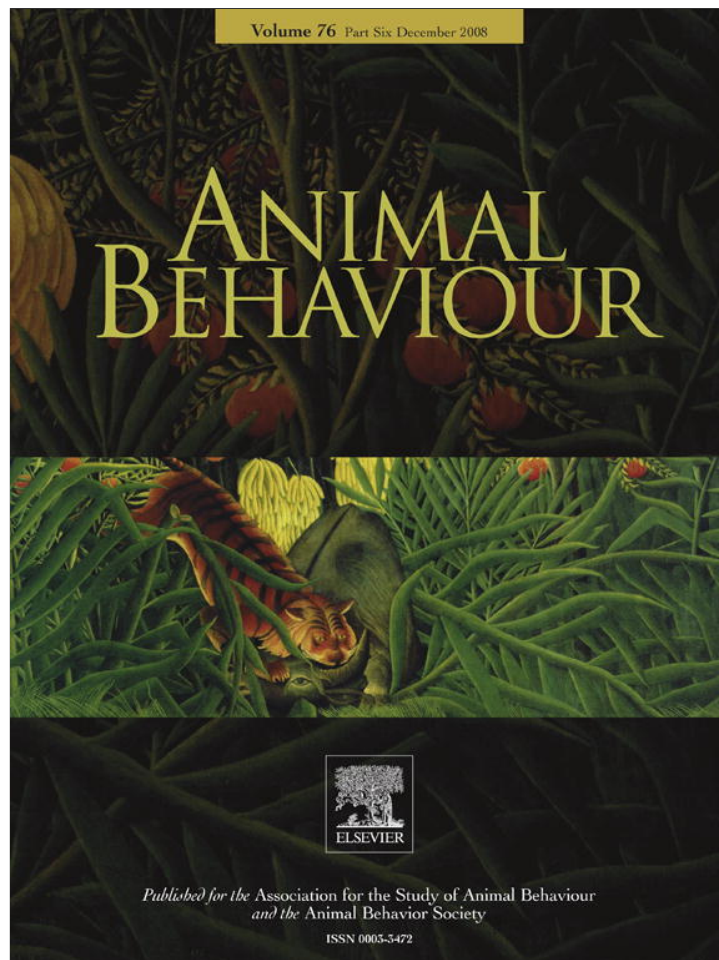


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Parental defence of an empty nest after catastrophic brood loss

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We studied parental care behaviour in a field population of convict cichlids, *Amatitlania siquia*, a fish with biparental care of its free-swimming young (fry). We simulated catastrophic brood loss by removing all of the young from 26 broods of various ages. We recorded parental defence behaviour for 5 min prerule and three consecutive 5 min postremoval intervals. We then returned all of the young and recorded 5 min of parent–offspring reunion behaviour. Following brood loss, both parents defended the empty territory and searched for missing young. Females spent more time in the empty territory and performed more attacks in defence of the empty territory than did males. Females searched and defended a significantly larger area than males did. During the 15 min fry-absent period, males increasingly spent more time away, whereas females maintained a constant level of investment in searching the brood area. Four of 26 males (15%) engaged in courtship with a new female within 15 min of brood loss. Attacks to repel potential predators from the brood area declined in frequency over the 15 min fry-absent period in both sexes. Standard length (age) of young was positively correlated with parental investment for females but not males. Number of young was positively correlated with parental investment for males but not for females. We conclude that post-brood-loss behaviours are search and recovery tactics that contribute to parental inclusive fitness in the event of incomplete brood predation.

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Keywords: *Amatitlania siquia*; brood defence; brood loss; brood value; convict cichlid; parental care; sex difference; territoriality

The economy of reproduction dictates that limiting resources such as energy, time, and mating opportunity invested in current reproduction are not available for future reproductive efforts (Williams 1966; Trivers 1972). In general, these predictions are based on one common argument. That is, when expected reproductive success from the current reproductive effort is high relative to expected future reproductive success, parental investment in current reproduction should increase to best capitalize on favorable reproductive potential. Conversely, when expected reproductive success from the current

reproductive effort is low relative to expected future reproductive success, parental investment should decrease so that finite resources can be better invested in future effort.

Fishes lend themselves well to the study of parental care because costs are simple to quantify (Sargent & Gross 1993). Generally, fish do not thermally incubate their young or lactate or provide their developing young with prey. The main form of parental investment in fishes is fanning of eggs and defence of young from brood predators (Sargent & Gross 1993). In contrast to other vertebrates, brood defence in fishes does not incur a substantial risk of predation. Because adult fish are hundreds to thousands of times the mass of their offspring, brood predators are generally smaller than guardian parents (McKaye 1981).

Convict cichlids, *Amatitlania siquia* (Schmitter-Soto 2007; in recent years, also known as *Archocentrus nigrofasciatus*, *Cryptoheros nigrofasciatus* and *Cichlasoma*

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nigrofasciatum, among others) are small freshwater fishes native to Central America (Bussing 1998). In Costa Rican streams, females typically breed only once per season, whereas males can breed up to four times, with a new female each time (Wisenden 1995). These fish form monogamous pair bonds and jointly excavate a lair from under a large stone or other solid object on the substratum. The female does much of the directed care during early development while the male peruses the territorial perimeter repelling intruders (Wisenden 1995). The eggs hatch into free-embryos (eleutheroembryos) with a large yolk sac and poorly developed fins. Free-embryos soon develop into free-swimming larvae that feed exogenously and form a shoal guarded by both parents for 4–6 weeks. By the end of the 6-week free-swimming period under parental care, the young have metamorphosed into juveniles ready for life independent of their parents. We use the vernacular term 'fry' as a collective moniker to refer to young under parental care, whether embryonic, larval or juvenile, because it is convenient to do so and because ontogeny is not the focus of this study (for formal definitions and terminology of ontogenetic stages see Balon 1999).

In Costa Rican streams, an average \pm SE of 67 ± 3.1 (max. = 136, $N = 123$ broods) free-swimming young emerge from the lair at 4.5–5 mm standard length (SL) and attain independence from parental care when they reach 10–12 mm SL (Wisenden 1994a, unpublished data). Families form a mobile territory defended by both parents. Parents and young move slowly along the bottom while the young pick at food items on the substratum. Brood success (defined as having at least one offspring reach independence from parental care) varies by habitat and has been estimated from 15% to 48% in Costa Rican streams (Wisenden 1994a,b) and 20% in Laguna Xiloá, Nicaragua (McKaye 1977; Alonzo et al. 2001). Brood loss occurs by means of one of two processes. The first process is brood predation by attrition, whereby the number of young is reduced gradually over time by numerous individual attacks by brood predators (Wisenden 1994a). The second process is absolute predation during a single catastrophic event, whereby the brood is decimated when parental defences are overwhelmed by brood predators (Meral 1973; Alonzo et al. 2001; Wisenden 1994a). Predator 'avalanches' (Meral 1973) result in consumption of some young and dispersal of other young from the brood area.

The current study stems from observations of a natural event of catastrophic predation and brood recovery in the Río Cabuyo, Costa Rica, on 27 March 1993 (control pair no. 36: Wisenden & Keenleyside 1995). The number of young in the brood was 51 in the early morning. In passing that same section of stream a while later (11 45 hours), we casually noticed that there was only one fry. Both parents actively guarded the brood area as if the entire brood was still intact. We revisited the brood periodically during the day to monitor its fate. There were three fry at 12 45 hours, six fry at 15 00 hours and seven fry at 15 50 hours. On 1 April, the brood contained 37 young. These observations led to our hypothesis that postpredation defence and searching an area that contains no

offspring may be a regular part of the reproductive ecology of this species. Postpredation parental care should be affected by the same factors that determine brood value; that is, offspring number, offspring age and sex differences in trade-offs between current and future reproductive success (Williams 1966; Trivers 1972; Sargent & Gross 1993). To test these ideas, we experimentally removed entire broods to quantify postpredation responses of parents. Specifically, we predicted that (1) searching behaviour and area defence would correlate positively with the number of young in the brood because large numbers of young represent high potential reproductive success relative to expected future reproductive success, (2) searching behaviour and area defence would correlate positively with brood age because larger (older) offspring have a greater probability of reaching independence than smaller (younger) offspring and represent greater potential for reproductive success from the current brood relative to expected future reproductive success, and (3) females would search with greater intensity and for greater duration than males because females have lower future reproductive potential than males.

METHODS

Convict cichlids are locally abundant in the Río Cabuyo, a small stream located in Lomas Barbudal Biological Reserve, Guanacaste, Costa Rica ($10^{\circ}30'21.62''N$, $85^{\circ}22'14.71''W$). During the dry season (December to May) the Río Cabuyo is fed by ground water creating conditions of high water clarity and stable flow. Physicochemical descriptors of the Río Cabuyo are described in Wisenden & Keenleyside (1994). We surveyed the Río Cabuyo in January 2008 to locate 26 broods in a range of stages of fry development. We systematically moved from downstream to upstream in our survey to ensure that we did not sample any brood more than once. We observed each brood against landmark objects on the substrate for a few minutes from a distance of 1–2 m. We then measured the diameter and brood depth with a tape measure. We recorded parental care behaviour for 5 min as a baseline measurement of parental investment (pre-brood-removal period). We recorded time away from the brood (more than three body lengths away), the number of attacks against territorial intruders and the frequency of feeding bites within the observable area. Two observers each recorded behaviours of one of the parents so that all behavioural recordings represent simultaneous behavioural sampling of male–female pairs. We then removed all of the young with the aid of mask, snorkel and hand nets. This was followed immediately by three 5 min focal follows of both parents simultaneously (by the same two observers), representing 0–5, 5–10 and 10–15 min post-brood-removal periods. During this time, a third researcher counted the number of young and measured the standard length (SL, rostrum to posterior limit of the caudal peduncle) of 10 arbitrarily chosen fry. At the end of the 15 min postremoval period, we returned all of the young to the parents using a clear plastic cylinder (ca. 11 cm diameter, 25 cm long). The cylinder was placed vertically on the substrate at the location on

the stream bottom whence the young had been taken. Young released into the open top of the cylinder settled quickly to the substratum. Once visual contact between young and parents was established (usually within 10 s), the cylinder was removed by lifting it vertically off the bottom, which allowed parents and young to be reunited. As soon as the family was reunited, we resumed recording parental care for a final 5 min period (postreunion period). When behavioural recording was complete, we measured the area actively defended by each sex during the 15 min postremoval period by measuring the distance between landmarks on the substratum.

We performed 2 × 5 factorial repeated measures ANOVAs to compare the effect of sex across the five observation periods on each behavioural variable of Time Away, Attack Frequency and Feeding Frequency (*N* = 17). For closer analysis, we performed 2 × 3 factorial repeated measures ANOVAs examining only the three observation periods of the fry-absent interval for which sample sizes were larger (*N* = 26). Areas defended were compared between sexes and times with paired *t* tests. Additional regression analyses were performed for sex–time subsets of data.

RESULTS

Effect of Number of Young and Fry Length

Both parents continued to defend their territory after complete brood loss, although females defended more than males (25 of 26 females versus only 10 of 26 males defended the area; Fisher's exact test: *P* < 0.001). Areas defended by males during the 15 min fry-absent period were for broods that had had significantly more fry (85.2 ± 12.1 , *N* = 10 versus 42.2 ± 4.4 , *N* = 16; $t_{24} = 3.92$, *P* < 0.001) but mean fry standard length had no effect (6.47 ± 0.6 mm, *N* = 10, versus 7.17 ± 0.6 mm, *N* = 16; $t_{24} = 0.82$, *P* = 0.420; Fig. 1). Females abandoned only 1 of 16 broods (with 45 fry of 10.45 mm SL). The mean for the remaining 15 broods was 59.3 ± 7 fry of 6.8 ± 0.4 mm.

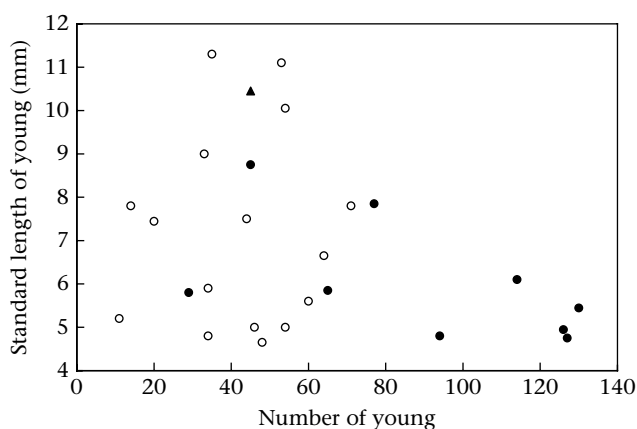


Figure 1. Number of young and fry standard length (mm) in broods for which the brood area was defended (solid symbols) and not defended (open circles) by the male during the 15 min postremoval period. Females defended the brood area for all removed broods except for the brood indicated by the triangular symbol.

Table 1. Statistical results for repeated measures 2 × 5 factorial ANOVA (2 sexes, 5 time periods) on three behaviours associated with defence of empty nests

	Effect	df	F	P
Time Away	Sex	1,14	20.577	<0.001
	Sex*Fry SL	1,14	8.082	0.013
	Sex*Fry No	1,14	13.610	0.002
	Time	4,56	0.300	0.877
	Time*Fry SL	4,56	1.833	0.126
	Time*Fry No	4,56	1.297	0.282
	Sex*time	4,56	0.517	0.723
Attacks	Sex	1,14	6.237	0.026
	Sex*Fry SL	1,14	1.519	0.238
	Sex*Fry No	1,14	1.156	0.300
	Time	4,56	0.652	0.628
	Time*Fry SL	4,56	0.283	0.888
	Time*Fry No	4,56	0.770	0.549
	Sex*time	4,56	1.812	0.139
Feeds	Sex	1,14	4.884	0.044
	Sex*Fry SL	1,14	10.793	0.005
	Sex*Fry No	1,14	1.311	0.271
	Time	4,56	1.895	0.124
	Time*Fry SL	4,56	2.269	0.073
	Time*Fry No	4,56	0.661	0.622
	Sex*time	4,56	1.240	0.319

Fry SL = fry standard length; Fry No = fry number. Significant Bonferroni-corrected *P* values (<0.025) are given in bold.

The initial area guarded by the intact pair was correlated with fry length ($F_{1,24} = 10.25$, *P* = 0.004) but not fry number ($F_{1,24} = 0.28$, *P* = 0.600). In the absence of fry, the area defended by females was not correlated with fry number ($F_{1,24} = 1.37$, *P* = 0.253) or fry length ($F_{1,24} = 0.15$,

Table 2. Statistical results for repeated measures 2 × 3 factorial ANOVA (2 sexes, 3 time periods) on three behaviours associated with defence of empty nests

	Effect	df	F	P
Time Away	Sex	1,23	6.129	0.021
	Sex*Fry SL	1,23	1.116	0.302
	Sex*Fry No	1,23	3.220	0.086
	Time	2,46	0.975	0.385
	Time*Fry SL	2,46	0.069	0.933
	Time*Fry No	2,46	0.218	0.805
	Sex*time	2,46	0.512	0.603
Attacks	Sex	1,23	5.827	0.024
	Sex*Fry SL	1,23	0.790	0.383
	Sex*Fry No	1,23	0.334	0.569
	Time	2,46	1.110	0.342
	Time*Fry SL	2,46	0.990	0.379
	Time*Fry No	2,46	1.787	0.179
	Sex*time	2,46	2.833	0.069
Feeds	Sex	1,23	1.591	0.220
	Sex*Fry SL	1,23	2.981	0.098
	Sex*Fry No	1,23	0.283	0.600
	Time	2,46	3.885	0.028
	Time*Fry SL	2,46	3.467	0.040
	Time*Fry No	2,46	0.581	0.564
	Sex*time	2,46	0.242	0.786

Fry SL = fry standard length; Fry No = fry number. Significant terms (*P* < 0.025) are given in bold.

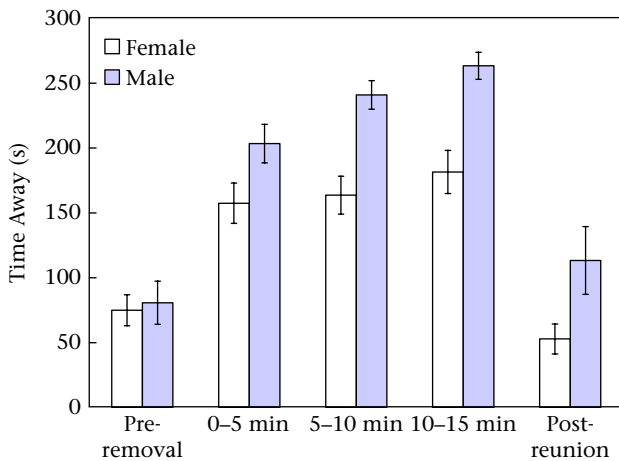


Figure 2. Mean \pm SE Time Away from the brood area for 5 min observation periods before brood removal, for three consecutive 5 min intervals after brood removal and for 5 min after brood recovery.

$P = 0.707$). Similarly, the area defended by males was not correlated with fry number ($F_{1,8} = 0.11$, $P = 0.750$) or fry length ($F_{1,8} = 1.54$, $P = 0.162$) in the absence of fry.

Effect of Sex

Males and females engaged in searching behaviours such as frequent pausing and close inspection of the substratum, particularly in areas of structural complexity (rock crevices, leaf litter, etc.) where fry might seek refuge. There was a significant effect of sex on Time Away and Attacks (Tables 1 and 2, Figs 2–4). Females spent more time with the brood and initiated more attacks than males did, especially during the 15 min period when fry were absent. During the 15 min fry-absent period, females searched a significantly larger area than males did (paired t test: $t_{24} = 3.20$, $P = 0.004$; Fig. 5). The actively defended area during the 15 min fry-absent period was significantly

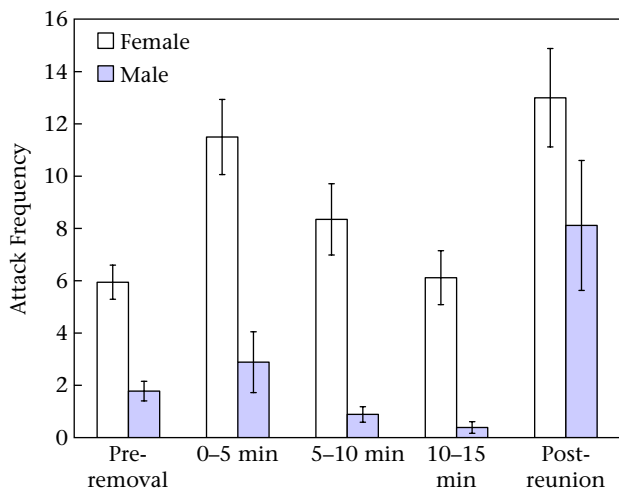


Figure 3. Mean \pm SE Attack Frequency in defence of the brood area for 5 min observation periods before brood removal, for three consecutive 5 min intervals after brood removal and for 5 min after brood recovery.

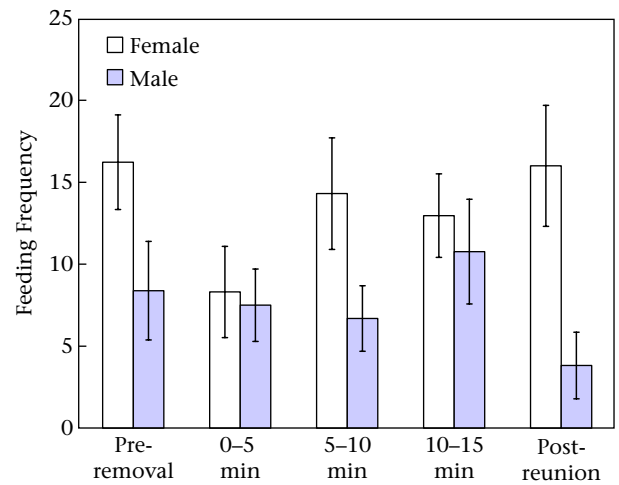


Figure 4. Mean \pm SE Feeding Frequency in view of the observer for 5 min observation periods before brood removal, for three consecutive 5 min intervals after brood removal and for 5 min after brood recovery.

larger than the area occupied by the brood during the pre-removal period for females (paired t test: $t_{25} = 4.72$, $P < 0.001$) but not for males ($t_{25} = 1.64$, $P = 0.114$). Four of 26 (15.4%) males engaged in courtship with a dark-phase female (i.e. nuptially coloured, indicating reproductive readiness; Wisenden 1995).

Complicating the interpretation of the effect of sex and brood age and size on post-brood-loss defence were significant interactions of sex*fry length, and sex*fry number on Time Away, and sex*fry length on Feeding Frequency (Table 1). When only the three fry-absent time periods were considered (for which larger sample sizes were available), these interactions disappeared (Table 2). More detailed regression analysis revealed the likely source of the significant interaction terms: brood age significantly influenced female behaviour, whereas fry number significantly influenced male behaviour (Table 3, Fig. 6). Males increased Time Away when fry number was small. Females tended to increase Time Away when fry length (age) was greater.

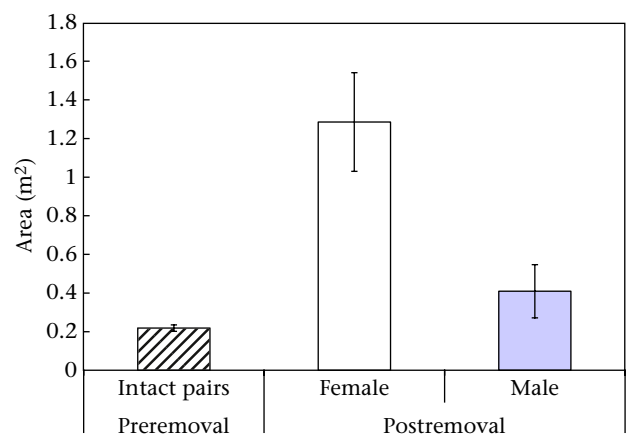


Figure 5. Mean \pm SE area of the brood for intact pairs (preremoval) and areas defended by females and males during the 15 min brood-removal period.

Table 3. Regressions of fry standard length (Fry SL) and fry number (Fry No) on the parental behaviours of Time Away, Attack Frequency and Feeding Frequency for each sex within each time interval

Dependent variable	Independent variable	Sex	Statistic	Preremoval	Observation period (5 min each)			Postreunion
					5 min	10 min	15 min	
Time Away	Fry SL	F	<i>F</i>	6.32	2.03	3.719	4.1	0.08
			<i>df</i>	1, 16	1, 24	1, 24	1, 24	1, 15
		<i>P</i>	0.023	0.167	<i>0.066</i>	<i>0.054</i>	0.783	
	M	<i>F</i>	0.08	3.54	1.58	2.56	0.1	
		<i>df</i>	1, 16	1, 24	1, 24	1, 24	1, 15	
		<i>P</i>	0.781	<i>0.075</i>	0.221	0.123	0.752	
Time Away	Fry No	F	<i>F</i>	2.45	0.17	0.49	2.32	0.66
			<i>df</i>	1, 16	1, 24	1, 24	1, 24	1, 15
		<i>P</i>	0.137	0.684	0.49	0.141	0.431	
	M	<i>F</i>	11.72	16.54	16.51	14.82	14.8	
		<i>df</i>	1, 16	1, 24	1, 24	1, 24	1, 15	
		<i>P</i>	0.003	<0.001	<0.001	<0.001	0.002	
Attack Frequency	Fry SL	F	<i>F</i>	0.02	2.24	0.03	2.3	0.97
			<i>df</i>	1, 16	1, 24	1, 24	1, 24	1, 15
		<i>P</i>	0.886	0.148	0.865	0.142	0.340	
	M	<i>F</i>	2.62	0.74	2.01	0.15	<0.01	
		<i>df</i>	1, 16	1, 24	1, 24	1, 24	1, 15	
		<i>P</i>	0.125	0.398	0.17	0.705	0.955	
Attack Frequency	Fry No	F	<i>F</i>	1.53	0.7	0.16	1.56	0.09
			<i>df</i>	1, 16	1, 24	1, 24	1, 24	1, 15
		<i>P</i>	0.233	0.41	0.696	0.223	0.768	
	M	<i>F</i>	0.01	7.39	15.11	1.59	2.59	
		<i>df</i>	1, 16	1, 24	1, 24	1, 24	1, 15	
		<i>P</i>	0.926	0.012	0.001	0.219	0.128	
Feeding Frequency	Fry SL	F	<i>F</i>	3.46	1.14	3.54	0.36	1.17
			<i>df</i>	1, 16	1, 24	1, 24	1, 24	1, 15
		<i>P</i>	<i>0.081</i>	0.297	<i>0.072</i>	0.549	0.296	
	M	<i>F</i>	<0.001	0.18	<0.001	1.47	0.66	
		<i>df</i>	1, 16	1, 24	1, 24	1, 24	1, 15	
		<i>P</i>	0.995	0.672	0.989	0.238	0.43	
Feeding Frequency	Fry No	F	<i>F</i>	7.92	0.81	1.72	2.01	0.14
			<i>df</i>	1, 16	1, 24	1, 24	1, 24	1, 15
		<i>P</i>	0.12	0.378	0.202	0.169	0.718	
	M	<i>F</i>	5.28	3.36	1.57	1.55	1.96	
		<i>df</i>	1, 16	1, 24	1, 24	1, 24	1, 15	
		<i>P</i>	<i>0.035</i>	<i>0.079</i>	0.221	0.226	0.182	

Significant Bonferroni-corrected *P* values (<0.025) are given in bold, trends (*P* < 0.10) are given in italics.

Pairwise comparisons between time periods showed that Time Away was greatest during the 15 min fry-absent period, whereas Attack rates were greatest just after the young were removed and just after the young had been returned (Figs 2 and 3, Table 4). When only the 15 min fry-absent period was considered, Time Away steadily increased and Attack rates steadily declined for each of the successive 5 min periods (Table 4). Feeding rates were consistent over the entire observation period.

DISCUSSION

When confronted with total brood loss, females and males continued to actively defend the empty territory for at least 15 min. Both sexes searched the immediate area

(examining crevices, peering under leaves) and repelled intruders. Females searched a larger area than males and they spent more time than males in the area formerly occupied by the brood. Females also performed more attacks in defence of the area than males did. Both sexes showed decreasing levels of investment over the three successive postremoval intervals. Males in particular were quick to decrease investment in area defence when the young were absent. These sex differences concur with previous studies in cichlids (e.g. Lavery & Keenleyside 1990; Jennions & Polakow 2001) and in biparental birds (e.g. Beissinger 1986; Winkler 1991).

Time Away from the brood area reflects two conflicting behavioural motivations: brood abandonment (low motivation) or brood searching (high motivation). When males were away from the brood area, they tended to

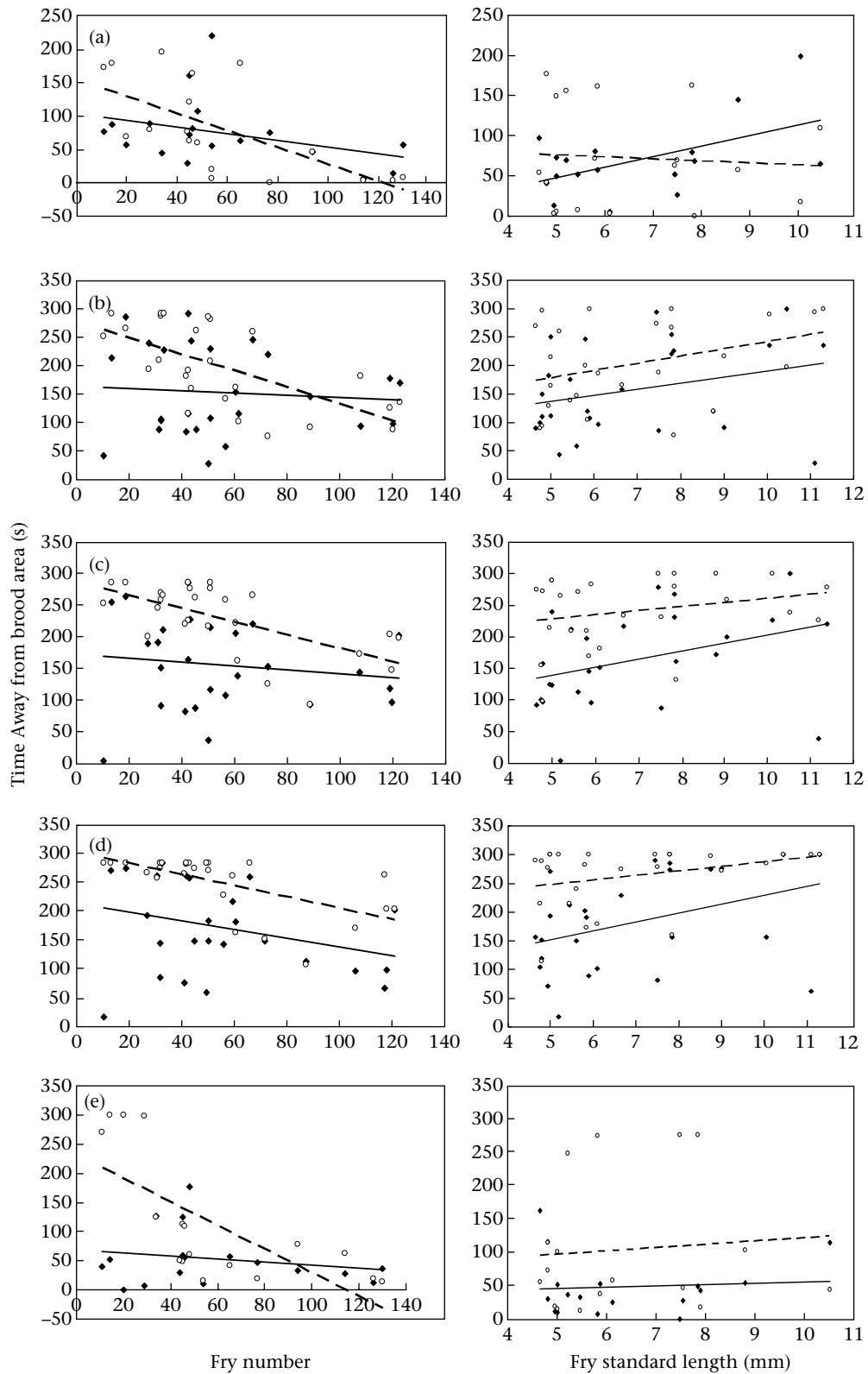


Figure 6. Effect of fry number and fry standard length on Time Away by parental female and male Convict Cichlids. Solid lines and filled symbols, females. Dashed lines and open symbols, males. (a) Preremoval, (b) 0–5 min postremoval, (c) 5–10 min postremoval, (d) 10–15 min postremoval and (e) postreunion.

Table 4. Bonferroni-corrected post hoc pairwise comparisons ($P < 0.025$) between time periods for repeated measures ANOVA comparing all five time periods (2×5 ANOVA) or only the three postremoval time periods (2×3 ANOVA)

Behaviour	2×5 ANOVA	2×3 ANOVA
Time Away	15 min > 10 min = 5 min > Postreunion = Preremoval	15 min > 10 min > 5 min
Attacks	Postreunion = 5 min > 10 min = 15 min = Preremoval	5 min > 10 min = 15 min
Feeds	No significant differences	No significant differences

Data from both sexes are combined in this analysis.

either forage or court new females. After the young were removed, 16 of the 26 (61.5%) males made no attempt to defend the brood area. When females were away, they defended a large area centred around the brood area. All but one female chased intruders from the area after the young were removed. These sex differences are consistent with theoretical predictions and empirical observations in a range of taxa. Males generally have a greater reproductive potential than females, and this is known to be the case for convict cichlids (Wisenden 1995). Males therefore pay a relatively high mating cost by remaining with a brood that is faring poorly or appears to be lost (Sargent & Gross 1993). Consequently, fry number is important in determining parental investment by males (Wisenden 1994b; Jennions & Polakow 2001) and this seems to extend to post-brood-loss parental investment. Pre-brood-loss fry number was not correlated with the level of parental investment by females, a result that concurs with the findings of Jennions & Polakow (2001) but not other studies (Carlisle 1985; Lavery & Keenleyside 1990).

Unlike fry number, fry length was important for parental investment by females in that females spent more time away for broods of large (older) fry than for broods with small (younger) fry. This might reflect that older young are better able to survive independently of parental protection as has been argued for mate desertion by males (Wisenden 1994b; Jennions & Polakow 2001). Fry standard length predicts the likelihood of gaining at least some reproductive success from the current brood, which is of greater value for females with relatively low future reproductive success. The reason for the lack of male response to fry standard length is not clear. Brood age is a significant predictor of male parental care in *A. coeruleopunctatus* (Jennions & Polakow 2001) and in an earlier study on male mate desertion in convict cichlids (Wisenden 1994b).

We observed 4 of 26 males courting dark-phase females within 15 min of brood removal. Dark colour phase is correlated with ovarian maturity (Wisenden 1995), female courtship (Wisenden 1995), female–female aggression in the laboratory (Beeching et al. 1998) and escalated female–female contests over male mates in the field (B. D. Wisenden, personal observation). Our observed rate of 15% of males engaging in extrapair courtship is remarkably similar to that reported for *A. coeruleopunctatus* in response to partial brood reduction (Jennions & Polakow 2001). In their field study, 9 of 45 males (20%) in experimentally reduced broods engaged in extrapair courtship.

This is the first report of parental defence of an empty nest in fish. Petyk (2004) described post-brood-loss parental care by a pair of golden-cheeked warblers, *Dendroica chrysoparia*, after a western scrub-jay, *Aphelocoma californica*, had eaten their nestlings (comprising one warbler and one brown-headed cowbird, *Molothrus ater*, nestling). Postpredation parental behaviours included calling and searching among tree branches in the vicinity of the nest. Parents continued to bring insect prey to the nest area for more than 4 h after the predation event and performed a distraction display to a jay 5 h after the nestlings had gone missing. The example of the golden-cheeked warbler behaviour is not exactly analogous to the current study because one unhatched egg remained in the nest during the 5 h period. Nevertheless, Petyk (2004) hypothesized that belated parental behaviours related to nestlings (delivery of insect prey) could result from parental inability to immediately extinguish parental behaviours in the absence of young, or, from an adaptive response to the possibility that recently fledged young may be in nearby branches. In our study, parental search behaviours were rewarded with full brood recovery within 15 min, after which both parents resumed normal parental care behaviour. If disappearance of the fry had been a result of real rather than simulated predation, area defence and searching behaviours would have been rewarded with fitness benefits and thus promote these behaviours by natural selection over generational time. The behaviours quantified in this study are similar to those that made repeated brood sampling possible in earlier studies of reproductive ecology in this system (Wisenden 1994a, 1995) and match anecdotal observations of a natural predation event observed in 1993.

In this study, fry number was reduced to zero and then returned to 100% of the original brood. Real predation events are likely to produce conditions of partial brood reduction and partial brood recovery. Parental care behaviours are influenced by the degree of brood reduction in cichlids (Carlisle 1985; Lavery & Keenleyside 1990; Jennions & Polakow 2001) other fishes (Pressley 1981; Coleman et al. 1985; Ridgway 1988, 1989; Lindström & Pampoulie 2005; Karino & Reiko 2006), and other vertebrates with parental care (Pöysä et al. 1997; Ackerman & Eadie 2003; Kosciuch et al. 2006). Further study is needed to explore the effect of the magnitude of brood reduction and the rate and magnitude of brood recovery on parental search and recovery behaviours.

A minimum of 29% of 292 broods sampled in the Río Cabuyo contained young from neighbouring families at some point during the period of parental care (Wisenden & Keenleyside 1992). The mechanism(s) by which

young become incorporated into foster care is not known. Ecological selection for brood-recovery behaviours in response to predation may have been a contributing factor to the evolution of brood adoption in this species. Young that become separated from their family by a catastrophic predation event could well find their way to neighbouring families by sight and subsequent olfactory imprinting (Wisenden & Dye, *in press*) or by active parental kidnapping (McKaye & McKaye 1977) selected for by the fitness benefits from alloparental care (Wisenden & Keenleyside 1994; Wisenden 1999). Further insights into the evolution of these behaviours are best acquired through field-based manipulation experiments on populations in the natural context in which these behaviours evolved.

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