



# Parental division of labour and the shift from minimal to maximal role specializations: an examination using a biparental fish

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In biparental species, parents often cooperate by emphasizing different parental roles. However, these parental sex differences often disappear when only one parent is present. For example, under natural conditions, the female convict cichlid fish, *Archocentrus nigrofasciatus*, typically remains with the offspring while the male spends most of his time patrolling the territory and chasing intruders. With the removal of the mate, either parent is capable of raising the offspring alone, and when doing so, they each perform all parental roles. We tested how the presence and absence of the mate and the presence and absence of an intruder influence parental sex-role specialization in *A. nigrofasciatus*. When presented with an intruder, widowed males left the offspring unattended more often and spent more time attacking the intruder compared with widowed females. For intact pairs, males showed a tendency to leave the offspring more than their mates but this sex difference was not significant. However, these paired individuals rarely left the offspring unattended. With an intruder present, paired males and females spent the least amount of time with the offspring (compared with widows and paired individuals without an intruder present), with males spending significantly more time with the intruder than females. Unlike pairs without an intruder, parents with an intruder changed roles only in support of the other parent. Thus, females rarely approached the intruder unless the male was also present and the male rarely approached the offspring without the female also being present. We speculated that the male's inability to remove the intruder caused females to support the male in attacking the intruder and the male returned to the offspring and joined the female during those periods when the intruder was least threatening.

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A hallmark of biparental care is the cooperation that two parents display when trying to raise the same offspring. While many studies concede its importance (e.g. both parents are required to provide sufficient food or protection; see review by Clutton-Brock 1991), few studies have examined this cooperation. In birds, where biparental care has received considerable attention, Gowaty (1996) observed that studies often ignore which parent does what in the nesting cycle. It is possible that the cooperation consists of each parent confining itself to its own sex-typical role. For example, Kendeigh (1952) suggested some degree of parental role specialization after observing females spending more time incubating eggs

and males emphasizing territory defence. Gowaty (1996) noted that although documentation is minimal, many investigators apparently accept that such sex differences occur throughout the parental stage. However, even with such sex differences in parental care, birds often raise their offspring when widowed, or when their mates reduce their participation in offspring care (e.g. see review by Sasvari 1986). These experiments suggest that the coordination of roles displayed in biparental birds is flexible and may depend on the presence and the behaviour of the other parent.

Perhaps similar to birds, a growing literature on several monogamous rodent species suggests that biparental behaviour also is coordinated such that one parent stays with the offspring if the mate is away foraging (e.g. Gubernick et al. 1993; Solomon 1993; Wang & Novak 1994; Wynne-Edwards 1995). This coordination serves to ensure that at least one parent remains with the pups and

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prevents them from suffering excessive heat loss, heat gain, or dehydration. Similarly, as in birds, there is evidence that parental role preferences or specializations disappear when one mate is removed. For example, in meadow voles, *Microtus pennsylvanicus*, single fathers perform the mothers' role of excluding unfamiliar males from the nest area (Storey et al. 1994) suggesting that these different sex-typical parental roles depend on the presence of the mate. In Djungarian hamsters, *Phodopus campbelli*, females are more likely to emphasize direct offspring care when their mates are present (Wynne-Edwards 1995). The most detailed studies on biparental care have been performed on humans and, here also, single human parents have been shown to be quite capable of performing many, if not all, of the necessary activities needed to raise their children, yet when paired, men and woman typically reflect the traditional parental roles (i.e. women tend to be more responsible for the care of the offspring than men; e.g. Jones & Heermann 1992; Hoffman & Kloska 1995). As for birds, the above studies also indicate that the expression of sex-typical cooperative parental behaviour appears dependent on the presence of the other parent.

Here, we examine the shift from minimal parental role specializations (as seen in single parents) to maximal specializations and cooperation (as seen in pairs) using the biparental convict cichlid fish, *Archocentrus nigrofasciatus*. In cichlid fish, where biparental care is common, field studies have revealed a coordination of parental activities, with females tending to remain with the offspring while males tend to defend the general area against intruders (e.g. Itzkowitz & Nyby 1982; Neil 1984; Wisenden 1994). Similar to studies on birds, experimental studies on biparental cichlids (Itzkowitz 1984; Lavery & Reebbs 1994) also revealed that widows do attempt to rear their offspring and that any tendency toward role specialization is dropped (Itzkowitz 1984; Lavery & Reebbs 1994). We considered two factors that we predicted would be influential: the presence or absence of the mate, and the presence or absence of an intruder. It seemed intuitively obvious that the presence of the other parent must be important because role specializations occur only when both parents are present. We considered the influence of intruders because biparental care in cichlids is thought to have evolved (along with the division of roles) to protect the offspring against intruders (e.g. Keenleyside & Mackereth 1992; Wisenden 1994).

Previous studies on biparental cichlids (Itzkowitz 1984; Lavery & Reebbs 1994) revealed that single male and single female parents behave similarly; both spend most of their time near the offspring. Given this similarity in offspring care by both single male and single female parents, we predicted that both sexes, when single, also would respond similarly to an intruder; that is, both would devote a similar amount of time to attacking the intruder. Alternatively, the single male and female may respond differently to the introduction of an intruder. In this case, we anticipated that each sex will revert to that pattern seen in pairs observed under natural conditions; that is, the male will emphasize defensive behaviour and

the female will spend more time with the offspring (Keenleyside et al. 1990; personal observations)

When both parents are present and in the absence of an intruder, both parents may stay with the offspring. In this case, paired parents would resemble single parents because each parent in a pair would be responding to the offspring and not to each other. Alternatively, with one parent staying near the offspring, the other parent may be free to patrol the territory in search of intruders or to forage. Although males in nature typically spend less time with the offspring, under these isolated conditions both parents may be more equitable in their offspring care.

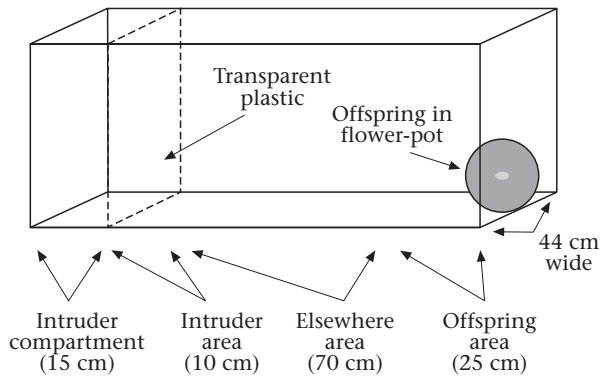
With the introduction of an intruder, we expected that role division would revert to that typically seen under natural conditions (personal observations) and laboratory conditions (e.g. Lavery & Keenleyside 1990). That is, the male will spend more time defending the area while the female spends more time with the offspring. Comparing the effect of intruders on pairs or single parents allowed us to determine the importance of the mate and the intruder on the division of roles. It is possible that both sexes develop their parental roles in response to the same stimuli. For example, if paired males and paired females spend the same amount of time near an intruder as single males and single females, we would conclude that the intruder, and not the presence of the mate, is responsible for the reduction in time both sexes spend near the offspring. Alternatively, if paired males and females spend more time with the intruder than single males and females, we would conclude that both the presence of the mate and the intruder have some type of additive or interactive effect. Other scenarios exist in which each sex responds differently to the presence of the mate and the intruder.

We also considered the effects of the mate on the defensive behaviour patterns used against an intruder. We predicted that the kinds of aggressive interactions used would depend on the presence of the mate. For example, threat behaviour in fish (e.g. lateral displays) is typically seen when size asymmetries are minimal; direct attacks (biting) increase when size asymmetries increase (e.g. Keeley & Grant 1993). When attacking a single intruder, a pair has a clear advantage and thus both parents should be less likely to threaten and more likely to make direct assaults than single fish.

## METHODS

### Study Animal

The convict cichlid is a monogamous, biparental, substrate-brooder that engages in extended care of the young. The young mature through three distinct stages termed egg, wriggler and free-swimming fry. The eggs hatch into wrigglers and remain at this stage for 4–6 days, until the yolk sacs have been absorbed. The young then become free-swimming fry. At the egg and wriggler stage, the female spends more time in direct care than the male, but as the young become free-swimming fry, parental activities are shared more equally by the parents (Smith-Grayton & Keenleyside 1978); this pattern is similar to



**Figure 1.** Sketch of the experimental tank. Parents kept their wrigglers within the flower-pot. When an intruder was placed within the intruder compartment, we recorded the location of each parent relative to three areas (i.e. offspring area, elsewhere area, intruder area). Because parents rarely entered the intruder area when the intruder was absent, we recorded the parents' locations as being within the offspring area or away from the offspring (=elsewhere area+intruder area). The lengths of three location areas are indicated with the width being the width of the tank (44 cm). The flower-pot was 15 cm wide and 15 cm long.

the behaviour found in other types of cichlids (Barlow 1974; Itzkowitz & Nyby 1982; Itzkowitz 1984).

All of the fish used in these experiments were raised in our laboratory and were descendants of stock purchased from local suppliers. The intruder fish were male convict cichlids. Previous studies have revealed that once offspring are present, both the male and the female parent respond aggressively to intruding convict cichlid males (M. Itzkowitz, J. Barnes & N. Santangelo, unpublished data). Also, although courting individuals tend to attack intruders of their own sex (see Haley 1987), our preliminary observations revealed that once offspring are present, parents do not differentiate between the sex of the intruder.

## Experimental Design

We maintained males and females separately in several 600-litre stock tanks. We placed three males of equal size, and three females each approximately 1 cm smaller than the males, into an experimental tank (470 litre). The experimental tank was divided into four areas (only linear measurements are provided because all areas extend the full width of the tank (44 cm) (see Fig. 1): (1) the 'offspring area' measured 25 cm and included a flower-pot, (2) the 'intruder compartment' opposite the offspring area measured 15 cm and was formed by a sheet of clear plastic that extended across the width of the tank, (3) the 'intruder area' extended 10 cm beyond the clear plastic partition towards the centre of the tank, and (4) the 'elsewhere area' was the 70-cm space between the intruder area and the offspring area.

At the onset of pair formation, we removed the four nonpaired fish. One of the nonpaired males was then placed into the intruder compartment at one end of the tank. A previous study has shown that placing a conspecific intruder behind such a partition increases the

likelihood that the pair will successfully produce eggs (Itzkowitz & Draud 1992). After eggs were laid in the flower-pot, we removed the intruder from the intruder compartment leaving the paired parents to raise the offspring ( $N=15$ ). For the single parent experiment, we removed either the male ( $N=10$ ) or female parent ( $N=10$ ). After the eggs hatched into wrigglers, we videotaped the paired parents or the remaining parent of the pair for 25 min before adding an intruder and videotaping for another 25 min. We used the first 5 days of the wriggler stage for analysis. On each test day we randomly selected an intruder that was approximately the same size as the male parent from a large stock population. After widowed or paired parents raised their offspring to the free-swimming fry stage, we placed them in a separate stock tank and did not use them again.

We were alert to the possibility that the smaller size of the female, relative to both her mate and to the intruder, might influence her parental role selection (i.e. she may be less inclined to attack the intruder). A previous study addressed this point (Itzkowitz et al., unpublished data) and will report that females marginally smaller than the male (as those in this study) behaved similarly to females that are the same size as their mates.

## Parental activities

Using a computer event-recording program, we transcribed the following events from the videotapes (see above).

*Time with offspring.* The total amount of time (in seconds) that a parent remained in the offspring area.

*Time with intruder.* The total amount of time (in seconds) that a parent remained in the intruder area.

*Time away.* The total amount of time (in seconds) that a parent was not in the offspring area. Time away was used when an intruder was not present because the parent rarely went near the empty intruder compartment and thus it was unnecessary to subdivide this area into intruder and elsewhere areas.

*Bite rate.* The total number of times a parent bit (i.e. mouth-open display) at the intruder compartment divided by the total amount of time the parent spent within the intruder area.

*Lateral display rate.* The total number of times a parent performed the lateral display divided by the total amount of time the parent spent in the intruder area. The lateral display is the typical threat display seen in fish in which the parent presents its side to the intruder while extending its unpaired fins and lowering its branchiostegals.

*Frontal display rate.* This behaviour is similar in form to the lateral display except the parent faces the intruder. Here also, we generated the rate by dividing the number

of frontal displays by the total amount of time a parent spent in the intruder area.

### Statistical Analysis

For all but one of the dependent measures, there were two experimental variables, sex (male–female) and testing context, alone or with the mate (single–pair). Although this results in four conditions (single male, single female, paired male and paired female), using a two-way factorial analysis of variance (ANOVA) was not possible as ordinary methods assume that the error terms are homogeneous and in this case they were not. When we tested fish singly (i.e. alone during testing), we randomly chose a group of 10 widowed males and a second group of 10 unrelated widowed females. But when we tested males and females in pairs (i.e. in the presence of the mate), we simultaneously recorded the behaviour of both the male and female from 15 randomly chosen pairs during each test session. Thus, for these intact pairs, because ‘pair’ became an additional blocking factor, we assessed the sex effect within pairs. If doing a separate ANOVA on the singles data (i.e. widows), we would test for sex effects with the appropriate independent groups error term ( $MS_{\text{Subjects within sex}}$ ); for the intact pairs we would test for sex effects with the appropriate sex by pair (i.e. treatment by block) interaction error term ( $MS_{\text{Sex} \times \text{Pair}}$ ). This more efficient heterogeneous design was preferred over increasing the sample sizes for the intact pairs and then, to achieve independence, using only one parent from each replicate.

The same hypotheses as tested in an ANOVA (i.e. main effects and interaction) can be tested in this heterogeneous design, but with error terms customized to our combination of independent groups and blocking. The tests are described below as  $t$  tests rather than  $F$  tests because of the more natural derivation of the appropriate error terms for  $t$ . The numerator of  $t$  is the difference to be tested, while the denominator is the standard error (SE) of that difference.

For any of the dependent measures we can easily derive the SE of the mean for any single group or any sums or differences among group means. For example, the SE for the difference between the means of two independent groups is the square-root of the sum of the squared SEs for the two groups being compared,  $SE_{\text{Mean}_1} - \text{Mean}_2 = \sqrt{SE_{\text{Mean}_1}^2 + SE_{\text{Mean}_2}^2}$ . For a blocking design, the SE of the difference between two means is the SE of the mean of the difference scores,  $SE_{\text{Mean Difference Score}}$  (e.g. we obtained the sex-effect differences by subtracting the female score from the male score in each pair). Since all experimental factors were bilevelled, each main effect and interaction represents a single difference and each can be tested with a  $t$  test. Since the SEs for the singles half of the data were derived differently from the SEs for the pairs half, the  $t'$  (i.e.  $t$  prime) approximation for heterogeneous variances was most appropriate (Snedecor & Cochran 1989). The adjusted degrees of freedom (Snedecor & Cochran 1989, page 97) are given with each  $t$  value, and exact  $P$  values based on the adjusted degrees of freedom were calculated by DATASIM.

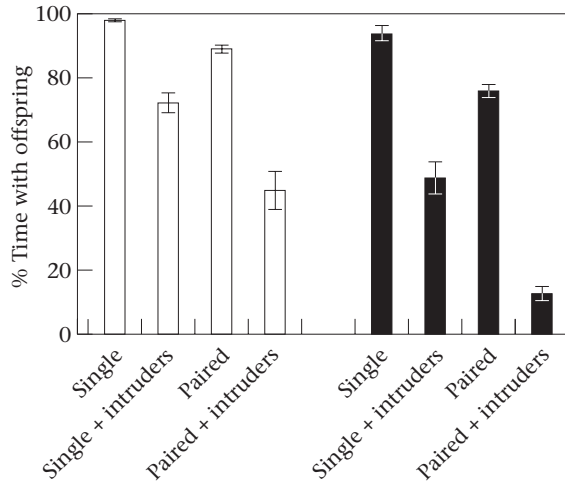
To test the interaction between sex (male–female) and testing context (single–pair), we obtained the numerator for the  $t$  test by subtracting the mean male–female difference for pairs from the mean male–female difference for singles (analogous to the unweighted means solution using an ANOVA). We obtained the denominator by first finding the SEs for the mean male–female difference for singles and for pairs. Since singles and pairs data are independent, the denominator for the interaction is the square-root of the sum of the two squared SEs. To test the main effect of sex, we obtained the numerator by summing the two mean male–female differences and we tested this difference with the same denominator as that used for the interaction (the variance of a sum of two independent variables is equal to the variance of the difference). Finally, to test the main effect of context (single–pair) we obtained the numerator by summing the mean male and female scores for singles and then subtracting the mean male+female scores for pairs. We then combined these SEs for these averages (singles and pairs) as indicated above for independent groups to provide the appropriate error term. The percentage of time with the offspring had a third experimental factor, intruder present or absent. Intruder present–absent is a within-subject or repeated measures factor; each fish was tested both with an intruder present and with an intruder absent. We analysed this measure as a three-way factorial design, also with error terms customized to take into account the difference in design for the singles data compared to the pairs data. To reduce type I error inflation because of the large number of tests (due to having five dependent variables) we evaluated all tests at the 0.01 level of significance.

Initially, we performed the above analyses using ANOVAs in which we presumed that the nonsignificant correlations between males and females in pairs indicated that they were also independent. With one exception, the result from these preliminary ANOVAs yielded the same significance scores as those generated from our above ‘customized’ tests. The one exception was that one main effect (the number of frontal displays) was significant in the ANOVA analysis but not significant in the customized error term analysis. We accepted the nonsignificant result.

## RESULTS

### Time with Offspring

With the exception of the triple interaction (male–female  $\times$  single–paired  $\times$  intruder absent–present) and one two-way interaction (male–female  $\times$  single–paired), all main effects and pairwise interactions were significant. The mean percentage of session time spent with the offspring for each condition is graphed in Fig. 2. When there was no intruder present and fish were alone in the tank with the offspring (single condition), there was no difference between the two sexes ( $t_{18}=1.26$ ,  $P=0.2232$ ), both males and females spent nearly all their time (over 94%) with the offspring. Introducing an intruder or placing the male and female fish of a pair together with

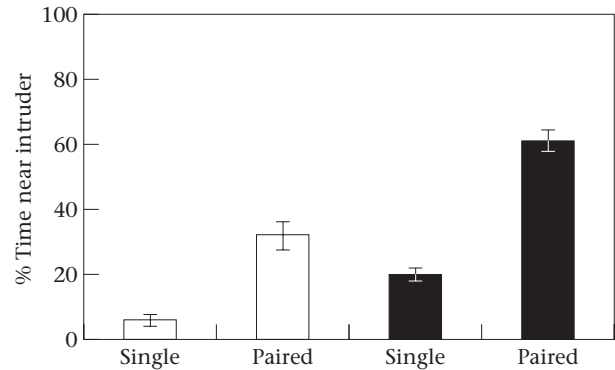


**Figure 2.** The mean±SE percentage of session time (session=approximately 1500 s) that females (□) and males (■) spent with the offspring when tested singly and in pairs with and without an intruder present. Single: one parent present; single+intruder: one parent present along with the intruder; pair: the other mate was also present in tank; pair+intruder: the other mate was present along with the intruder.  $N=10$  for single male and single female parents,  $N=15$  for paired parents.

the offspring dramatically decreased the percentage of time each parent spent with the offspring, especially for males.

As expected, on average, females spent a higher percentage of session time with the offspring (76%) than the males (58%) ( $t_{31.73}=7.21$ ,  $P<0.0001$ ). Also as expected, presence of an intruder reduced the time with the offspring for both sexes (from 89% without the intruder to 45% with the intruder;  $t_{27.15}=22.40$ ,  $P<0.0001$ ). But a significant interaction ( $t_{27.55}=5.17$ ,  $P<0.0001$ ) showed that the presence of an intruder reduced the time with the offspring more for males (from 85% when no intruder was present to 31% when the intruder was present) than for females (from 93% when no intruder was present to 59% when the intruder was present; Fig. 2). Thus, in the presence of an intruder, males mostly abandoned the offspring while females mostly remained with the offspring.

Pairing ('testing context') also affected time spent with the offspring, with paired fish averaging less session time with the offspring (56%) than single fish (78%) ( $t_{30.61}=7.76$ ,  $P<0.0001$ ). Pairing interacted with the presence or absence of an intruder ( $t_{27.15}=4.45$ ,  $P=0.0001$ ), but not with sex ( $t_{31.73}=1.80$ ,  $P=0.081$ ) (see Fig. 3). When an intruder was introduced, time with the offspring dropped more for paired fish (from 82% when no intruder was present to 29% when an intruder was present) than for single fish (from 96% when no intruder was present to 60% when an intruder was present). Thus, it appears that single fish were reluctant to leave the offspring even in the presence of an intruder. While pairing decreased the time with the offspring somewhat more for males (from 94% when single to 76% when paired) than for females (from 98% when single to 89% when paired), the lack of a significant interaction



**Figure 3.** The mean±SE percentage of session time that female (□) and male (■) parents were in the intruder area. See Fig. 2 legend for more details.

between pairing and sex indicates that this difference was not significant. Thus, pairing seems to release the fish of both sexes from being tied to the offspring, but this effect was greater when an intruder was present (a specific reason to leave the offspring) than when an intruder was not present.

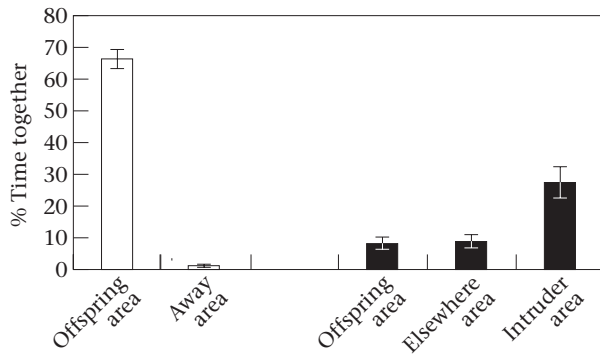
### Time Near the Intruder

Both main effects (male–female, single–paired) and the interaction were significant. Consistent with the analysis of time with the offspring, time spent near the intruder was higher for males (40%) than for females (19%) ( $t_{22.46}=7.68$ ,  $P<0.0001$ ). Paired fish spent a higher percentage of session time near the intruder (46%) compared with single fish (13%) ( $t_{18.73}=9.42$ ,  $P<0.0001$ ). The significant interaction ( $t_{22.46}=2.83$ ,  $P=0.0096$ ), indicates that male fish spent more time near the intruder when paired than when single (61% when paired versus 20% when single) compared with female fish (32% when paired versus 6% when single; Fig. 3). Particularly when paired, male fish spent proportionally more time near the intruder than female fish.

Thus, when male and female fish were tested singly and there was no intruder present, both spent almost all their time with the offspring. However, when fish were tested in pairs, both parents reduced the time they spent with the offspring. Introducing an intruder further reduced the time each parent spent with the offspring but to a greater degree for males than for females. Conversely, when an intruder was present, each parent increased the time spent near the intruder, especially the males.

### Time Together

We also considered the time both parents were together with the offspring or the intruder. Two outcomes seem plausible. The pair might tend to trade off roles (e.g. while the female is with the offspring, the male is more free to leave the offspring and deal with the intruder, and vice versa). Or the pair might coordinate their movements together (i.e. they might tend to stay with the offspring together and approach the intruder together).

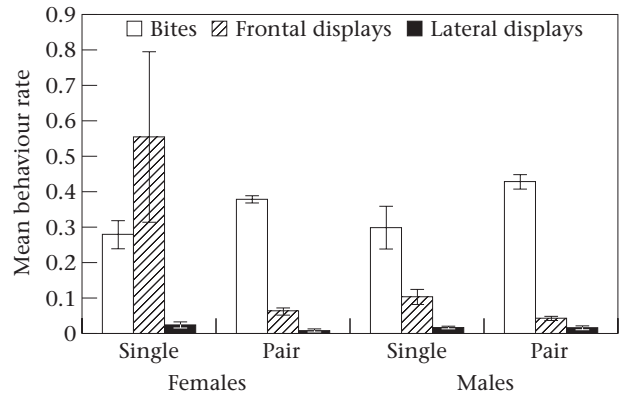


**Figure 4.** The mean  $\pm$  SE percentage of session time that both parents were present at each location (note: away area=elsewhere area+intruder area) when no intruder was present ( $\square$ ) and when intruders were present ( $\blacksquare$ ).  $N=15$  pairs.

We calculated the probabilities of both fish being together either with the offspring, near the intruder, or elsewhere (the large area in the middle of the test tank between the offspring and the intruder end sections) by dividing the total time the pair was together at the three different sites by the total session time (Fig. 4). If there were no coordination of behaviour, then male and female behaviour would be independent, and the time they are together with the offspring would be predictable from knowing the time each of them spend with the offspring separately. In particular, if the male in a pair spent 50% of session time with the offspring and independence holds, we would predict that the male would be with the offspring 50% of the time whether the female was also with the offspring or not. If the conditional probability of the male being present was higher when the female was also present, then we could conclude that there was a tendency for the male and female of a pair to stay with the offspring together. If the conditional probability of the male being present was lower when the female was also present, then we could conclude that there was a tendency for the male and female of a pair to trade off roles; while one was with the offspring the other would be more likely to leave the offspring.

With no intruder present, both members of a pair spent most of the session time with the offspring (76% for males and 89% for females), although as expected, females spent more time with the offspring than males ( $t_{14}=6.15$ ,  $P<0.0001$ ). However, males also spent less time with the offspring when the female was also with the offspring (74%) than when the female was not with the offspring (88%) ( $t_{14}=4.09$ ,  $P=0.0011$ ). Similarly, females also spent less time with the offspring when the male was with the offspring (86%) than when the male was not with the offspring (94%) ( $t_{14}=4.06$ ,  $P=0.0012$ ). Thus, when an intruder was not present the male and female of a pair 'trade off' roles (i.e. they were more likely to be apart than expected by chance).

We conducted this same analysis on pairs when the intruder was present. The data indicate that, overall, in the presence of an intruder, the male spent little time (13%) with the offspring, while the female spent almost



**Figure 5.** The mean  $\pm$  SE number of bites/s, frontal displays/s and lateral displays/s for females and males, when single or paired. Rate=number of aggressive events/total time in seconds in the intruder area.  $N=10$  for single males and females,  $N=15$  for pairs.

half the session with the offspring (45%) ( $t_{14}=5.52$ ,  $P<0.0001$ ). However, when the female was with the offspring, the male was almost twice as likely to be with the offspring (21%) as when the female was not with the offspring (11%), although this difference was not significant at the 0.01 level ( $t_{14}=2.45$ ,  $P=0.0283$ ). Similarly, the female was more likely to be with the offspring when the male was also with the offspring (71%) than when the male was not with the offspring (43%) ( $t_{14}=4.01$ ,  $P<0.00013$ ). The same pattern was observed for time spent near the intruder data. Overall, males spent the majority of their session time near the intruder (61%) while females spent only about one-third of their time (32%) near the intruder ( $t_{14}=5.98$ ,  $P<0.0001$ ). However, when the female was near the intruder, the male spent even more time near the intruder (85%) compared with when the female was not near the intruder (47%) ( $t_{14}=5.61$ ,  $P<0.0001$ ). Similarly, the female was more likely to be near the intruder when the male was also near the intruder (47%) than when the male was not near the intruder (9%) ( $t_{14}=5.73$ ,  $P<0.0001$ ). Thus, in contrast to pairs without an intruder, in the presence of an intruder the male and female of a pair tended to stay together more than expected by chance, either with the offspring or near the intruder.

### Aggressive Behaviour Patterns

When an intruder was present, we recorded three additional measures of aggression: bites/s, frontal displays/s, and lateral displays/s. For each of these measures, for each fish separately, we divided the total number of counted behaviours by the total time the fish was near the intruder (Fig. 5). Thus, these measures provide information that is statistically independent of how much time each fish spent in the presence of the intruder. Each design was a 2 (sex, male–female)  $\times$  2 (testing context, single–pair) factorial design, and we analysed each by testing main effects and interactions using the customized error terms described above.

For the mean number of bites/s (total number of bites/total number of seconds each fish was near the intruder) (see Fig. 5), paired fish exceeded single fish by 40% with means of 0.40 for paired and 0.29 for single fish ( $t_{24,87}=3.04$ ,  $P=0.0056$ ). There was no significant main effect of sex ( $t_{24,28}=0.99$ ,  $P=0.3296$ ), nor a significant interaction between testing context (i.e. single and paired) and sex ( $t_{24,28}=0.47$ ,  $P=0.6461$ ).

For the mean number of frontal displays/s (total number of frontal displays/total number of seconds each fish was near the intruder), none of the three effects was significant (main effects: sex:  $t_{18,06}=1.87$ ,  $P=0.0775$ ; pairings:  $t_{18,11}=2.28$ ,  $P=0.029$ ; sex  $\times$  pairings:  $t_{18,06}=1.78$ ,  $P=0.0911$ ; Fig. 5). Thus, the number of frontal displays/s directed towards the intruder was not significantly affected either by sex or by testing context.

Finally, for the mean number of lateral displays/s (total number of lateral displays/total number of seconds each fish was near the intruder), again, none of the three effects was significant (main effects: sex:  $t_{21,47}=0.16$ ,  $P=0.8759$ ; pairings:  $t_{29,95}=1.09$ ,  $P=0.2844$ ; sex  $\times$  pairings:  $t_{21,47}=1.466$ ,  $P=0.1571$ ; Fig. 5). As for frontal displays, the number of lateral displays directed towards the intruder was not significantly affected either by sex or by testing context.

## DISCUSSION

### Sex Similarities and Differences

These experiments revealed that sex differences in the selection of parental roles were based on a sex's inherent dispositions, the availability of alternative parental roles, and the presence or absence of the other parent. As seen in previous studies, when intruders were absent, both males and females as single parents responded similarly by accepting the only available parental role (i.e. staying with the offspring), and rarely accepting a nonparental alternative that left the offspring unattended (e.g. such as meandering around the tank). With the addition of the intruder, both sexes as single parents significantly reduced their time with the offspring. However, contrary to our prediction that the single parents of both sexes would respond similarly to an intruder, males were more likely than females to leave the offspring unattended and defend against the intruder.

In the absence of an intruder, paired males spent more time than single males meandering around the tank, suggesting that the females 'released' them from some direct offspring care. Although paired females had a tendency to spend less time away from the offspring than did males, there was no significant difference between the sexes in how much pairing reduced time with offspring compared to single individuals. The addition of an intruder produced the most dramatic effect on both sexes in the paired context in that each member of the pair spent significantly less time with the offspring than widowed parents, with or without an intruder, or paired parents without an intruder. Paired males were more affected by an intruder and spent significantly more time near the intruder and away from the offspring than did

females. For example, compared with single parents without an intruder, the combined effect of the presence of a mate and the intruder caused males to reduce their time with their offspring by about 86% while the female's reduction was about 54%.

With regard to aggressive behaviour, our prediction that both parents would respond similarly to the presence of the mate was partially supported. For example, although there were no sex differences in bite rates, both sexes increased their bite rate when their mate was present. However, sex and pairing had no effect on frontal and lateral display rates. The analysis of these two displays clearly did not support our prediction because the presence or the absence of the mate did not influence the lateral display rate. In other species of cichlids, single males perform lateral displays of greater duration than single females (Itzkowitz 1985), but this is not the case for convict cichlids (M. Itzkowitz & N. Santangelo, unpublished data).

In summary, our experiments revealed that both the presence of the mate and the presence of an intruder had a similar effect on both sexes; however, role specialization was evidenced by these stimuli having quantitatively different effects on the sexes.

### Role Specializations and Support Roles

Little attention has been paid to parental role specialization in the animal literature where the emphasis has been on the sharing of a task (e.g. both parents providing food or protection to offspring). However, in one of the more detailed analyses of biparental cooperation, Wynne-Edwards (1995) observed that female Djungarian dwarf hamsters are more likely to emphasize direct offspring care when paired than when alone, and both parents often engage in the same activity. In humans, social scientists have observed that men and women traditionally take on different parental roles and those parents that change roles often do so in a support capacity (e.g. Pedersen et al. 1987). Our study revealed that convict cichlid parents also show a division of roles coupled with each parent often switching roles to support the other parent. Previous studies on biparental cichlids (e.g. Itzkowitz 1984; Rangeley & Godin 1992) have emphasized that a parent periodically may relieve its mate of its sex-typical role (e.g. the male might remain with the offspring allowing the female to move around the territory and forage). This role trade-off was evident in the present study when the intruder was absent (i.e. offspring were left unattended only 1% of the session time). Such role exchanges are commonly observed in nature and, similar to our experiments, typically occur when neither parent is defending against an intruder (M. Itzkowitz & N. Santangelo, unpublished data). Thus, while we could see no external stimulus that might have attracted the male or female parent away from the offspring, the presence of one parent with the offspring induced the other to leave the offspring for some time.

With the addition of an intruder, the female's time away from the offspring depended mainly on joining the

male in attacking the intruder. Similarly, the male typically was with the offspring only in the presence of the female. Thus, in the presence of an intruder, the impetus to change roles was caused by an individual joining a mate and not switching roles with the mate; the effect was to leave either the offspring or the intruder unattended. Although this suggests that both sexes have become parental role specialists and change roles only in support of the other parent, in nature it is quite rare for both parents to attack an intruder simultaneously (M. Itzkowitz, personal observation). Exceptions (when both parents do attack together) do occur, however, as when an intruder manages to approach the young undetected. Also, both parents will respond to an intruder that is slow to retreat after being attacked by one parent. This situation typically occurs when other cichlid parents (often different species) that are defending free-swimming fry intrude and are slow to retreat.

The high frequency with which the female supported the male in attacking the intruder in our experiment was probably caused by the persistent presence of the intruder. Because the intruder will eat the offspring if given the opportunity, it is not surprising that both parents will attack any intruder that cannot be removed by a single parent. However, it remains unclear why the male sometimes left the intruder to join the female near the offspring. Parents spent much less time together with their offspring than they spent together near the intruder (i.e. about 70% less time). Quite possibly, these brief periods occurred when the intruder was not actively threatening the pair, and thus during these periods, their behaviour more closely resembled that of pairs without an intruder.

Under our conditions, the division of roles seen in convict cichlids resembles the division of a single task often described in other biparental species (i.e. both parents are required to perform an essential activity such as feeding fast-growing offspring; Clutton-Brock 1991). That is, while male and female convict cichlids do emphasize different parental roles, each sex does possess considerable flexibility that allows them to change roles whenever it is imperative to support the other parent, or, in particular, when the other parent is not present or missing.

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