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The response of convict cichlids to chemical alarm cues: an integrated study of behaviour, growth and reproduction

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Predation is an important agent leading to the evolution of accurate risk assessment. In fishes, one of the best studied modes of threat assessment is the use of damage release cues from consumed or damaged individuals. These cues act as sources of public information alerting both conspecific and heterospecific individuals in the immediate area of a possible predation threat. Responses to damage release cues can be behavioural (e.g. avoidance of the cue or increased schooling), morphological (e.g. change in body shape), and potentially reproductive (e.g. altered patterns of breeding and reproductive investment). In the current study we documented the response of convict cichlids (*Archocentrus nigrofaciatus*) to damage release cues from conspecifics, unknown heterospecifics (swordtail, *Xiphophorus helleri*), and distilled water. In short term behavioural trials we found that cichlids exhibited an antipredator response to injured conspecifics, while they exhibited a foraging response to injured swordtails and no response to distilled water. In longer term trials (41 days) we found that cichlids exposed to conspecific cues grew significantly less than those in the other treatments. Finally, we found that reproductive patterns were influenced by the treatments. Cichlids bred faster in the presence of predation cues (conspecific skin extract) and food cues (swordtail skin extract) than the control treatment (distilled water).

Introduction

The effects of predation permeate every aspect of a prey animal's life including its behaviour, morphology and reproduction (for review *see* Lima & Dill 1990, Kats & Dill 1998, Lima 1998). Animals must therefore be able to accurately assess their current level of predation risk to maximize fitness and minimize costs associated with antipredator behaviour (Kats & Dill 1998). For example, guppies (*Poecilia reticlulata*) from populations with different types of predation maximize fitness by adapting strategies to fit the threat of predation (Reznick & Endler 1982). Guppies from areas with high adult predation breed quickly, produce smaller fry and divert much of their energy stores to reproduction, when compared with guppies from populations containing high juvenile predation or low predation (Reznick & Endler 1982).

Numerous species of fishes from a wide diversity of taxa have been shown to alter their behaviour (Chivers & Smith 1998) or morphology (Brönmark & Miner 1992) in response to damage release cues. For example, several field studies have demonstrated that fishes will avoid areas recently marked with damage release cues (review Tremaine *et al.* 2005). One such study by Mathis and Smith (1993) demonstrated that fathead minnows (*Pimephales promelas*) will avoid areas containing not only their own damage release cues but they will also avoid damage release cues of known heterospecifics with which they co-occur and share predators (i.e. prey guild members). While the vast majority of studies examining damage release cues have concentrated on behaviour (Chivers & Smith 1998) an important few have examined morphological responses (Brönmark & Miner 1992, Brönmark & Petterson 1994). Brönmark and Petterson (1994) concluded that chemical cues alone were enough to cause crucian carp (*Carassius carassius*) to develop deeper bodies in an attempt to avoid predation. They postulate that the deeper body, while energetically expensive in movement, limited the ability of predatory fish to grasp and swallow their prey. Upon further examination Stabell and Lwin (1997) concluded that the odour of a damaged conspecific alone was enough to instigate this inducible defence.

A few studies have examined the effects of predation on reproduction in fishes. For example, Jones and Paszowski (1997) found that male fathead minnows reduce nest guarding in the presence of predators. Likewise, Chivers *et al.* (1995) showed that Iowa darters (*Etheostoma exile*) reduce courtship and spawning in the presence of predators. In a study on wild Trinidadian guppies, Godin (1995) found that males under high predation pressure were more likely to engage in sneak matings than they were in longer, "riskier" courtship displays. While these studies demonstrate that predation can affect the reproductive ecology, no studies have addressed whether damage release cues affect reproductive behaviour. The current study will attempt to address these shortcomings with a study examining the effects of damage release cues on the antipredator behaviour, morphology and breeding behaviour of convict cichlids (*Archocentrus nigrofasciatus*).

The convict cichlid is a substrate brooder native to Central America, from Guatemala to northeastern Panama (Bussing 1987). Both parents defend their young for up to 7 weeks in the lab (Williams 1972). Females lay approximately 200 eggs per clutch; these hatch into wrigglers which are transferred to previously dug pits. When their yolk sacs have been absorbed (3–4 days) the young become free-swimming fry and feed on algae and small particles on the substrate (Lavery & Keenleyside 1990).

Studies by Alemadi and Wisenden (2002) documented the ability of convict cichlid fry to respond to damage release cues. They found that convict cichlid young of a size typically defended by parents engaged in area avoidance and grouping behaviors in response to conspecific damage cues and did so as effectively as young that would typically be independent of parental care. Moreover, an earlier study by Wisenden and Sargent (1997) exposed convict cichlids to conspecific and unknown heterospecific damage release cues and found that juvenile cichlids exposed to conspecific cues not only significantly increased their antipredator behaviours but also significantly decreased the frequency of aggressive interactions. Brown *et al.* (2004) showed that cichlids show stronger intensity antipredator responses to cues of conspecifics in better body condition than to those in poorer condition.

Our study was conducted in two parts; first we documented the behavioural response of adult cichlids to the damage release cues of conspecifics, unknown heterospecifics (swordtail) and a blank control. We did this in short term behavioural trials in which feeding response and change in movement was recorded. Second, we documented the morphological and reproductive response of pairs of adult convict cichlids to the same three stimuli in a 41 day study. We documented the effects of these cues on cichlid breeding including time to initiate breeding, number of broods laid during the study, and the survival rate of the offspring. We also took several morphological measurements prior to the start of the study and immediately after to determine if the cues affected growth and morphology.

In the current study we hypothesize that the presence of conspecific skin extract will label an area as dangerous and therefore we predict that the cichlids may alter their temporal patterns of reproduction and parental investment in comparison with fish in the unknown heterospecific treatment or the blank control treatment. Furthermore, we predict that the indication of danger may affect their morphology; cichlids may develop an antipredator morphology (i.e. spine growth, an increase in body depth to length ratios, etc.). Moreover, the behavioral responses to predation cues may reduce foraging efforts, and consequently cichlids exposed to conspecific cues may have reduced growth. Given differential male and female roles in reproduction and territorial defense, we may expect gender differences in growth and morphology.

Materials and methods

Experiment 1

The purpose of Experiment 1 was to test the behavioral response of adult cichlids to damage release cues. We tested adult convict cichlids for their response to one of four chemical stimuli. Experiments were conducted in May 2003. All cichlids tested were in breeding condition (i.e. displaying typical breeding colouration and were observed to be engaging in typical nesting behaviour), but had not yet bred. Fish were from a laboratory population and originated from the same brood (i.e. full siblings). Conspecific skin extract donors were also from our stock population and were either siblings from the same brood as the test fish or were younger siblings from the same parents. Swordtails were obtained from a commercial supplier and held under the same conditions as the cichlids.

Skin extracts were prepared by collecting skin from four large cichlids (mean standard length ± 1 S.D. = 6.88 ± 0.68 cm), 11 small cichlids (3.08 ± 0.46 cm) and 10 swordtails (5.20 ± 0.98 cm). For each skin extract, donor fish were killed with a blow to the head (in accordance with Concordia University Animal Care protocol # AC-2002-BROW) and skin filets were removed from either side and immediately placed into 100 ml of chilled, glass distilled water. Skin samples were then homogenized and filtered through polyester floss (to remove any remaining tissue) and the final volume adjusted with the addition of glass distilled water. We collected a total of 29.52 cm^2 (in 332 ml) of large cichlid skin, 19.46 cm^2 (in 220 ml) of small cichlid skin and 45.17 cm^2 (in 508 ml) of swordtail skin. All skin extracts were frozen at –20 °C in 20 ml aliquots until needed. As an additional control, we also froze 20 ml aliquots of distilled water.

Behavioural trials were conducted in 37-liter glass aquaria with a gravel substrate, equipped with a single airstone mounted along the back wall. Attached to the airstone was an additional length of tubing, which allowed us to inject the stimuli from behind a black plastic viewing curtain. Tanks were covered on three sides with brown paper to ensure visual isolation from neighboring test tanks.

Single adult cichlids (mean ± S.E. standard length at time of testing = 7.24 ± 0.5 cm) were placed into the test tank and allowed 24 hrs for acclimation. During the acclimation period, test cichlids were fed *ad libitum* with brine shrimp and cichlid pellets. In addition, test cichlids were fed with brine shrimp one hour prior to testing in order to reduce the potential confound of a trade-off between foraging and predator avoidance (Brown & Smith 1996).

Trials consisted of a 10 minute pre-stimulus injection period and a 10 minute post-stimulus observation period. Prior to the pre-stimulus observation, we withdrew and discarded 60 ml of tank water through the stimulus injection tube (to remove any stagnant water) and then withdrew and retained an additional 60 ml. Following the pre-stimulus injection period, we injected 10 ml of one of the three experimental stimuli (or 10 ml of the distilled water control) and slowly flushed it into the tank with the retained 60 ml of tank water. Dye tests demonstrated that the stimulus was fully dispersed throughout the test tank within approximately 18 to 20 seconds. We tested a total of 10 cichlids per stimulus (N = 40) and all trials were videotaped. Videotapes

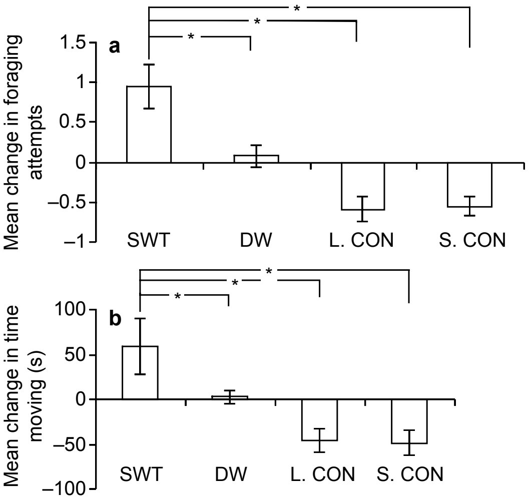

Fig. 1. Mean ± S.E. change in (**a**) foraging attempts and (**b**) time spent moving.

were labeled such that all data were recorded blind to the stimulus being tested.

During both the pre-stimulus and post-stimulus observation periods, we recorded two behavioural measures: foraging and time spent moving. A foraging attempt was recorded when the test fish pecked at the substrate with the body in an inclined (> 45°) position. Since we did not provide additional food during the observation periods, we recorded all pecking at the substrate as foraging attempts. Foraging rate is expressed as the number of attempts per minute. A decrease in foraging rate and time spent moving is indicative of an antipredator response in convict cichlids (Wisenden & Sargent 1997).

For both foraging rate and time spent moving, we calculated the difference between the post-stimulus and pre-stimulus injection periods and used the difference scores as dependant variables in subsequent analyses. We compared the rate of foraging and time spent moving across the treatment conditions using one-way ANOVA. Post hoc comparisons were made with Fisher's Protected Least Square difference test.

Experiment 2

The purpose of the current experiment was to test the effects of damaged release cues on the growth, morphology and breeding ecology of pairs of convict cichlids.

Cichlids were obtained from commercial dealers, as well as breeding stock from the University of Saskatchewan and Concordia University. At the start of the experiment (March 2003) 58 females and 58 males were anesthetized with MS-222 and morphological measurements were taken. We measured standard length, body depth, weight, dorsal spine length, pelvic fin length and longest pelvic spine length. We also calculated body condition (weight/length^3) and body depth index (length/height). Following the 41 day breeding period we remeasured each fish for the same suite of morphological characters recorded prior to the experiment and calculated the percent change during the experiment. Researchers were blind to the experimental treatments while measuring fish before and after the study. The percent change was analyzed using a two-way ANOVA with skin extract and gender as factors. All calculations were done using SPSS version 11.5 including Bonferroni post hoc comparisons.

In the wild, convict cichlids exhibit size assortative mating (Wisenden 1994); for this reason males were paired with females closest to their own standard length. Care was taken to ensure couples were not from the same population or that females were not bigger than males. Following the measurements, pairs were put into 37-liter aquaria containing a corner box filter (with an airstone), a clay pot (11 cm diameter), and a substrate of ~1 cm of granite chips. Cichlid pairs were treated daily with one of three treatments: convict cichlid skin extract, swordtail skin extract, or distilled water.

To prepare the convict cichlid skin extract ten adult convicts (SL + 1 S.D. = 7.49 ± 0.94 cm) were sacrificed by a blow to the head (University of Saskatchewan Committee on Animal Care and Supply, Protocol Number 19970077) and a skin filet was removed from both sides of each fish producing 423.86 cm^2 of skin in total. The skin was placed into 500 ml of distilled water and homogenized. The sample was filtered through glass wool to remove any solid particles and diluted with 4003 ml of distilled water for a total of 4238.60 ml. The extract was divided into sample bags containing 100 ml each and immediately frozen at –20 °C. We used the same procedure to produce an extract from swordtails (SL = 3.84 ± 0.78 cm). Distilled water was used to control for the disturbance of an injection into the tank. Cues were injected into the tanks using a 5 ml pipette at 16:00 daily.

As well as being treated daily, each couple was fed 0.5 g of Wardley's Cichlid Pellets at 9:00 and checked each day at 15:00 at which time we recorded the appearance and number of eggs, the transition of the offspring from one stage to another (i.e. wriggler to fry), and any deaths of either the adults or offspring. Time to first breeding attempt was analyzed using a paired Kolmogorov-Smirnov (K-S) test, as well as the length of time the offspring survived. The number of breeding attempts made throughout the study was analyzed using a Chi-square goodness of fit test. All calculations were made using SPSS v. 11.

Results

Experiment 1

For both behavioural measures, we found a significant effect of treatment (foraging: $F_{3,36}$ = 13.52, $p < 0.0001$; time moving: $F_{3,36}$ = 7.20, p = 0.0007). In response to both large and small cichlid skin extracts, test cichlids significantly decreased their foraging rates and time spent moving (Fig. 1). The intensity of the antipredator response was similar when exposed to either large or small conspecific skin extract. However, when exposed to swordtail skin extract, large cichlids significantly increased both foraging rate and time spent moving, suggesting an increase in foraging behaviour. There was no change in either behavioural measure in response to the distilled water control.

Experiment 2

Morphology

Of the 58 pairs of cichlids established at the beginning of the experiment there were nine tanks where one of the fish died. Deaths occurred equally among treatments and these pairs were dropped from the analysis. The causes of death were not determined by post-mortem analysis but in many cases appeared to result from agonistic interactions.

Of the three measures of body growth we found treatment effects for percent change in standard length, body depth and weight (Table 1). However, we failed to find gender effects or an interaction between gender and treatment in any of the same variables (Table 1). We did, however, note a strong trend indicating an interaction between gender and treatment affecting depth ($p = 0.064$; Fig. 2b).

Post hoc multiple comparisons show that fish exposed to swordtail skin extract grew sig-

Table 1. Results (*p* values) of the two-way ANOVA testing differences between morphological measurements taken before and after the study. Values in boldface are statistically significant.

	p	d.f.	*F*
Standard length (SL)			
Treatment	**0.009**	2	5.117
Gender	0.615	1	0.256
Treatment × Gender	0.192	2	1.691
Depth			
Treatment	**0.002**	2	7.102
Gender	0.148	1	2.145
Treatment × Gender	0.064	2	2.872
Weight			
Treatment	**0.021**	2	4.113
Gender	0.934	1	0.007
Treatment × Gender	0.304	2	1.214
Body Condition Index (BCI)			
Treatment	0.684	2	0.383
Gender	0.860	1	0.031
Treatment × Gender	0.651	2	0.432
Body Depth Index (BDI)			
Treatment	0.495	2	0.710
Gender	**0.029**	1	4.995
Treatment × Gender	0.286	2	1.277
Longest Dorsal Spine (LDS)			
Treatment	0.072	2	2.734
Gender	**0.035**	1	4.644
Treatment × Gender	0.118	2	2.21
Longest Pelvic Spine (LPS)			
Treatment	0.349	2	1.071
Gender	0.609	1	0.265
Treatment × Gender	0.420	2	0.879
Pelvic Fin Length (PFL)			
Treatment	**0.002**	2	6.918
Gender	0.161	1	2.006
Treatment × Gender	0.753	2	0.285

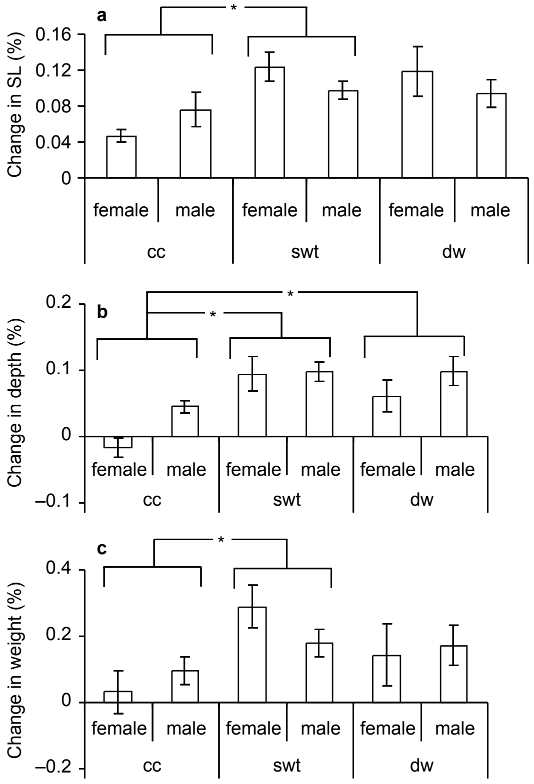

Fig. 2. The change in (**a**) standard length, (**b**) depth and (**c**) weight of male and female convict cichlids exposed to convict cichlid cues, swordtail cues and distilled water.

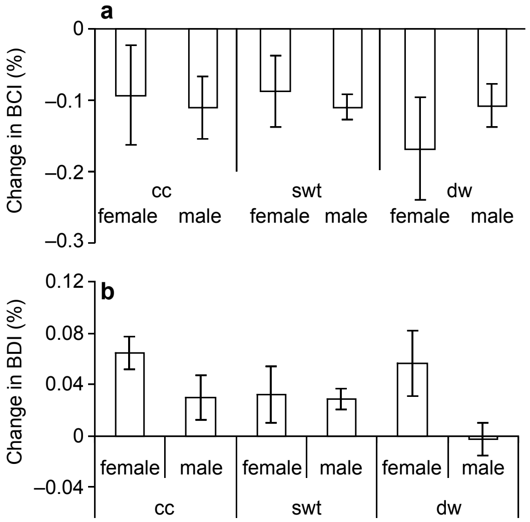

Fig. 3. The change in (**a**) body condition index (BCI) and (**b**) body depth index (BDI) of male and female convict cichlids exposed to convict cichlid cues, swordtail cues and distilled water.

nificantly longer than fish exposed to conspecific cues ($p = 0.014$; Fig. 2a) and tended to grow longer than fish exposed to distilled water cues ($p = 0.053$; Fig. 2a). Cichlids exposed to convict cichlid cues also showed significantly reduced growth in depth when compared with cichlids exposed to either swordtail cues ($p = 0.004$; Fig. 2b) or distilled water ($p = 0.013$; Fig. 2b). They also gained significantly more weight when exposed to swordtail cues when compared with conspecific cues ($p = 0.019$; Fig. 2c).

Of the two body index calculations, body condition index failed to produce differences attributed to treatment, gender or an interaction, while there was a significant effect due to gender on the body depth index. Females had a significantly greater increase in BDI than did males ($p = 0.029$; Fig. 3b).

Of the three measures of fin growth (longest dorsal spine (LDS), longest pelvic spine (LPS) and pelvic fin length (PFL)) we found a significant effect of treatment on PFL and an effect of gender on LDS. The pelvic fins of fishes exposed to convict cichlid cues grew significantly less than fishes exposed to swordtail cues ($p = 0.001$; Fig. 4c) and tended to grow less than fishes exposed to distilled water ($p = 0.053$; Fig. 4c). The dorsal spines of male cichlids tended to grow longer than females regardless of treatment ($p = 0.035$; Fig. 4a).

Reproduction

First breeding attempts

In our study 47 of 48 pairs made at least one reproductive attempt. In most pairs multiple reproductive attempts were made.

Pairs exposed to swordtail skin extract were quicker to attempt reproduction than the cichlids exposed to either convict cichlid skin extract (K-S test: $Z = 2.348$, $p < 0.001$ (two-tailed)) or distilled water (K-S test: $Z = 2.795$, $p < 0.001$ (two-tailed)). Moreover, cichlids exposed to cichlid extract attempted to breed earlier than the cichlids exposed to distilled water (K-S test: $Z = 1.901$, $p = 0.001$ (two-tailed); *see* Fig. 5).

Number of eggs laid

Results of data comparing the number of eggs laid indicated no significant difference between treatments for individuals breeding for the first time (one-way ANOVA: df = 2, $p = 0.413$). Insufficient sample size made analysis of the egg number in second breeding attempts tenuous, and results were therefore not calculated.

Number of breeding attempts

Results of a Chi-square Goodness of Fit test indicated that the number of pairs in each treatment that made at least one breeding attempt did not differ ($\chi^2 = 1.57$, $p > 0.25$) (Fig. 6). However, there was a difference in the number of pairs that attempted to breed a second time ($\chi^2 = 6.67$, $p < 0.05$) and third time ($\chi^2 = 21.16$, $p < 0.001$). Significantly more pairs exposed to swordtail cues made two breeding attempts than pairs exposed to convict cichlid cues ($\chi^2 = 6.62$, $p < 0.025$). In regard to third breeding attempts, pairs exposed to swordtail cues made significantly more attempts than pairs exposed to distilled water ($\chi^2 = 9.00$, $p < 0.005$) or convict cichlid cues ($\chi^2 = 16.95$, $p < 0.001$). We caution readers that interpreting the number of breeding attempts is somewhat problematic as captive cichlids frequently cannibalize their offspring. The stage at which this occurs could have a significant influence on the subsequent breeding attempts.

Offspring survival

The survival of the offspring was analyzed using a Kolmogorov-Smirnov (K-S) test to examine treatment differences in the time of survival from egg laying to consumption by the parents, or removal following 14 days as fry (Fig. 7). Results indicate a significant difference between all treatments. Survival among treatments was similar during the egg stage (until approximately day 8). This was followed by a significant decline in survival of cichlids in the swordtail treatment as compared with that of both the cichlid treatment (K-S test: $Z = 0.697$, $p = 0.006$) and the distilled water treatment (K-S test: $Z = 1.556$, $p = 0.016$). By day 13, survival in the distilled water treatment had fallen significantly below that in the cichlid treatment (K-S test: $Z = 1.414$, $p = 0.037$).

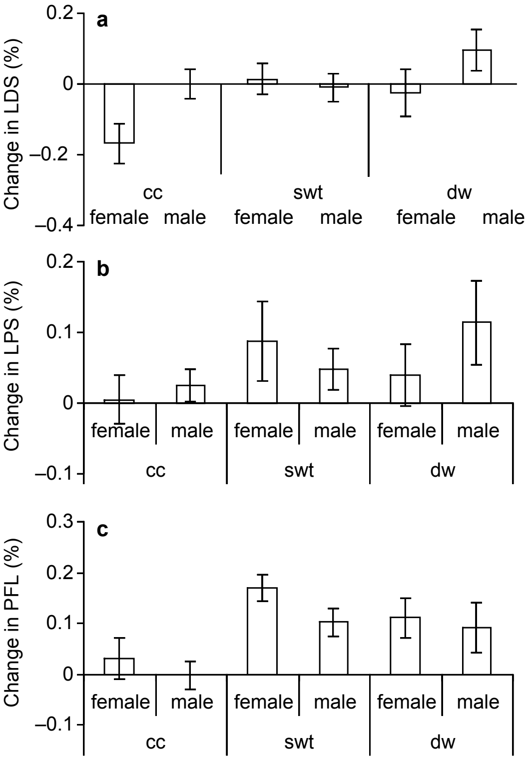

Fig. 4. The change in (**a**) length of the longest dorsal spine (LDS), (**b**) longest pelvic spine (LPS) and (**c**) pelvic fin (PFL) of male and female convict cichlids exposed to convict cichlid cues, swordtail cues and distilled water.

Discussion

The results of Experiment 1 demonstrate that cichlids exposed to conspecific cues ingest less food and engage in less movement when compared with cichlids exposed to either distilled water or swordtail skin extracts. These behaviours are most likely caused by the antipredator response to conspecific damage release cues as such responses have been documented in numerous species including convict cichlids (for review *see* Chivers & Smith 1998). Results indicating that cichlids exposed to swordtail skin extracts

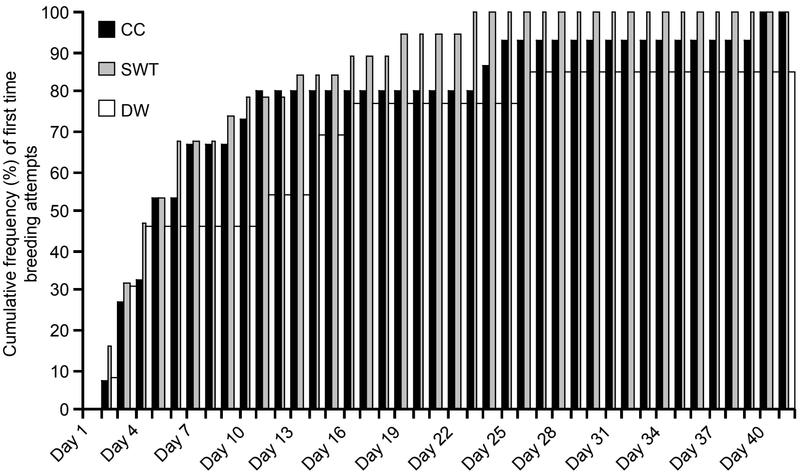

Fig. 5. The cumulative percent frequency of first time breeding attempts made by cichlid pairs exposed to convict cichlid cues, swordtail cues and distilled water as a function of time.

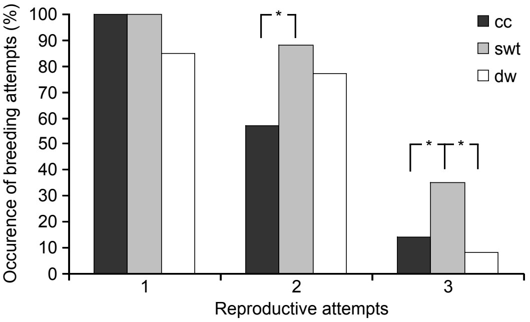

Fig. 6. The occurrence of 1st, 2nd, and 3rd breeding attempts by cichlid pairs exposed to convict cichlid cues, swordtail cues and distilled water.

increase foraging rates over a blank control can be explained in two ways. Exposure to swordtail cues could indicate that an unknown heterospecific competitor has entered the cichlid's territory with the consequence that food resources may soon become scarce and therefore should be rapidly consumed. It may also be that swordtail damage release cue itself is viewed as a novel food source to be exploited. Further experimentation, similar to Experiment 2, is required to differentiate these possibilities.

From our results we conclude that chemical cues affect growth of cichlid pairs. Exposure to conspecific cues had a negative effect on growth for convict cichlids with regard to length, weight and depth. As suggested by the results of Experiment 1, cichlids exposed to swordtail cues gained more weight, and grew longer and deeper than convicts exposed to conspecific cues. There was, however, no difference in growth rate between cichlids exposed to the swordtail cues and those exposed to distilled water. We interpret the reduction in growth in the cichlid treatment as a cost of antipredator behaviour (Skelly 1994). Cichlids exhibiting an antipredator response to cichlid cue may have reduced growth as a result of reduced food intake.

The ability of fish to change their morphology in response to predation risk has been documented in crucian carp (Brönmark & Miner 1992). The fish became significantly deeper bodied in ponds containing predatory northern pike (*Esox lucius*) when compared with carp allopatric with pike. Subsequently, Brönmark and Petterson (1994) demonstrated that it was the piscivorous diet of the predator, and not the predator odour alone, that caused the shift in morphology. In both studies the change in morphology was an increase in body depth believed to be a response to a gape limited predator. In our study there was no effect of treatment on body depth index or on spine growth and hence there appears to be no adaptive phenotypic change in morphology. It is possible that such effects take longer to develop and hence our experiment was too short to adequately identify such effects. It is also possible that convict cichlids lack the plasticity to induce morphological change and instead invest in behavioural responses and reproductive output.

Our study documented several significant effects on the reproductive behaviour of our

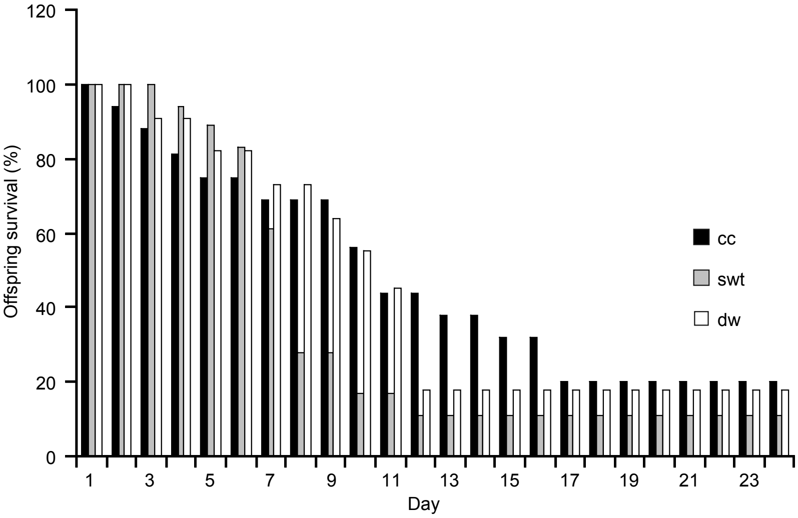

Fig. 7. Cumulative frequency of offspring survival through time.

cichlid pairs caused by chemical cues. We noted a significant difference in the time it took until breeding attempts were made, as well as a significant difference in the number of breeding attempts made in the 41 day duration of the study, and finally a significant difference in the survival of the offspring.

Previous studies have shown that female convict cichlids will adjust their brood size relative to perceived predation risk. Wisenden (1993) demonstrated that the security of nest sites significantly affects the number of eggs females will lay in each brood. Based on this finding we made the logical prediction that tanks receiving the conspecific skin extract (a high predation risk cue) would result in a reduction in the number of eggs laid and a delay in time to initiate breeding. However, we found no difference in number of eggs laid in the first breeding attempts. Moreover, there was faster reproduction in the cichlid treatment than the distilled water control. It seems likely that exposing the cichlids to a high intensity predation cue for a long duration caused them to breed faster, perhaps because the perceived predation risk was very high; delaying reproduction may be maladaptive if the probability of survival until the next reproductive event is low.

As stated above, the swordtail skin extract may have represented a source of food or a source of competition. If cichlids perceive the swordtail cues as food, and the area high in resources, then breeding should be entered into as early as possible. Alternatively, if the odour could have represented a competitive threat we could predict early breeding to monopolize existing nest sites and resources. Conversely delaying reproduction to wait for reduction in competition density is also possible. An experiment designed to measure the speed and frequency of breeding in response to high and low quality food in the absence and presence of a competitive threat should answer the question of whether the swordtail cue is perceived as food or a competitor.

Our results indicate that significantly more cichlid pairs exposed to swordtail skin extract made a second breeding attempt when compared with pairs receiving cichlid skin extract. Similarly, cichlid pairs exposed to swordtail cues were significantly more likely to attempt a third breeding episode, than were pairs exposed to cichlid skin extract, and those pairs exposed to cichlid cues were significantly more likely to attempt a third breeding than the pairs exposed to distilled water. Again, this may indicate that the pairs perceived that this was a food rich area worthy of energy expenditure or a highly competitive area in which resources must rapidly be monopolized. An alternative, and perhaps the simplest explanation, is that the swordtail cue indicated competition for food which caused an increase in food consumption leading to an increase in reproductive output.

Our final set of data deals with the survival of the offspring. In nature, there can be heavy selective pressure for efficient parental care. In Lake Jilóa, Nicaragua, only 20% of convict cichlid pairs were successful at rearing their brood to independence (McKaye 1977). In our study only 9 pairs (18.8%) successfully reared fry to 2 weeks of age. The cause of mortality in our study was likely consumption by one or both of the parents, as evidenced by the lack of bodies found in tanks. However, we cannot discount the fact that the entire brood may have succumbed to other factors and sunk into the gravel. The choice of the parents to eat the offspring may be directly related to their perception of the likelihood that they could successfully raise the fry, or more simply cannibalism could be related to stress. As the occurrence of cannibalism was relatively high in all treatments we again caution readers against drawing conclusions regarding reproduction data past the first breeding attempt as the energy or experience gained from cannibalism may have influenced subsequent events. Cichlids may engage in adaptive cannibalism if they are in a confined tank and their offspring are unable to disperse.

Our data indicates little variation in survival at the egg stage and wriggler stage (up to approximately day 8) attributable to the skin extracts. However, at the fry stage (day 9 onwards) tanks treated with heterospecific cues had significantly lower survival when compared with that in tanks with the other two cues. This was followed by a significant drop in survival of offspring exposed to distilled water cues. Studies have shown that parents invest different levels of care at different stages of offspring development (Sargent & Gross 1986) and that predation is believed to be most intense on small mobile fry (McKaye & Barlow 1976). Further experimentation investigating the link between cannibalism and predation risk is required.

Taken together, these data indicate threat-sensitive trade-offs between perceived local risk and reproduction patterns. Under conditions of high perceived risk (conspecific chemical skin extracts), cichlids reproduced earlier and had fewer reproductive events. In addition, we observed the lowest levels of growth in the conspecific alarm cue treatments. Thus, under conditions of increased predation risk, breeding pairs appear to invest more in reproduction (at a cost of growth rate and future reproduction). By doing so, they are able to maintain direct fitness (i.e. fecundity), at least for the first reproductive event.

Cichlids exposed to swordtail extract, however, exhibited the highest rate of reproduction (i.e. reproducing earlier and more often). Cichlids exposed to swordtail skin extracts exhibited the highest increase in growth and thus may have been able to allocate a higher proportion of energy to reproduction. It is possible that under conditions of low risk and high perceived resource availability, available energy is shifted to earlier reproduction. Though speculative, our results are suggestive and merit further examination.

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