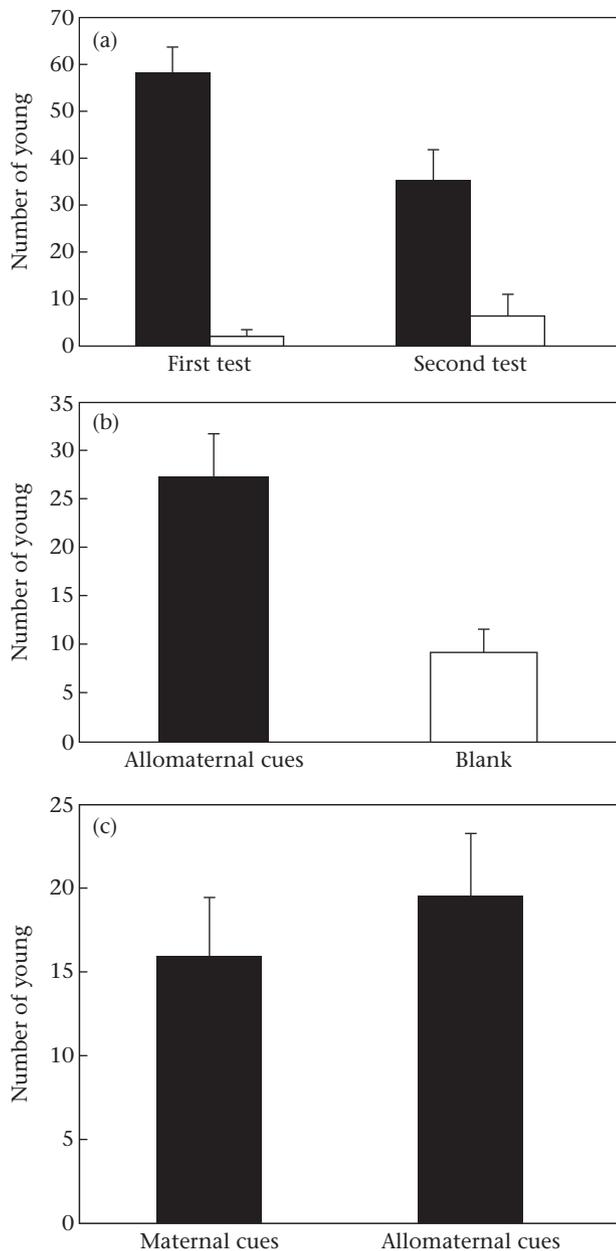


Figure 2. (a) Mean \pm SE number of convict cichlid young that responded to odour cues from both parents (solid bar) or a blank water control (open bar) in the Y-maze (repeated on reverse sides to control for side bias). (b) Mean \pm SE number of young that responded to odour cues from a hormonally maternal unrelated female or a blank water control in the Y-maze. (c) Mean \pm SE number of young that responded to odour cues from their biological mother or from an unrelated allomaternal female in the Y-maze.

DISCUSSION

We found that displaced young convict cichlids can use the signature odour of an individual parent, without sibling cues or home tank odours, to orient back to the relative safety of parental protection. In previous studies, sibling odours (Lee-Jenkins & Godin, 2013) or sibling odours combined with parental odours in a ‘family cue’ (Lee-Jenkins et al., 2014; Wisenden & Dye 2009) were used for orientation by young convict cichlids. In the present study, we also found that young can and do follow an odour trail of any hormonally maternal female that is not necessarily their biological parent. When given a choice between their biological parent and a

hormonally maternal but unrelated fish, young convict cichlids showed no overall preference, although there were interesting size effects (see below). Taken together, our results reveal that olfaction is an important proximate mechanism by which displaced convict cichlid offspring orient to intact families, and therefore, is also a mechanism by which young may become incorporated into foster broods, leading to alloparental care.

Our results parallel those of Barnett (1977), who tested responses of displaced free-swimming Midas cichlid young (aged 1–10 days) to parental odours cues in a Y-maze similar to maze used in our experiment design. He also found that young preferred maternal cues and allomaternal cues over blank water, but he found no difference in attraction between maternal and allomaternal cues. Lee-Jenkins and Godin (2013) and Lee-Jenkins et al. (2014) found that small young less than 7 mm SL either failed to discriminate among odours on the basis of familiarity or kinship (Lee-Jenkins & Godin, 2013), or failed to return to their family even for very short distances of displacement (Lee-Jenkins et al., 2014). In the present study, young of all sizes responded to test odours in our dichotomous test apparatus. The responsiveness of small young in the present study and in Barnett’s (1977) study may result from dim lighting conditions during testing. We deliberately conducted our tests in a room lit only by the subdued glow of light emanating from six, bilevel rows of aquaria each lit from overhead fluorescent lights. The main room lights were turned off. Subdued lighting more closely matches the natural lighting of the shaded low-order headwater streams of Guanacaste, and we have noticed in previous studies that fish behave more naturally under dimly lit conditions (Alemadi & Wisenden, 2002; Wisenden & Dye, 2009). Moreover, although displaced convict cichlid offspring respond more readily in the laboratory than they do in the field (Lee-Jenkins et al., 2014), field data show that young are commonly adopted when they are about 5 mm SL (Wisenden & Keenleyside, 1992), indicating that very small young do indeed orient to foster families. The responses by small young in the present study were not a laboratory artefact. Another factor that may have contributed to the difference in responsiveness of young used in our tests versus those used in Lee-Jenkins et al.’s (2014) study is that we tested groups of five fish whereas Lee-Jenkins et al. (2014) tested isolated individuals.

Although displaced young use visual cues for orienting to parents in the laboratory (De Gannes & Keenleyside, 1992; Hay, 1978; Lavery, Mackereth, Robilliard, & Keenleyside, 1990; Lee-Jenkins et al., 2014; Sheenan, Waas, & Lavery, 1994), they do so to a lesser degree in the field (Lee-Jenkins et al., 2014). Lee-Jenkins et al. (2014) noted that displaced young in the field sought refuge and remained in hiding for the duration of the observation period (5 min). This is an adaptive behavioural response when the risk of predation is high. Young may hide in the substratum until a brightly marked parental fish comes searching for them (Wisenden et al., 2008), or until dusk when they can safely emerge from hiding and follow a chemosensory gradient to join a nearby family unit. Alternatively, displaced young may creep towards an adoptive family while under the cover of leaf litter where they will be safe from predators, but unable to use vision to locate a nearby family.

Although there was no overall difference in the number of young attracted to cues from a biological parent versus an alloparent, there was a significant effect of size. Small young were more attracted to cues from their biological mother (or more averse to the cues of an allomother) relative to larger, older young. Barnett (1977) also noted that the strength of attraction to maternal cues waned in free-swimming Midas cichlids from day 1 to day 10. Barnett (1977) hypothesized that there may be an ontogenetic shift from olfaction to vision as the dominant sensory modality used for orienting in the environment. This differential response of young cichlids may also be linked to risks associated with joining a foster

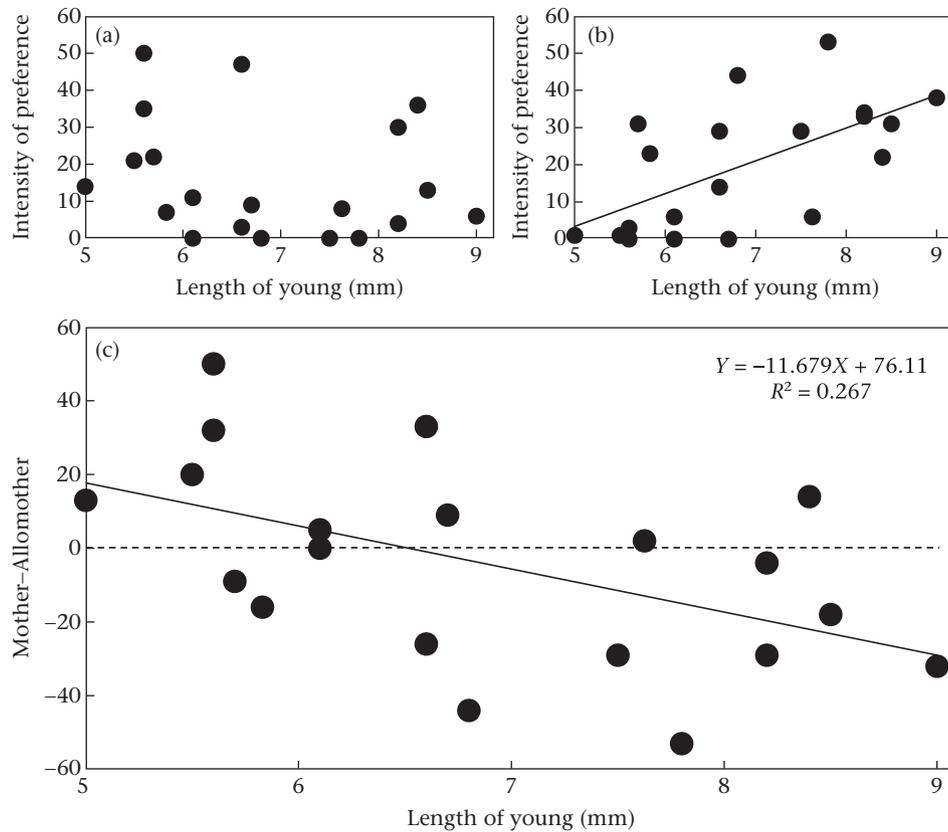


Figure 3. Relation between the size of convict cichlid young (total length) and the intensity of their attraction to cues from (a) their biological mother and (b) an unrelated allomother. (c) The strength of preference for the biological mother (total number of young that responded to cues from the biological mother minus the total number of young that responded to cues from the allomother).

family whose young do not match them in size. Large young that join a family with younger/smaller offspring risk being rejected by the adoptive parents (Wisenden & Keenleyside, 1992). Parental rejection may occur because large and small young differ in swimming ability, making smaller host young more vulnerable to brood predators (Wisenden & Keenleyside 1992, 1994), or because large young may physically attack small young (Fraser, Wisenden, & Keenleyside, 1993). Thus, small young that join a family with older/larger offspring also risk physical attack from the host brood's offspring. In either case, rejected young would have to start a new search, but the costs are not the same for small and large young because swimming performance abruptly improves at around 7 mm SL in the Guanacaste stream system (Wisenden & Keenleyside, 1992, 1994; Wisenden et al., in press). Young smaller than 7 mm SL have a poorly ossified skeleton and relatively slow swimming velocity and acceleration, whereas fish greater than 7.5 mm in length are uniformly quick (Wisenden et al., in press). Given the effect of development on the cost of abandonment, selection should favour the distinction between maternal and allomaternal cues during stages of ontogeny when swimming ability is poorly formed but decrease as antipredator competence improves. Our findings in the present study indicate that the switch from favouring maternal cues to favouring allomaternal cues occurs when free-swimming young are approximately 6.52 mm SL, which closely agrees with the switch point in roaming behaviour of young in the field. The area defended by parents of intact brood in the Río Cabuyo, Costa Rica, increases until the young reach 6.45 mm SL, because this is the size at which maximum antipredator competence (i.e. swimming performance) is attained (Wisenden et al., in press).

Alloparental care is a major component of the reproductive ecology of convict cichlids and many other species of fish with parental care because of its low cost and its fitness benefits (Wisenden, 1999). Fish are generally not burdened with the cost of direct provisioning of food in the way that nidicolous birds or placental mammals are. With low additive costs to parental care (i.e. adding extra young adds little to the cost of brood defence) and potential benefits through risk dilution and differential predation, there is little selection for parents to reject wayward young that may join their brood. Young, on the other hand, have low probability of survival without parental protection, which creates strong selection for the ability to detect and orient towards nearby families. Young are likely to seek and successfully join foster families when parental care does not require parental food provisioning, a condition met most often by fishes and precocial birds (e.g. Bustnes & Erikstad, 1991; Wisenden, 1999).

Acknowledgments

Funding for this project was provided by the College of Science, Health and the Environment, Minnesota State University Moorhead, through faculty research grants to B.D.W. and student research grants to E.A.M., C.N.S. and N.J.B.

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