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## Past reproductive effort affects parental behaviour in a cichlid fish, *Cichlasoma nigrofasciatum*: a comparison of inexperienced and experienced breeders with normal and experimentally reduced broods

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**Abstract** Defensive and parental care behaviour of convict cichlids that differed in past effort was compared. Before testing, some fish were bred three times while others were not bred. Age was held constant; all individuals in this study were approximately 20 months old ( $\pm 2$  months) at test time. Furthermore, half of the pairs in this study had their broods experimentally reduced by 50%. Results indicated that past effort across breeding attempts affects investment in the current brood. Experienced pairs were more aggressive toward a model predator than inexperienced parents. However, no major differences were observed in depreciable care (i.e. fanning). Contrary to previous studies, brood size had minor effects on parental care. This discrepancy could be due to the age of the parents; individuals in this study were significantly older than fish tested in previous studies. The results support parental investment theory and suggest that past effort is not only important within breeding episodes but also within an animal's lifetime.

**Key words** Parental investment · Behaviour · Past effort · Cichlidae

### Introduction

To maximize lifetime reproductive success, animals that breed more than once, must decide on how much to invest in each brood. Parental effort is known to be affected by a variety of factors inherent to parents and

offspring (see Sargent and Gross 1986; Montgomerie and Weatherhead 1988). For instance, older parents have been shown to be more committed to the current brood than younger parents (Pugesek 1981; but see Nur 1984), in effect supporting parental investment models (Williams 1966; Pianka and Parker 1975). If current reproduction reduces the capacity for future reproduction, animals may base investment decisions on past effort.

Trivers (1972) argued that parents should adjust current care in relation to past investment in order to minimize loss of reproductive effort. Dawkins and Carlisle (1976) and Boucher (1977) suggested that parents should adjust current care not to past costs but to prospective benefits. More recently, Sargent and Gross (1986) have argued that past investment may be a reliable index of future expected benefits if past investment reduces the parents' capacity for further expenditures. Therefore, animals may appear to be basing expenditures on past investment, while in fact their behaviour is indirectly related to prospective benefits.

To date, behavioural studies have only manipulated past investment within a breeding episode. They show that animals do assess the amount of past investment in allocating resources to current care (Weatherhead 1979, 1982; Dawkins and Brockmann 1980; Coleman et al. 1985; Lavery and Keenleyside 1990a). Because parental age and past effort are usually correlated, it is difficult to test for the effects of past effort across breeding attempts. Furthermore, parental investment theory predicts that parental care should increase with both age and past effort (Pianka 1983). Field studies have shown that older and more experienced birds lay earlier and have higher reproductive success than younger and less experienced birds (Crawford 1977; Finney and Cooke 1978; Middleton 1979). This result could be due to the greater foraging efficiency and competitive ability of experienced birds (Stutchbury and Robertson 1988; constraint hypothesis) or a decline in future

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reproductive potential (Pugesek 1981, 1983; restraint hypothesis).

In this study, parental age was kept constant while manipulating past reproductive effort; before testing, some convict cichlids were bred three times while others were not bred. Therefore, it is possible to determine whether past effort across breeding attempts, independent of parental age, affects parental expenditure in the current brood. In this paper, I use past effort and breeding experience interchangeably because the two factors are inevitably linked. Because brood reductions result in a decrease in parental defense or filial cannibalism in the convict cichlid (Lavery and Keenleyside 1990a, b), broods were also reduced in half of the inexperienced and experienced pairs. Therefore, I attempted to determine if parents with different prospective benefits differ in their response to a low quality brood.

## Methods

### Study animal

The convict cichlid is a Central American substrate spawner. Although mate desertion and bigamy have been reported (Keenleyside 1991), usually both parents provide care for several weeks. However, females provide more direct care (i.e. fanning) than males during the embryonic period (egg, wriggler). During the larval period, both parents care for the young; although parents aid their young in acquiring food by fin-digging, the predominant form of care is defence.

The fish used in this study were approximately 5–6 generations removed from Costa Rica, Guanacaste Province.

### Experimental groups

Fish were raised and held in large holding tanks (248 l). To facilitate pair formation, females were put in breeding tanks (61 × 31 × 31 cm, 59 l) 4 days before males. Each pair had its own tank. Breeding tanks were placed side by side so that each pair could visually interact with one neighbouring pair. Placement of pairs was randomized. During the experiment each fish received a pellet of food (Tropic Aquaria Inc. stock # A149) a day. Larvae received brine shrimp nauplii, *Artemia salina*. Each tank contained a clay flowerpot for spawning, gravel and an airstone. A room heater kept the water temperature of all tanks at 27±2°C. Lighting was provided by overhead fluorescent tubes (LD 12:12).

I used a 2 × 2 factorial ANOVA design; the four groups were: (1) experienced, control; (2) experienced, brood reduced; (3) inexperienced, control; (4) inexperienced, brood reduced. The sample size was 10 pairs in each of the four groups. All individuals in these groups were 20 (±2) months old.

Individuals in the experienced group were allowed to raise three broods before they were used in this study. Males and females were given new partners for each breeding episode and were allowed to raise a brood for 2 weeks. In between each reproductive episode, males and females were kept in holding tanks for approximately 2 weeks. They were never video-taped or introduced to a model predator before their fourth brood. Individuals in the inexperienced group were kept in holding tanks until the experiment began; they had never raised a brood. Every time individuals from the experienced group were netted, inexperienced individuals were chased around their holding tank with a net.

After inexperienced and experienced pairs were weighed and measured, they were randomly assigned to either control or brood reduced groups. Within 12 h of spawning, pairs in the brood reduced groups had their clutch of eggs reduced by 50%. Eggs of control groups were removed for the same amount of time (approx. 2 min). All egg clutches were photographed.

### Parental behaviour

Behaviour of both males and females was videotaped twice during both the embryonic (egg, wriggler) and larval periods (day 2, day 5) to determine the effects of breeding experience on parental care behaviour. I quantified the following behaviour patterns with an event recorder: percentage time spent away from brood (two body lengths), percentage time spent fanning, and the frequencies of mouthing, foraging, fin-digging, and retrieving larvae. Mouthing is considered an embryo cleaning behaviour (Keenleyside 1991); the parent nips at the embryo and thus removes debris. Fin-digging involves stirring the substrate by moving the pectoral fins forward while simultaneously beating the caudal fin; it is believed to provision the young with food. Retrieving larvae only occurs during the larval period; a parent picks up a stray larva with its mouth and returns it to the centre of the brood.

Each 10 min observation period was followed by a defense test. The test consisted of presenting a model predator for 2 min and video-taping the behaviour of the parents. The model was a preserved *Gobiomorus maculatus*, (12.6 cm in total length, see Helfman 1983 for preparation) and had never been encountered by the parents in this study. The model was suspended by a steel rod attached to a piece of wood that rested on top of the aquarium; it was presented 10 cm from the brood. I quantified biting, frontal displaying, headshaking, percentage time spent away from the brood and model (two body lengths), and the latency till an aggressive act toward the model predator was exhibited (see Lavery and Colgan 1991 for descriptions).

After the final defence test, the fry were counted and the parents were weighed.

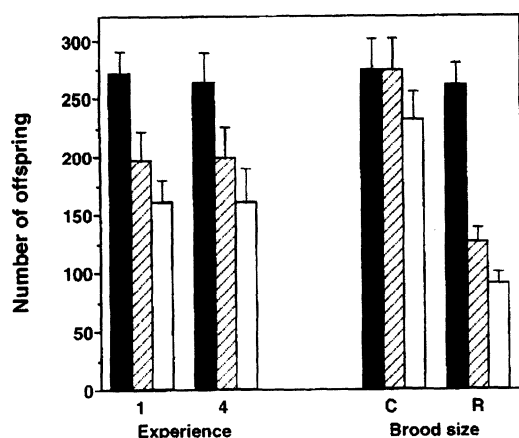
### Data analysis

If the data did not meet the assumptions of the parametric tests, the data was  $\ln(x + 1)$  transformed. Within each developmental period (embryonic, larval) the data were averaged. Two-way ANOVAs with two repeated measures (sex, brood period) were used to analyse the data. The main factors were experience and brood size. The parental weight data were analysed with ANCOVAs with pre-weight (weight before the fish were put in the breeding tanks) as the covariate. Because male fanning and mouthing embryos were infrequent, I analysed the sexes separately for these two behaviour patterns. Furthermore, brood period was eliminated as a factor from the statistical model for behaviour patterns that occurred during only one developmental brood period (i.e. fan, mouth and retrieve larva).

## Results

### Brood size

Before the broods were reduced, there was no difference in clutch size among groups (two-way ANOVA, experienced vs inexperienced  $F=0.07$ ,  $P=0.788$ ; control vs. brood reduced:  $F=0.14$ ,  $P=0.707$ , Fig. 1). After the broods were reduced in size, there was no difference in clutch size between experienced and inexperienced



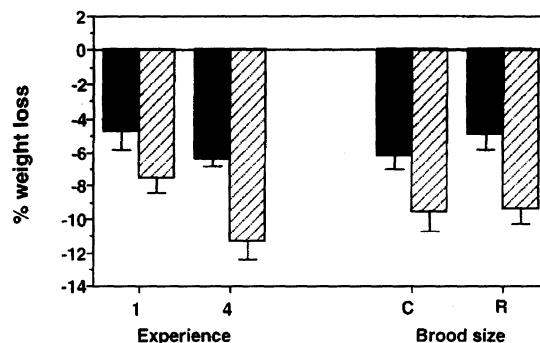
**Fig. 1** Mean ( $\pm$ SE) number of young by experimental group. *Black bars* mean ( $\pm$ SE) number of eggs after spawning, *hatched bars* mean ( $\pm$ SE) number of eggs after the spawning were experimentally reduced, *open bars* mean ( $\pm$ SE) number of fry at the end of the experiment; experience: 1 inexperienced breeders on first breeding attempt, 4 experienced breeders on fourth attempt; brood size C control group, R=brood reduced group. In each column  $n=20$  because I used a  $2 \times 2$  ANOVA to analyze the data. The data from the control and reduced groups are combined in each of the 1 and 4 columns. Likewise, the data from the inexperienced and experienced groups are combined in each of the control and brood reduced groups

groups ( $F=0.01$ ,  $P=0.935$ ); however, pairs which had their broods reduced had significantly smaller clutches than control pairs ( $F=29.93$ ,  $P<0.001$ , Fig. 1). From the beginning of the experiment to the end, all groups lost young ( $F=13.40$ ,  $P=0.001$ ) at the same rate (experience  $\times$  brood loss:  $F=0.01$ ,  $P=0.934$ ; brood size  $\times$  brood loss:  $F=0.04$ ,  $P=0.847$ , Fig. 1).

### Parental weights

At the start of the experiment, inexperienced females were heavier than experienced females ( $x \pm \text{SE}$ :  $8.1 \pm 0.4$  g,  $7.0 \pm 0.4$  g, respectively;  $F=4.15$ ,  $P=0.049$ ). Experience had the same effects on male weight (inexperienced,  $14.0 \pm 0.6$  g; experienced,  $11.8 \pm 0.5$  g;  $F=7.72$ ,  $P=0.009$ ). At test time, inexperienced fish were larger than experienced fish in the holding tanks, suggesting that reproduction affects somatic growth in an indeterminate grower. Control pairs and pairs with reduced broods did not differ (females:  $F=0.20$ ,  $P=0.657$ ; males:  $F=2.26$ ,  $P=0.142$ ).

A comparison of adult weight before and after the experiment revealed that all groups lost weight (repeated measure ANOVA,  $F=197.96$ ,  $P<0.001$ , Fig. 2). However, females with past breeding experience lost a greater proportion of their body weight than inexperienced females ( $F=7.90$ ,  $P=0.008$ , Fig. 2), while experienced and inexperienced males did not differ ( $F=1.77$ ,  $P=0.191$ ). Brood size had no significant effects on adult weight loss (females:  $F=0.021$ ,  $P=0.886$ ; males:  $F=1.11$ ,  $P=0.298$ , Fig. 2).



**Fig. 2** Mean ( $\pm$ SE) percent weight loss of males (*black bars*) and females (*hatched bars*) by experimental group;  $n=20$  in each column. (Experience: 1 inexperienced breeders on first breeding attempt, 4 experienced breeders on fourth attempt; brood size: C control group, R=brood reduced group)

### Defensive behaviour: group effects

Only past breeding experience had significant effects on defensive behaviour ( $P$  values for brood size effects were all greater than 0.410). Experienced pairs bit ( $F=11.22$ ,  $P=0.002$ , Fig. 3a), displayed ( $F=28.37$ ,  $P<0.001$ , Fig. 3b) and headshook ( $F=9.42$ ,  $P=0.004$ , Fig. 3c) more at the model predator than inexperienced pairs. Experienced pairs also spent less time away from the brood and predator ( $F=15.61$ ,  $P<0.001$ , Fig. 4a) and took less time to display at the model ( $F=18.60$ ,  $P<0.001$ , Fig. 4b) than inexperienced pairs.

### Sex differences

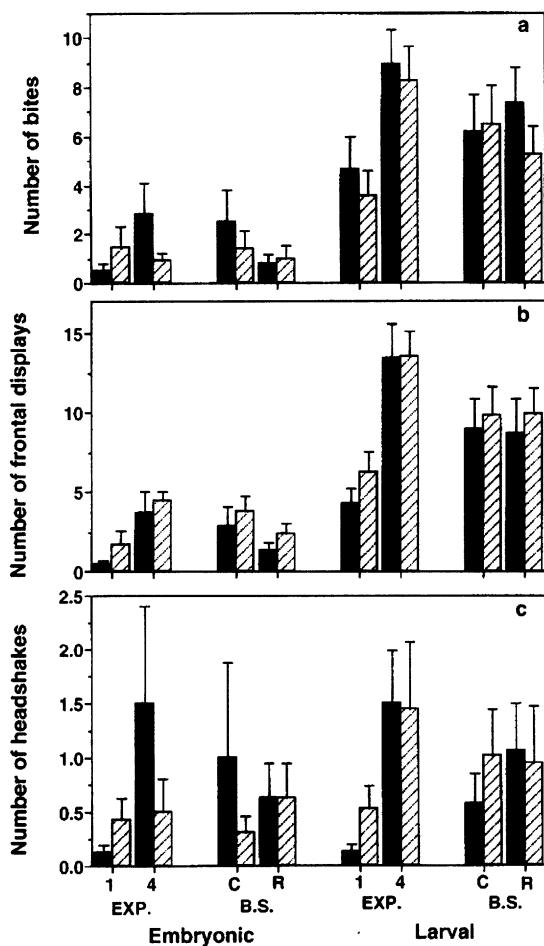
Across all groups, females were more committed to the brood than males; they performed more frontal displays (repeated measures ANOVA,  $F=5.05$ ,  $P=0.031$ ), spent less time away from the predator ( $F=47.40$ ,  $P<0.001$ ) and took less time to confront the predator ( $F=5.96$ ,  $P=0.020$ ) than males (Figs. 3 and 4).

### Brood period effects

Except for the number of headshakes, brood defense increased with offspring age in all groups. During the larval period, males and females bit (repeated measures ANOVA,  $F=101.25$ ,  $P<0.001$ ), displayed ( $F=106.40$ ,  $P<0.001$ ), spent less time away ( $F=70.03$ ,  $P<0.001$ ), and took less time to confront the predator ( $F=78.22$ ,  $P<0.001$ ) than during the embryonic period (Figs. 3 and 4).

### Direct parental care: group effects

Experienced males spent more time fanning embryos than inexperienced males ( $F=4.01$ ,  $P=0.053$ , Fig. 5a). Males with reduced broods did not differ in fanning behaviour from control males ( $F=0.04$ ,  $P=0.953$ ). There were no group differences in the frequency of

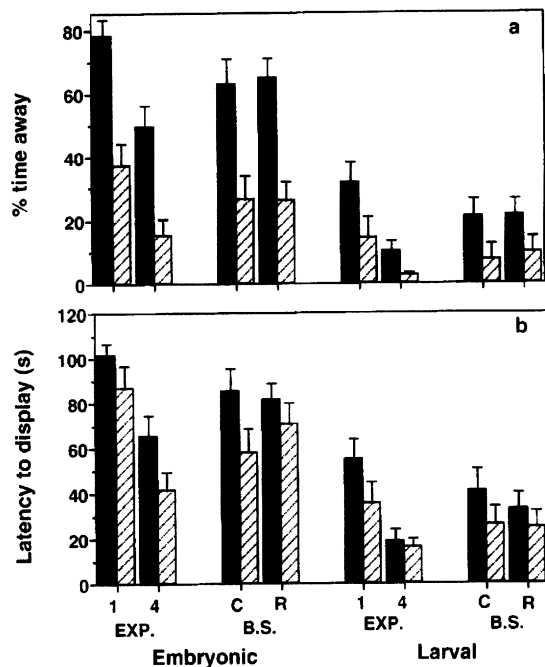


**Fig. 3** Mean ( $\pm$ SE) number of **a** bites, **b** frontal displays and **c** headshakes by males (black bars) and females (hatched bars) for each experimental group during both the embryonic and larval periods ( $n=20$  in each column). [Experience (Exp.): 1 inexperienced breeders on first breeding attempt, 4 experienced breeders on fourth attempt; brood size (B.S.): C control group, R brood reduced group]

mouthed embryos (experience:  $F=1.30$ ,  $0.262$ ; brood size:  $F=0.58$ ,  $P=0.453$ , Fig. 5b).

Experienced females did not differ from inexperienced females in the time spent fanning ( $F=0.931$ ,  $P=0.341$ , Fig. 6.5a) and in the frequency of mouthing embryos ( $F=1.41$ ,  $P=0.242$ , Fig. 5b). However, females with reduced broods spent less time fanning ( $F=8.92$ ,  $P=0.005$ , Fig. 5a) and mouthed embryos ( $F=8.84$ ,  $P=0.005$ , Fig. 5b) more than control females.

Experienced males and females did not differ from inexperienced pairs in the time spent away from the brood ( $F=2.97$ ,  $P=0.093$ , Fig. 5c), the frequency of foraging ( $F=0.31$ ,  $P=0.580$ , Fig. 6a) and in the frequency of retrieving larvae ( $F=1.32$ ,  $P=0.258$ , Fig. 6c). However, experienced pairs fin-dug more than inexperienced pairs ( $F=5.12$ ,  $P=0.030$ ); Fig. 6b reveals that the effect is largely due to differences in male behaviour.



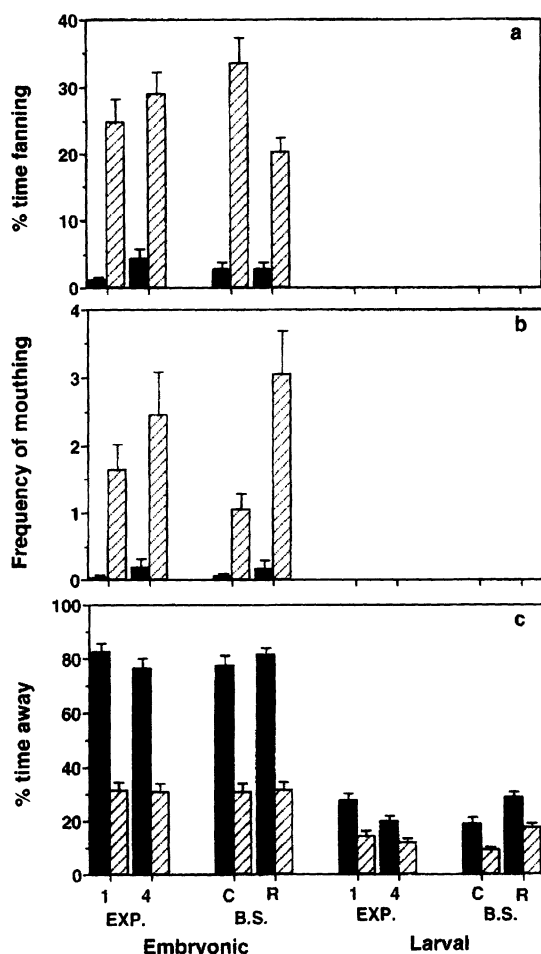
**Fig. 4** Mean ( $\pm$ SE) **a** percent time spent away from brood and predator and **b** latency till display (s) at the predator by males (black bars) and females (hatched bars) for each experimental group during both the embryonic and larval periods ( $n=20$  in each column). [Experience (Exp.): 1 inexperienced breeders on first breeding attempt, 4 experienced breeders on fourth attempt; brood size (B.S.): C control group, R brood reduced group]

Brood reduction had only one significant effect on parental behaviour; during the larval period males and females with reduced broods spent more time away from the brood than control pairs (brood period  $\times$  brood size:  $F=9.69$ ,  $P=0.004$ , Fig. 5c).

#### Brood period and sex effects

During the larval period, males and females spent less time away from the brood ( $F=130.10$ ,  $P<0.001$ , Fig. 5c), foraged more ( $F=16.32$ ,  $P<0.001$ , Fig. 6a) and fin-dug more ( $F=19.83$ ,  $P<0.001$ , Fig. 6b) than during the embryonic period. During the larval period, pairs also began to retrieve larvae; however there were no group differences (brood size and experience) in the frequency of this behaviour pattern (Fig. 6c). Females retrieved more young than males ( $F=58.54$ ,  $P<0.001$ ).

There was a significant sex and brood period interaction for the frequency of foraging ( $F=8.25$ ,  $P=0.007$ ) and fin-digging ( $12.80$ ,  $P=0.001$ ), indicating that only during the larval period were females foraging and fin-digging more than males (Fig. 6). Also for the time spent away from the brood ( $F=6.87$ ,  $P=0.013$ ), there was a significant sex and brood period interaction; compared to females, males spent considerably less time away during the larval period than they did during the embryonic period (Fig. 5c).

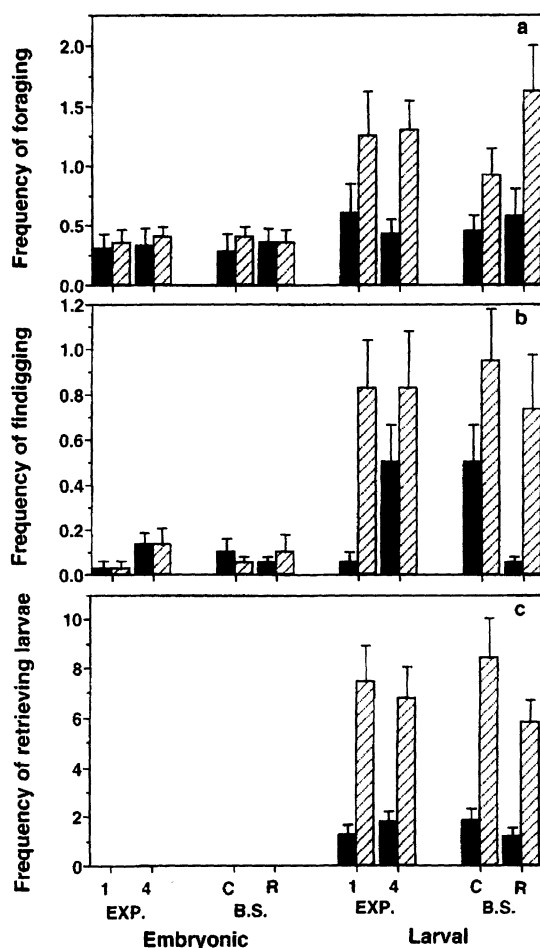


**Fig. 5** Mean ( $\pm$ SE) **a** percent time spent fanning, **b** mouthing frequency and **c** percent time spent away from brood by males (black bars) and females (hatched bars) for each experimental group during both the embryonic and larval periods ( $n=20$  in each column). [Experience (Exp.): 1 inexperienced breeders on first breeding attempt, 4 experienced breeders on fourth attempt; brood size (B.S.): C control group, R brood reduced group]

## Discussion

The results show that past effort affects expenditure in the current brood. Experienced parents performed more defensive behaviour toward a model predator than inexperienced parents during both the embryonic and larval periods. If past effort reduces a parent's capacity for further expenditure, experienced convict cichlids have more to lose if the brood fails and consequently are increasing their expenditure in the current brood. Within breeding episodes, animals have been shown to adjust care to past investment. For instance, Coleman et al. (1985) have shown that bluegill sunfish adjust current care to both brood size and past investment (also see Weatherhead 1979, 1982; Lavery and Keenleyside 1990a).

Besides group differences in male fin-digging and fanning rates, I found no major effects of breeding experience on depreciable care, suggesting that experience



**Fig. 6** Mean ( $\pm$ SE) **a** foraging, **b** fin-digging and **c** retrieving larvae frequency by males (black bars) and females (hatched bars) for each experimental group during both the embryonic and larval periods ( $n=20$  in each column). [Experience (Exp.): 1 inexperienced breeders on first breeding attempt; 4 experienced breeders on fourth attempt; brood size (B.S.): C control group, R brood reduced group]

does not have any major effects on brood maintenance activities in this species (see also Colgan and Salmon 1986; Reeb and Colgan 1991). With that in mind, it is unlikely that past investment within the breeding episode differed substantially between groups to account for the results. Furthermore, it has been suggested that parental care is less costly to old parents with experience because they may be more competent and efficient than young parents (Sargent and Gross 1986; Clutton-Brock 1991). Because foraging frequency did not differ between groups, and inexperienced parents were actually larger than experienced parents, it is doubtful that experienced parents performed more defensive behaviour due to a greater resource budget size. Furthermore, none of the individuals had seen the model predator before; therefore, it is unlikely that the results are due to differences in experience with predators.

Contrary to previous studies (see Montgomerie and Weatherhead 1988; Clutton-Brock 1991), brood size had little effect on defensive behaviour. Lavery and Keenleyside (1990a) have shown that convict cichlid parents with larger broods were more aggressive than parents with reduced broods (see also Carlisle 1985). However all these parents were inexperienced breeders and approximately a year younger than parents used in this study. The difference between the studies could be due to the age of parents; older parents regardless of experience may expend more energy in the current brood because the prospects for future broods may be reduced (Pugesek 1981, 1983; Thornhill 1989; Trumbo 1991). Alternatively, the discrepancy between studies may be due to differences in brood size. In this study, parents had larger brood sizes; therefore, brood reductions were less dramatic in terms of the absolute number of young remaining. After the brood reductions, parents still had over 125 offspring (Fig. 1). It is not known whether cichlid parents assess the absolute number of offspring or the relative number for their given body size.

Both experienced and inexperienced pairs increased defensive behaviour and brood care (i.e. fin-digging, time with brood) with brood age. The increase in defensive behaviour with brood age is not due to parents becoming more confident towards the model predator (revisitation hypothesis), as Lavery and Colgan (1991) controlled for repeated model presentations, and found that convict defensive behaviour still increased with brood age regardless of the amount of past experience with a model predator.

It is interesting that past effort had the same effects on both sexes; both males and females increased care with breeding experience. However, males invested considerably less than females in this study. They performed less depreciable care (i.e. fanning) and took longer to confront the model predator than females. Males also performed less frontal displays and spent less time attacking than females (Figs. 3 and 4). It is not surprising that females lost proportionally more weight than males, especially in the experienced group (Fig. 2). In the wild, males can breed up to four times in a season while females rarely breed twice (Wisenden 1993); therefore, the current brood is relatively more valuable to females than males.

In conclusion, I have shown that past effort affects parental care in both male and female convict cichlids. The results are not due to differences in parental age, resource budget size, predator encounter rates, and brood characteristics (size and age). Because this is a laboratory study, I was not able to determine if the differences in parental behaviour translate into differences in reproductive success. However, there are many field studies on the effects of parental age, with past effort as a confounding variable, that show that older parents are reproductively more successful than

younger parents. The results of these studies indicate that young parents are often constrained by environmental factors and maybe less competent than old parents. If the important variables can be controlled, it is possible that young animals may also show reproductive restraint.

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## References

- Boucher DH (1977) On wasting parental investment. *Am Nat* 111: 786–788
- Carlisle TR (1985) Parental response to brood size in a cichlid fish. *Anim Behav* 33: 234–238
- Clutton-Brock TH (1991) The evolution of parental care. Princeton University Press, Princeton
- Coleman RM, Gross MR, Sargent RC (1985) Parental investment decision rules: a test in the bluegill sunfish. *Behav Ecol Sociobiol* 18: 59–66
- Colgan PW, Salmon AB (1986) Breeding experience and parental behaviour in convict cichlids. *Behav Processes* 13: 101–118
- Crawford RD (1977) The breeding biology of year-old and older female red-winged and yellow-headed blackbirds. *Wilson Bull* 89: 73–80
- Dawkins R, Carlisle TR (1976) Parental investment, mate desertion and a fallacy. *Nature* 262: 131–133
- Dawkins R, Brockmann HJ (1980) Do digger wasps commit the Concorde fallacy? *Anim Behav* 28: 892–896
- Finney G, Cooke F (1978) Reproductive habits in the snow goose: the influence of female age. *Condor* 80: 147–158
- Helfman GS (1983) Resin-coated fishes: a simple model technique for in situ studies of fish behaviour. *Copeia* 1983: 547–549
- Keenleyside MHA (1991) Parental care. In: Keenleyside MHA (ed) *Cichlid fishes: behaviour, ecology and evolution*. Chapman and Hall, London, pp 191–208
- Keenleyside MHA, Baily RC, Young VH (1990) Variation in the mating system and associated parental behaviour of captive and free-living *Cichlasoma nigrofasciatum* (Pisces, Cichlidae). *Behaviour* 112: 202–221
- Lavery RJ, Colgan PW (1991) Brood age and parental defence in the convict cichlid, *Cichlasoma nigrofasciatum* (Pisces: Cichlidae). *Anim Behav* 41: 945–951
- Lavery RJ, Keenleyside MHA (1990a) Parental investment of a biparental cichlid fish, *Cichlasoma nigrofasciatum*, in relation to brood size and past investment. *Anim Behav* 40: 1128–1137
- Lavery RJ, Keenleyside MHA (1990b) Filial cannibalism in the biparental fish *Cichlasoma nigrofasciatum* (Pisces: Cichlidae) in response to early brood reductions. *Ethology* 86: 326–338
- Middleton ALA (1979) Influence of age and habitat on reproduction by the American goldfinch. *Ecology* 60: 418–432
- Montgomerie RD, Weatherhead PJ (1988) Risks and rewards of nest defence by parent birds. *Q Rev Biol* 63: 167–187
- Nur N (1984) Increased reproductive success with age in the California gull: due to increased effort or improvement of skill? *Oikos* 43: 407–408
- Pianka ER (1983) *Evolutionary ecology*. Harper and Row, New York
- Pianka ER, Parker WS (1975) Age-specific reproductive tactics. *Am Nat* 109: 456–464

- Pugesek BH (1981) Increased reproductive effort with age in the California gull (*Larus californicus*) Science 212 : 822–823
- Pugesek BH (1983) The relationship between parental age and reproductive effort in the California gull (*Larus californicus*). Behav Ecol Sociobiol 13 : 161–171
- 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
- Sargent RC, Gross MR (1986) William's principle: an explanation of parental care in teleost fishes. In: Pitcher TJ (ed) The behaviour of teleost fishes. Johns Hopkins University Press, Baltimore, pp 275–293
- Stutchbury BJ, Robertson RJ (1988) Within-season and age-related patterns of reproductive performance in female tree swallows (*Tachycineta bicolor*). Can J Zool 66 : 827–834
- Thornhill R (1989) Nest defense by red jungle fowl (*Gallus gallus spadiceus*) hens: the roles of renesting potential, parental experience and brood reproductive value. Ethology 83 : 31–42
- Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual selection and the descent of man 1871–1971. Aldine, Chicago, pp 136–179
- Trumbo ST (1991) Reproductive benefits and the duration of paternal care in a biparental burying beetle, *Necrophorus orbicollis*. Behaviour 117 : 82–105
- Weatherhead PJ (1979) Do savannah sparrows commit the Concorde fallacy? Behav Ecol Sociobiol 5 : 373–381
- Weatherhead PJ (1982) Risk-taking by red-winged blackbirds and the Concorde fallacy. Z Tierpsychol 60 : 199–208
- Williams GC (1966) Natural selection, cost of reproduction and a refinement of Lack's principle. Am Nat 100: 687–690
- Wisenden BD (1993) The reproductive ecology of convict cichlids in Costa Rica. Ph.D. thesis. University of Western Ontario, London, Canada