

Young convict cichlids use visual information to update olfactory homing cues

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Abstract In this study, we tested the tendency of young cichlids to orient towards their parents using chemical cues. Convict cichlids have biparental defence of their free-swimming young. If young become separated from their family they must rejoin their family within minutes to have any chance of survival. Here, we used a dichotomous Y-maze to test if displaced convict cichlid young can use chemical cues to orient to their family. First, we showed that young preferentially orient toward water taken from their home tank versus blank water taken from a tank that contained no fish. Second, we showed that young prefer home tank water to water from a tank containing another family of convict cichlids. In a third experiment, we placed young convict cichlids in a small aquarium inserted within a larger aquarium. The large aquarium contained either their parents or no fish. The small insert aquarium contained blank water from a tank that had never contained fish. After 20 min in the insert tank, young convict cichlids were placed in the Y-maze and given a choice between either their home tank water or water from the insert tank. Convict cichlids that did not see their parents during the 20-min conditioning period oriented strongly toward chemical cues of their home tank water. Young that saw their parents during the 20-min conditioning period oriented strongly toward the chemical cues of the insert tank. These data indicate that young convict cichlids use visual cues to learn and reset the smell of “home” in less than 20 min.

Keywords Homing · Chemical cues · Visual cues · Cichlid · Parental care · Learning

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Introduction

Parental care is maintained by natural selection because care increases the probability of offspring survival, thereby contributing to parent fitness (Clutton-Brock 1991). Because parents and offspring are occasionally spatially separated, it is important for offspring and parents to have a mechanism for regaining close proximity. Mother-offspring odour recognition is well known in mammalian systems (see Schaal 1988 for review). For example, displaced mouse pups use odour cues to find their way back to the nest (Honeycutt and Alberts 2005). Recognition and attraction to the odour of home-nest bedding is learned and malleable by prenatal social context (Honeycutt and Alberts 2005). Parental crab spiders knocked out of their nest atop a flower stalk use visual landmarks and previously established silk lines to relocate their nest and resume defence of their young (Morse 1991).

Cichlids are unusual among fishes in the degree to which they practice care (Keenleyside 1991). Many forms of care exist among cichlids, from New World biparental egg-layers that defend their young from brood predators, to maternal mouth brooders that release their young only when the young are ready for independent life. Most New World cichlid species exhibit extended parental care in the form of post-hatch defence of free-swimming young. Offspring, for their part, depend on parental care and seek it out, particularly in times of crisis or threat. The young are small at first hatch and their survival is completely dependent upon parental protection from brood predators. For example, in a study where parental convict cichlids were experimentally removed, median time to complete brood annihilation by predators was between 2 and 3 min (Alonzo et al. 2001). Thus, young cichlids are under strong selection to remain near their parents. Several studies have demonstrated experimentally that displaced young orient

strongly to visual representations of their parents (e.g. Hay 1978; Lavery et al. 1990; De Gannes and Keenleyside 1992; Sheenan et al. 1994).

The convict cichlid is a biparental New World cichlid native to streams and lakes of Guatemala to Panama (Bussing 1987). Historically this species has been referred to as *Cichlasoma nigrofasciatum*, but in the past 15 years it has been reclassified several times to *Cryptoheroes*, to *Archocentrus*, and, of late, to *Amatitlania siquia* (Schmitter-Soto 2007). This species is similar to many other New World cichlids in that they form monogamous pair bonds and practice biparental care of their eggs and free-swimming young (Keenleyside 1991). Together the female and male jointly prepare a spawning site by excavating a small cavity beneath a large rock, a crevice between rocks, or overhanging surface. The female attaches rows of adhesive eggs to the roof of the spawning site that are in turn fertilized by the male until 200–300 eggs are deposited. The eggs hatch in a few days into yolk-laden “wrigglers” (free-embryos or eleutheroembryos, sensu Balon 1999) that have poorly developed fins. In a few more days, the young absorb the remaining yolk, and with their developing fins, gain the ability to swim freely in the water column. At this time, they commence exogenous feeding and become larvae. In Costa Rican streams, young emerge from the relative safety of their natal nest cavity at a size of 4.5 to 5 mm total length (Wisenden 1995). Biparental defence of the young continues for 4 to 6 weeks (depending on growth rate of the young) of larval and juvenile development (Wisenden 1994a, Alonzo et al. 2001).

Convict cichlid families in Costa Rican streams typical comprise 2 parents and an average (\pm SE) of 48 ± 1.3 young ($n=635$) over all stages of ontogeny in the Río Cabuyo and Quebrada Amores, Costa Rica (Wisenden unpublished data). The family forms a mobile territory that travels about the stream bottom during the day, up to 13.7 m from the natal lair, before returning to the refuge of natal territory every night (Wisenden 1995). During this interval mortality to brood predation is high in spite of parental defence, ranging from 52 to 85% brood failure in Costa Rican streams (Wisenden 1994a) to 80% (McKaye 1977; Alonzo et al. 2001) in Lake Xíloa, Nicaragua. Evidence to date suggests that families maintain social cohesion largely by visual contact (Hay 1978). Orientation to parent cichlids is facilitated by starkly contrasting (aposematic) vertical banding patterns adopted by adults during the parental phase of reproduction. Parents have also evolved several forms of calling signals such as head shakes and fin-flicks to induce antipredator responses in their young such as increase in shoal cohesion, movement toward the parents and toward the substratum (Lavery et al. 1990; Sheenan et al. 1994). These parental calling behaviours are visual

signals that may also incorporate mechano-sensory stimulation of the lateral line, and chemical cues.

When a family is attacked by a single brood predator, the parents drive it off and the family remains intact. However, very large predators, or alternatively, swarms of small brood predators can overwhelm the parents' ability to defend their brood (Meral 1973; Wisenden pers. obs.). In these instances, young that are not consumed in the onslaught disperse in every direction. Parents in field populations soon regain control of their territory, defend it, and search for missing young for at least 15 min even in the event of complete brood loss (Wisenden et al. *in press*). Young that become separated from their family have no hope of survival unless they quickly relocate their family. Visual contact with parents can be lost when the substratum is highly heterogenous and structured as occurs commonly in rocky substrata where cichlids breed and rear their young. Moreover, catfish attack cichlid broods at night (*Rhamdia nicaraguense* in Nicaraguan Lakes: McKaye and Barlow 1976; *R. guatemalensis* in the Rio Cabuyo: Wisenden pers obs) that could disperse young from their home site at a time when visual cues are absent. Even during the day there may also be a limit to the distance that young cichlids can see, especially during turbid conditions that typically follow rain. In these instances, young cichlid could rely on chemical information carried on water currents. There is no shortage of precedent for cichlids using chemical cues. For example, parent cichlids use chemical cues to locate and recognize their eggs and young (Myrberg 1966; McKaye and Barlow 1976; Barnett 1977; Reeb and Colgan 1991, 1992). There is also evidence that young cichlids use chemical cues for the assessment of predation risk (Wisenden and Sargent 1997; Alemadi and Wisenden 2002; Foam et al. 2005; Pollock et al. 2005).

The ability of young cichlids to orient to their family by tracking chemical cues has not been tested. In this study, we tested if displaced convict cichlid young use chemical cues to locate their family, and if the smell of “home” is fixed or labile.

Methods

Convict cichlids used in this study were second and third generation offspring derived from wild-caught fish from Quebrada Amores and the Rio Potrero, both found near the Lomas Barbudal Biological Reserve, Guanacaste, Costa Rica ($10^{\circ} 30' 21.68''$ N, $85^{\circ} 22' 14.71''$ W). The laboratory facility at Minnesota State University Moorhead maintains the fish on a 12:12 L:D cycle and fed daily with commercial flake diet. Holding aquaria were 190 L in volume with a thin layer of naturally coloured gravel, fragments of clay flower-pots, heater and internal power filters. Breeding aquaria were 75 L in volume ($30 \times 60 \times 42$ cm high) with naturally

coloured gravel substratum, clay flower pot, heater and internal power filter.

Chemosensory-based homing behaviour was determined with a dichotomous choice Y-maze (Fig. 1). The Y-maze was made from white polyvinyl chloride (PVC) tubing with an internal diameter of 7.5 cm, and a total length of 96 cm. The tubing was cut in half lengthwise to create a trough. The drain tube, which formed a stand pipe at the base of the stem of the Y, was adjusted so that the maximum depth in the centre of the trough of 1.8 cm and surface width of 6.5 cm. Cross-sectional area of water in the trough was 8.67 cm², thus total water volume in the maze was 1.38 L. Separate airline tubing hoses siphoned water from two elevated 37 L aquaria at a rate of 8.08±0.03 ml/s (*n*=10) into each arm of the Y-maze. Current speed in the maze was therefore about 0.93 cm/s in the arms of the maze and 1.86 cm/s in the stem of the maze.

Experiment 1: Homing behaviour based on olfactory cues of home

Young were removed from their home tank and placed in groups of five siblings in the start chamber of the Y-maze (Fig. 1). Siphons were started so that each arm of the maze received water of a different chemical signature. After 1 min of acclimation time, the removable mesh gate (Fig. 1) was raised and the fish swam upstream past the junction of the arms and up one of the arms of the maze. We recorded the number of young in each arm and the number of young that remained in the stem of the maze after the 4-min run time (5 min total elapsed time exposed to test cues). Fish that stayed in the stem of the maze were classified as undecided. We first conducted a preference test (*n*=11) between water from the home tank versus blank water

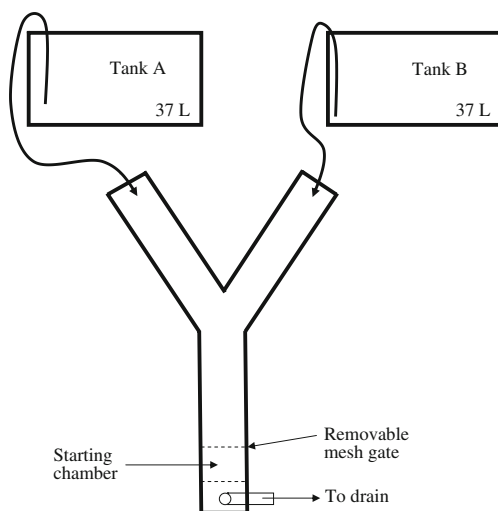


Fig. 1 The dichotomous Y-maze used for measuring chemically-oriented homing behaviour in young convict cichlids

(from an tank identical in every way to the home tank except that it had never contained fish since it was set up). The siphon hoses from stimulus tanks were reversed to the opposite arms of the maze for each successive trial to control for side bias. Four genetically different broods supplied young for this experiment. We conducted a second experiment (*n*=10), with identical set-up, in which young convict cichlids were given a choice between water from their home tank versus the odour from a tank that contained another family of adults and similar-aged young. Five genetically different broods provided young for this experiment. Data were analysed by subtracting the number of fish entering the maze arm receiving cue of the home tank from the number of fish entering the maze arm receiving the alternative cue, and comparing the difference against zero with Wilcoxon matched-pairs signed-ranks tests (Siegel and Castellan 1988). We used this test instead of a paired *t*-test because the fish shoaled together and influenced each other's behaviour. Therefore, behaviour of individual fish was not statistically independent of other fish within a trial.

Young used in the first set of trials comparing home tank water versus blank tank water were 14.14±0.53 mm (mean±1 SE) total length (TL). The focal fish used in the second set of trials comparing home tank water versus tank water from another family were 9.62±0.14 mm TL. The size of fish used as the other family was size-matched by eye, but not measured.

Experiment 2: Homing behaviour based on learned association of visual and olfactory cues

Here, we tested if young convict cichlids preferentially homed to chemical cues of their parents or whether they preferentially oriented to the odours of siblings and their microhabitat. We used two genetically different broods to provide young for this experiment. Five siblings were removed from their family and placed in a glass box (20×20×37 cm high=14.8 L) that could be inserted into a standard breeding tank. Water inside the insert tank was that of standard breeding tank that contained gravel, heater, filter, and fresh water that had never come in contact with fish. We ran 12 trials using 12 sets of five new sibling fish. Each set of five siblings was tested twice. We tested each set for a preference for home tank water versus insert tank water, then reversed the sides of the maze that received each test stimulus, and ran the test a second time on the same set of fish. Switching sides controlled for side bias. Preference scores of the two trials were averaged to produce one preference score for each set of five siblings. For half of the trials (*n*=6) the small tank with the five young was inserted into a breeding tank that contained no fish. For the other half of the trials (*n*=6) the small tank was

inserted into a novel breeding tank that contained their parents (but no siblings). After 20 min, the focal young were immediately tested in the Y-maze for homing preference between odour of their original home tank (odour of parents, siblings, tank microhabitat) versus the odour of the water taken from the insert tank (their own odour, but no odour of parents, siblings or home tank microhabitat). Young that could see their parents during the 20-min conditioning period were 9.99 ± 0.13 mm SL. Young that could not see their parents during the 20-min conditioning period were 9.92 ± 0.22 mm SL ($t_{58} = 0.27$, $P = 0.785$). Preference for home tank water was calculated by subtracting the number of fish in the arm receiving insert tank water from the number of fish in the maze arm receiving home tank water. The effect of parent presence/absence was tested by comparing preference for home tank water between treatment groups using a Wilcoxon–Mann–Whitney test (Siegel and Castellan 1988). For directional preferences within each treatment group, we used Wilcoxon matched-pairs signed-ranks tests. All P values reported in this study are based on two-tailed probability distributions.

Results

Experiment 1: do young convict cichlids use chemical cues to find home?

Young went up the maze arm that received home tank water significantly more than the arm receiving blank water (Wilcoxon matched-pairs signed-ranks test, $T^+ = 54$, $n = 10$, $P = 0.002$) or receiving water from the tank of another

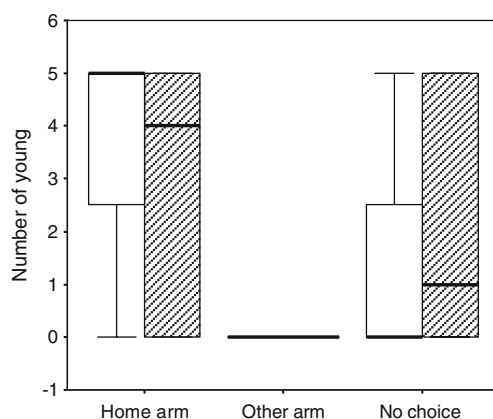


Fig. 2 Median (\pm quartiles, range) number of young per trial present in each arm of the maze after 4 min. One arm of the maze received water from their home tank (*Home arm*). The other arm received either (1) blank water from a fishless tank (open fill) or (2) tank water from a tank that contained another breeding pair and their young (hatched fill). Some young remained at the base of the maze and made no choice

family ($T^+ = 28$, $n = 7$, $P = 0.008$, Fig. 2). Thus, young convict cichlids clearly demonstrated an ability to home on the basis of chemical cues and that they can discern between the odour of their own family's tank and the chemical signature of another family's tank.

Experiment 2: do young convict cichlids learn the smell of home?

During the 20-min conditioning period, parents (especially the female) approached their young in the small tank. Presence and absence of parents significantly affected orientation in the maze (Wilcoxon–Mann–Whitney test $W_x = 21$, $n = 12$, $P = 0.004$). Young that had not seen their parents in the 20-min conditioning period oriented toward their home tank water (Wilcoxon matched-pairs signed-ranks test $T^+ = 21$, $n = 6$, $P = 0.031$), while young that had seen their parents during the 20-min conditioning period switched their homing preference to the water of the insert tank ($T^- = 21$, $n = 6$, $P = 0.031$, Fig. 3). Preference strength was not altered when the maze arm receiving each cue was switched ($T^- = 24.5$, $n = 9$, $P = 0.910$).

Discussion

Young convict cichlids can orient to their family solely on the basis of chemical cues and discern between the smell of their own family's tank and the smell of another family's tank. When held in a chemically-sealed tank within a fishless breeding tank for 20 min, young convict cichlids

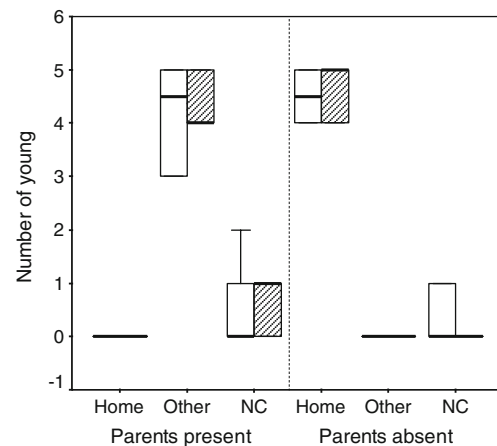


Fig. 3 Median (\pm quartile, range) number of young per trial present in each arm of the maze after 4 min. One arm of the maze received water from their home tank (*home*), the other arm received water from the small insert tank (*other*) that housed the focal fish for 20 min. Some fish made no choice (NC). Each group of five fish was run twice. The first run is represented by hollow fill, the second trial, in which the arms receiving each stimulus was reversed, is shown in hatched fill. Statistics are based on averaged scores of the two runs

retained a strong preference to orient toward the smell of their natal tank. However, when young in the same small tank were able to view their parents for 20 min, the young updated the chemical signature of “home” to that of the water inside the small insert tank, and preferred to orient toward these new cues over the odour of their home tank.

Because broods of convict cichlids in Costa Rican streams are mobile and range over large areas (Wisenden 1995), the smell of home changes frequently and thus, young update homing cues within periods of less than 20 min. This learning mechanism is adaptive in the ecological context in which this behaviour evolved. When displaced (out of sight of their parents), young retain the most recent chemical image of home and seek it out. When not displaced (within sight of their parents) young continually update the chemical bouquet of home.

Survival of young cichlids is dependent on parental protection from brood predators. Even with this protection, convict cichlid young in Costa Rican streams die at an average rate of 2.58 ± 0.13 ($n=391$ broods) young per day, a rate affected by age of young, number of young in the brood, and prevailing predation climate in their habitat (Wisenden 2001). Young that are scattered by predatory attack must find their way to the safety of their parents’ protection. The lab data from the current study suggests that one way that convict cichlid young can find their back to their family is to orient to the background chemical signature of the microhabitat in which the parents were last seen. Once within visual line of sight of the parents, young can orient visually toward the family (Hay 1978; Sheenan et al. 1994). This leads to several new questions for future investigation. First, how far are young convict cichlids dispersed when a brood is attacked by a predator? Second, what proportion of dispersed young is able to return safely to the protection of their parents? We know of no data to address these questions.

Convict cichlids adopt conspecific young from neighbouring families (Wisenden and Keenleyside 1992; Alonzo et al. 2001). In a survey of 292 broods in Costa Rican streams, 29% contained unrelated young (Wisenden and Keenleyside 1992). However, parents accrue fitness benefits by adopting unrelated young because defence of a few adopted young adds little to the cost of care while there are demonstrable benefits to parents from dilution of predation risk (Wisenden and Keenleyside 1992, 1994). Moreover, because parents selectively adopt young that are smaller than their own, adopted young are weaker swimmers. When predators attack the brood, adopted young suffer a disproportionate rate of predation (Wisenden and Keenleyside 1992, 1994). There are likely multiple mechanisms by which young may find themselves in the care of foster parents. Parents may actively kidnap young from each other (McKaye and McKaye 1977). If one mate deserts and

leaves its mate in a cruel bind, the remaining mate may lead the young toward a neighbouring brood and cause the broods to merge (Wisenden and Keenleyside 1992; Wisenden 1994b). A third possibility is that catastrophic attacks on a brood overwhelm parental defence and lead to flight and dispersal by the young (Meral 1973; Wisenden pers. obs). Regardless of the mechanism by which young may find themselves in foster care, the data from the current study suggests that adopted young would soon reset the smell of “home” using the sight of new parental fish, whether the parents are their biological parents or not. Once young are adopted into foster care, the smell of its biological family becomes immaterial because its best chance of survival depends on remaining with the foster parents. A flexible mechanism for learning the smell of home is superior to one governed by a kin-based template.

Adopted young are at a disadvantage (Wisenden and Keenleyside 1992, 1994). Moreover, if young approach a new family with relatively small young, the parents will reject them by chasing them away or eating them (Wisenden and Keenleyside 1992). Because entering into foster care is risky or fatal, young should always prefer their biological family when given the choice. In our experiment, young clearly demonstrated this preference.

Future work should also be directed toward exploring the role of ontogeny on homing ability. A limitation of the current study is that the young used were at the large end of the typical range of sizes of young under parental care. Fish smaller than 7 mm SL refused to run the maze, preferring instead to remain huddled against the mesh in the starting chamber. A different experimental set-up will be needed to test orientation of small young. Another avenue of research left unanswered by the current study is that we did not attempt to determine retention time of imprinted olfactory cues. Because young rapidly acquire a new smell of home, they may also forget olfactory information just as quickly. It might also be the case that olfactory cues need constant reinforcement to be retained. We can only conclude from our data that the chemical signature of home is retained for at least 20 min. Moreover, we do not know if resetting the chemical smell of home requires the sight of the biological parents, or if the sight of any parental fish would suffice. The widespread occurrence of alloparental care in this species and some lab studies (De Gannes and Keenleyside 1992) would seem to suggest the latter.

We admit to surprise that the role of chemical cues for homing is so apparent. Under normal daylight conditions with good water clarity, visual cues alone should suffice for young convict cichlids to orient to their aposematically-coloured parents. Thus, the role of olfactory cues in homing may occur only under special circumstances when visual cues are not available. For example, visual information is not available at night when nocturnal predators such as

Rhamdia catfish are active or during conditions of high water turbidity. Spates during the wet season render water conditions opaque with allochthonous silt. During these intervals, predators remain active and displaced young would be largely dependent on olfactory cues to orient to home. It may be the case that a steep selection gradient on finding parental fish has acted upon all sensory modalities.

Young in our experiments may have recognised their own chemical signature in the insert tank test stimulus. For example, three-spined stickleback orient by self reference based on odours associated with shared diet or recent habitat use (Ward et al. 2004, 2005; Webster et al. 2007). However, their own chemical signature was present in both test cues (insert tank water and home tank water) and response to these cues was conditional upon the presence or absence of the visual presentation of the parents, thus, self-referencing, per se, does not explain the observed homing behaviour.

Learning plays a significant role in behavioural ecology by allowing animals to optimally adjust behaviour to prevailing environmental conditions and maximize fitness benefits (Ward et al. 2005). Three-spine stickleback select shoalmates based on chemical cues indicating common diet or habitat use (Ward et al. 2004, 2005; Webster et al. 2007). Acquisition and recognition of shared habitat-specific chemical cues occurs in less than 4 h, but longer than 2 h (Webster et al. 2007). Young in our experiment clearly demonstrated a learned response within 20 min. Future research might experiment with shorter association times. The relatively short time required by young cichlids to orient to a new odour probably reflects the relative intensity of selection in the two systems. Young cichlids pay the ultimate fitness cost, within minutes (Alonzo et al. 2001), by failing to orient to their family. Stickleback pay only a mild fitness penalty in that fish that miscue in shoaling decisions do not shoal as cohesively (Webster et al. 2007) or forage as efficiently (Ward et al. 2002).

The form of learning revealed in this study differs from olfactory imprinting that occurs in salmonid parr and smolt in that salmonids imprint on only one bouquet of cues, imprint permanently and home toward these cues only as migrating adults (e.g. Cooper et al. 1976). A well-studied aspect of olfactory learning in fish is the association between chemical alarm cues and novel indicators of predation (Brown 2003). Predation reliably damages epidermal tissue. Chemical cues released from injured epidermal tissue alert nearby conspecifics of the presence of predation risk and provide an opportunity to associate predation risk with odours (Magurran 1989), images (Chivers and Smith 1994) or sounds (Wisenden et al. 2008a) correlated with predation risk. The form of learning observed in our study shares two qualities with learned associations with predation risk. First, (unlike salmonid imprinting) both types of learning occur throughout a fish's

life (see Brown 2003 for exceptions). Learning is not restricted to a brief window of time during ontogeny. Second, both forms of learning are achieved in a single, brief association without reinforcement. However, learned associations with predation risk are near-permanent because in most cases the information about predation risk stays salient for the rest of the fish's life. Here, we showed that young cichlids quickly substitute old chemical bouquets associated with home with new chemical bouquets.

These data lead to new questions about how much the chemical signature of one area of a stream bottom might differ from nearby areas. Convict cichlid broods wander up to 13.7 m away from their lairs during the day (Wisenden 1995). Are sections of streams separated by this distance sufficiently distinct to permit young cichlids to use microhabitat-specific cues to home to their family? Fathead minnows can associate predation risk with the chemical signature of a section of stream and distinguish it from water samples collected 15 m apart (Chivers and Smith 1995), suggesting that some predators are habitat-specific and create microhabitat-specific levels of predation risk. Minnows benefit from this fine resolution of risk because predation exerts such a profound selection pressure on prey. Similarly, young cichlids are under intense selection to avoid predation. From the perspective of young cichlids, predation risk is lowest in the place where their parents are. Subtle changes in background microhabitat cues may guide young within visual range of their parents.

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References

- Alemadi SD, Wisenden BD (2002) Antipredator response to injury-released chemical alarm cues by convict cichlid young before and after independence from parental care. *Behaviour* 139:603–611
- Alonzo JJ, McKaye KR, van den Berghe EP (2001) Parental defense of young by the convict cichlid, *Archocentrus nigrofasciatus*, in Lake Xiloá, Nicaragua. *J Aquaric Aq Sci* 9:208–227
- Balon EK (1999) Alternative ways to become a juvenile or a definitive phenotype (and on some persisting linguistic offenses). *Environ Biol Fish* 56:17–38
- Barnett C (1977) Chemical recognition of the mother by the young of the cichlid fish, *Cichlasoma citrinellum*. *J Chem Ecol* 3:461–466
- Brown GE (2003) Learning about danger: chemical alarm cues and local risk assessment in prey fishes. *Fish Fish* 4:227–234
- Bussing WA (1987) Peces de las aguas continentales de Costa Rica. Editorial de la Universidad de Costa Rica, San Jose, Costa Rica
- Chivers DP, Smith RJF (1994) Fathead minnows, *Pimephales promelas*, acquire predator recognition when alarm substance is associated with the sight of unfamiliar fish. *Anim Behav* 48:597–605

- Chivers DP, Smith RJF (1995) Fathead minnows (*Pimephales promelas*) learn to recognize chemical stimuli from high-risk habitats by the presence of alarm substance. *Behav Ecol* 6:155–158
- Clutton-Brock TH (1991) *The Evolution of Parental Care*. Princeton University Press, New Jersey
- Cooper JC, Schalz AT, Horrall RM, Hasler AD, Madison DM (1976) Experimental confirmation of the olfactory hypothesis with homing artificially imprinted coho salmon (*Onchorhynchus kisutch*). *J Fish Res Bd Can* 33:703–710
- De Gannes GC, Keenleyside MHA (1992) Convict cichlid fry prefer the more maternally active of two parental females. *Anim Behav* 44:525–531
- Foam PE, Mirza RS, Chivers DP, Brown GE (2005) Juvenile convict cichlids (*Archocentrus nigrofasciatus*) allocate foraging and antipredator behaviour in response to temporal variation in predation risk. *Behaviour* 142:129–144
- Hay TF (1978) Filial imprinting in the convict cichlid fish *Cichlasoma nigrofasciatum*. *Behaviour* 65:138–160
- Honeycutt H, Alberts JR (2005) Housing pregnant mice (*Mus musculus*) in small groups facilitates the development of odor-based homing in offspring. *J Comp Psychol* 119:418–429
- Keenleyside MHA (1991) Parental care. In Keenleyside, MHA ed. *Cichlid Fishes: Behaviour, Ecology and Evolution*. Chapman and Hall, New York, pp 191–208
- Lavery RL, Mackereth RW, Robilliard DRC, Keenleyside MHA (1990) Factors determining parental preference of convict cichlid fry, *Cichlasoma nigrofasciatum* (Pisces: Cichlidae). *Anim Behav* 39:573–581
- Magurran AE (1989) Acquired recognition of predator odour in the European minnow (*Phoxinus phoxinus*). *Ethology* 82:216–223
- McKaye KR (1977) Competition for breeding sites between the cichlid fishes of Lake Jilóá, Nicaragua. *Ecology* 58:291–302
- McKaye KR, Barlow GW (1976) Chemical recognition of young by the midas cichlid, *Cichlasoma citrinellum*. *Copeia* 1976:276–282
- McKaye KR, McKaye NM (1977) Communal care and kidnapping of young by parental cichlids. *Evolution* 31:674–681
- Meral GH (1973) *The adaptive significance of territoriality in the New World Cichlidae*. Ph.D. dissertation, University of California, Berkeley
- Morse DH (1991) Homing by crab spiders *Misumena vata* (Aranea: Thomisidae) separated from their nests. *J Arachnol* 19:111–114
- Myrberg AA (1966) Parental recognition of young in cichlid fishes. *Anim Behav* 14:565–571
- Pollock MS, Zhao X, Brown GE, Kusch RC, Pollock RJ, Chivers DP (2005) The response of convict cichlids to chemical cues: an integrated study of behaviour, growth and reproduction. *Ann Zool Fennici* 42:485–495
- Reebs SG, Colgan PW (1991) Nocturnal care of eggs and circadian rhythms of fanning activity in two normally diurnal cichlid fishes, *Cichlasoma nigrofasciatum* and *Herotilapia multispinosa*. *Anim Behav* 41:303–311
- Reebs SG, Colgan PW (1992) Proximal cues for nocturnal egg care in convict cichlids, *Cichlasoma nigrofasciatum*. *Anim Behav* 43:209–214
- Schaal B (1988) Olfaction in infants and children: developmental and functional perspectives. *Chem Sen* 13:145–190
- Schmitter-Soto J (2007) Phylogeny of species formerly assigned to the genus *Archocentrus* (Perciformes: Cichlidae). *Zootaxa* 1618:1–50
- Sheenan MGC, Waas JR, Lavery RJ (1994) The warning signals of parental convict cichlids are socially facilitated. *Anim Behav* 47:974–976
- Siegel S, Castellan NJ Jr (1988) *Nonparametric statistics for the behavioural sciences*. McGraw-Hill, New York
- Ward AJW, Axford S, Krause J (2002) Mixed-species shoaling in fish: the sensory mechanisms and costs of shoal choice. *Behav Ecol Sociobiol* 52:182–187
- Ward AJW, Hart PJB, Krause J (2004) The effects of habitat- and diet-based cues on association preferences in three-spined sticklebacks. *Behav Ecol* 15:925–929
- Ward AJW, Holbrook RI, Krause J, Hart PJB (2005) Social recognition in sticklebacks: the role of direct experience and habitat cues. *Behav Ecol Sociobiol* 57:575–583
- Webster MM, Goldsmith J, Ward AJW (2007) Habitat-specific chemical cues influence association preferences and shoal cohesion in fish. *Behav Ecol Sociobiol* 62:273–280
- Wisenden BD (1994a) Factors affecting reproductive success in free-ranging convict cichlids (*Cichlasoma nigrofasciatum*). *Can J Zool* 72:2177–2185
- Wisenden BD (1994b) Factors affecting mate desertion by males in free-ranging convict cichlids (*Cichlasoma nigrofasciatum*). *Behav Ecol* 5:439–447
- Wisenden BD (1995) Reproductive behaviour in free-ranging convict cichlids, *Cichlasoma nigrofasciatum*. *Environ Biol Fish* 43:121–134
- Wisenden BD (2001) Brood defense and optimal brood size in convict cichlids *Cichlasoma (Archocentrus nigrofasciatus)*, a species with biparental care. *J Aquaric Aq Sci* 9:303–320
- Wisenden BD, Keenleyside MHA (1992) Intraspecific brood adoption in convict cichlids: a mutual benefit. *Behav Ecol Sociobiol* 31:263–269
- Wisenden BD, Keenleyside MHA (1994) The dilution effect and differential predation following brood adoption in free-ranging convict cichlids (*Cichlasoma nigrofasciatum*). *Ethology* 96:203–212
- Wisenden BD, Sargent RC (1997) Antipredator behavior and suppressed aggression by convict cichlids in response to injury-released chemical cues of conspecifics but not to those of an allopatric heterospecific. *Ethology* 103:283–291
- Wisenden BD, Pogatschnik J, Gibson D, Bonacci K, Schumacher A, Willett A (2008a) Sound the alarm: learned association of predation risk with novel auditory stimuli by fathead minnows (*Pimephales promelas*) and glowlight tetras (*Hemigrammus erythrozonus*) after single simultaneous pairings with conspecific chemical alarm cues. *Environ Biol Fish* 81:141–147
- Wisenden BD, Sneker JL, Stumbo AD, Leese JM (2008b) Post-predation parental care: defense of an empty nest after catastrophic brood loss. *Anim Behav* (in press)