

Biparental division of roles in the convict cichlid fish: influence of intruder numbers and locations

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The convict cichlid fish (*Archocentrus nigrofasciatus*) has a parental division of roles in which the male spends much of his time defending the territory while the female remains near to the offspring. This division is not obligate because both parents do switch roles for brief periods and, in the absence of the mate, both sexes will perform all roles. We predicted that the division of roles depended on each parent being able to successfully complete its task. If a task could not be completed by a single parent, role specializations would be reduced resulting in a division of labor. That is, both parents would perform the same task. We modified the relative importance of the defensive role by changing the number and location of conspecific intruders. When we increased the number of distant intruders from one to two, we found that the division of roles was unaffected. Neither parent increased its defensive activities, although they did attack both intruders. Furthermore, when females did attack an intruder, it was usually the same intruder being attacked by the male. This too resembled pairs attacking single intruders. We concluded that, for distant intruders, both sexes seemed to invest a fixed amount in protecting the territory and the division of roles remained unchanged when intruder numbers changed. Placing one intruder near to the offspring greatly escalated the amount of time both parents spent attacking the intruder resulting in less time either parent spent near the offspring. A second intruder placed at a greater distance to the offspring was largely ignored by both parents. We believe we succeeded in modifying the division of roles by increasing the importance of one parental task and, in this way, the parental care in the convict cichlid resembled a division of labor around a single task.

KEY WORDS: division of roles, division of labor, Cichlidae, *Archocentrus nigrofasciatus*, offspring defense, offspring care.

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INTRODUCTION

The division of biparental labor has largely been studied in birds where it is assumed to have evolved because neither parent is capable or willing to provide all of the parental investment required to successfully rear the offspring. To test the flexibility of a parent's investment pattern, a host of field experiments have been performed on biparental birds that either removed or handicapped one parent (e.g., SASVAI 1986; BART & TORNES 1989; DUNN & HANNON 1989; WRIGHT & CUTHILL 1989, 1990; SCHWAGMEYER et al. 2002; LYNN & WINGFIELD 2003; see also GOWATY 1996). These studies generally indicate some decline in offspring survival suggesting that the unmanipulated mate did not boost its investment sufficiently to compensate for the reduction in its mate's parental care. In spite of this apparent inflexibility of parental investment, other studies on birds suggest that the parental care behavior can be flexible. HALKIN (1997) showed that female northern cardinals use songs to coordinate the male's parental care, thus illustrating that considerable flexibility exists in how and when the male directly participates in offspring care. KILNER (2002) and LESSELLS (2002) showed that male and female birds seemed to follow different provisioning rules and even showed some degree of flexibility in which offspring got preferential treatment. Overall, biparental care in birds seems to be a division of labor in which both parents perform the same general activity (food provisioning), although each parent may differ in when and who it feeds.

Unlike the division of labor, the division of parental roles found in other species is much less studied and poorly understood. In comparison with a division of labor where both parents perform the same activity, a division of roles may occur when there are several important competing activities. For example, the presence of a division of labor in birds may reflect the importance of both parents in provisioning the offspring. Perhaps a division of roles appears when several parental activities must be performed at the same time and, unlike food provision in some birds, each activity can be successfully performed by one parent.

Here we examine how shifting the relative importance of different parental roles influences the division of roles in the convict cichlid (*Archocentrus nigrofasciatus*). In convict cichlids the division of roles is pronounced with males emphasizing territorial defense while females spend more time near the offspring. These are not obligate activities because parents switch roles for brief periods and, in the absence of the other parent, both sexes will perform all activities (ITZKOWITZ et al. 2001).

If the difference between a division of labor and a division of roles is the number of mutually exclusive roles that must be performed, we predicted that biasing the importance of one role would cause both parents to act on that role and, in this way, resemble a division of labor. This prediction does not preclude the possibility that both parents may avoid the role and shift their activities to another role. For example, both parents may avoid offspring defense when the intruder threatens both parents. Here also, the parents' increased overlap in performing a secondary

role would resemble a division of labor. Finally, emphasizing the importance of one role may cause a more extreme division of roles where both parents would be less likely to switch roles (i.e., increase role separation). For example, increasing the threat to the offspring may cause one parent (the male) to emphasize his defensive role while the other parent (the female) persists in her typical nurturing role near the offspring. We modified the importance of the defensive role by changing the location and numbers of conspecific intruders. For convict cichlids, the presence of a conspecific intruder represents an important threat because they are common predators of offspring under natural conditions (KEENLEYSIDE et al. 1990, WISENDEN 1995, SANTANGELO & ITZKOWITZ pers. obs). Changing intruder numbers and locations was predicted to change the threat level and thus vary the difficulty for the male to cope with the intrusions.

Although role overlap may increase if both male and female increase their attacks against multiple intruders, the coordination of their defensive responses may be quite different than with a single intruder. For single intruders, females seem to assist the male and thus she is more likely to attack while the male is already attacking rather than attack independently (ITZKOWITZ et al. 2001). If the female is 'programmed' to assist the male, she may tend to attack only the intruder that is being attacked by the male. Alternatively, with multiple intruders, the female may attack the intruder that is not being attacked by the male. Females are certainly capable of independent action as seen when widowed females attack intruders (ITZKOWITZ et al. 2001). Thus, in one sense it is possible that there may be more role overlap because both parents may attack the intruders, perhaps the same intruder, but they may subdivide defensive responsibilities by attacking different intruders.

METHODS

Subjects. Convict cichlids occur naturally in Central America and field studies have been done mainly in Costa Rica (WISENDEN 1995). Our field observations indicate that pairs form first and then establish territories that they defend against all other species of fish. They are serially monogamous. They exhibit the typical substrate brooding behavior described for many other species of cichlids in which parents lay eggs within a small cave with the walls scraped clean. After approximately 3 days, the eggs hatch into nonmotile individuals called wrigglers. The parents transfer the wrigglers to pre-dug pits (in our experiments, the parents keep the wrigglers inside a flower pot). At the end of the 6 day wriggler stage, the offspring have absorbed their yolk-sacs and become free-swimming fry. The fry remain with the parents a variable period of days and then disperse.

The subjects used in this experiment were obtained either from several commercial suppliers or were bred from our own stock. Our breeding stock was a combination of adults from both commercial suppliers and from wild caught individuals (from Costa Rica). Unisex groups of adults were housed in 473 liter stock tanks. Pairs were used only once while the intruders were returned to the stock tanks.

The intent of the experiment was to provide a stimulus to the pair that would clearly threaten the offspring but not threaten the pair or the pair's territory. As intruders, we chose conspecific males that were approximately the same size as the paired male. At that size, the intruder was no threat to either parent and certainly would eat the offspring. Under laboratory and field conditions, such intruders were never observed to attack a pair with offspring and if ventured too close to the pair, were always quickly chased from the territory (ITZKOWITZ & SANTANGELO, pers obs). Although the female was smaller than the male and the intruder, her relative size should not have affected her behavior. A previous study (ITZKOWITZ et al. 2005)

that considered an assortment of male, female, and intruder sizes revealed that the division of roles remained largely unchanged except under the very unusual condition in which both the female and the intruder was much larger than the male parent.

The Experimental tank. Fig. 1 gives a sketch of a 284 liter experimental tank. The pairs typically deposited their eggs inside the small flower pot. We positioned three small transparent boxes inside the tank; two boxes at each corner at the far end of the tank and one box at the corner across from the flower pot. All plastic boxes were 15 cm sq and 30 cm high. Boxes B and C were separated by 14 cm and were separated from Box A by approximately 90 cm. The edge of the 15 cm long flowerpot was separated from Box A by 14 cm. The plastic used to construct the boxes was completely transparent (e.g., transmits UV light). We also drilled numerous 1.0 cm holes. In this way we hoped to minimize the distortion of visual, auditory, and chemical communication signals between parents and intruder(s).

Experimental design. Three males and three females were placed in an experimental tank and a pair was allowed to form. The nonpaired fish were immediately removed. After several days, eggs were typically laid on the upper inside surface of the flower pot. Irrespective of where the eggs were initially laid, the parents always placed the newly hatched wrigglers into the flowerpot where they remained for the 6 days. On the 2nd day of the wriggler stage, the manipulations began with the placing of one or two conspecific male(s) in the plastic boxes. When two intruders were used, each one was placed in a separate box. Four combinations of intruders and locations were used: (1) one intruder in the box near the offspring (site A), (2) one intruder in a more distant box (site B), (3) two intruders, one in the near box (site A) and the other in a distant box (site B), and (4) both intruders in the distant boxes (sites B and C). The four combinations were presented to a pair on each of the next four days. The sequence of presentations was randomized. The entire tank was videotaped for 25 min, after which, the intruders were removed.

Behavioral activities. The behavioral activities were transcribed using the BEAST event-recording program (1998, vers. 1.01A, Univ. Hawaii, Windward Technologies). The activities included the following: the total amount of time a parent remained within the flower pot (i.e., with the offspring), 10 cm from any of the intruder boxes, and the total number of bites directed against an intruder box. We did not record the lateral or frontal displays (typical threat displays used by these fishes) because we could not determine which intruder was the intended receiver of the display.

Both male and female convict cichlids do interact directly with the offspring (e.g., fanning, moving them). We were unable to accurately observe and quantify these activities and

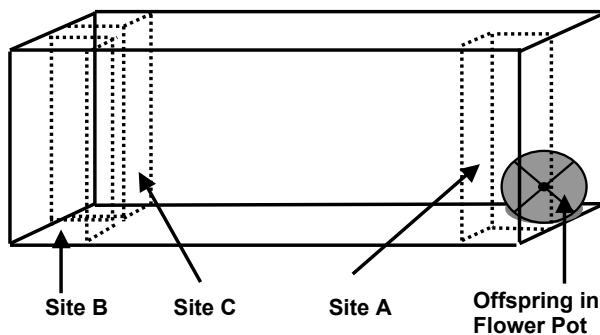


Fig. 1. — A sketch of the experimental aquarium. The stippled lines outline the plastic intruder boxes. See Methods for the dimensions of the tank and the boxes.

thus we relied on the location of the parent as an indicator of a parent's role. ITZKOWITZ et al. (2001, 2002) observed the coordination of parental roles were largely based on the location of the parents because in convict cichlids location seems to be a good indicator of the kind of role a parent performs.

Statistical analyses. We analyzed two measures, time in different areas of the experimental tank (which we have found to be a good indicator of parental behavior) and number of bites directed at the intruder (a direct measure of aggression). The time measure was divided into time near the offspring (parental nurturing behaviors) and time near the intruder (parental defensive behaviors). There were four intruder placement conditions: one intruder near the offspring; one intruder distant from the offspring; two intruders, one near and one distant from the offspring; two intruders, both distant from the offspring. We performed several repeated measures ANOVAs, testing ten intact parental pairs over four consecutive test days. When sphericity was violated (using Mauchly's Test of Sphericity at the 0.05 level of significance) we used the Greenhouse-Geisser correction (SPSS for Windows, Standard Version, Release 10.0.5, Nov. 27, 1999). In most cases the sphericity violation is caused by or exacerbated by mean percentages in one of the conditions being near zero (a floor effect). The Greenhouse-Geisser correction adjusts the degrees of freedom for both numerator and denominator of the F test, and the F tests corrected for sphericity violation can be identified by the decimal degrees of freedom. The comparisons between pairs of intruder location conditions cannot violate sphericity and so required no correction.

RESULTS

Time near the offspring

To assess the effect of the different intruder location conditions on how much time the parents spent near the offspring (Fig. 2) we performed a 2 (sex) \times 4 (intruder location conditions) repeated measures ANOVA. There was a significant main effect of sex, $F_{(1, 9)} = 10.07$, $P < 0.011$, with females staying near the offspring more than males. Intruder locations also had a main effect, $F_{(3, 27)} = 20.13$, $P < 0.001$. Pairwise comparisons indicated that only the presence versus the absence of a near intruder had a significant effect. Thus, parents spent less time near the offspring in the condition with a single near intruder compared to the conditions with one distant intruder, $F_{(1, 9)} = 24.24$, $P = 0.001$, or with two distant intruders, $F_{(1, 9)} = 23.09$, $P = 0.001$. If there was a near intruder, adding a second distant intruder did not significantly change time near the offspring, $F_{(1, 9)} = 2.07$, $P > 0.05$. Similarly, there was no significant difference between one or two distant intruders in the amount of time a parent spent near the offspring, $F_{(1, 9)} = 1.38$, $P > 0.05$. There was no significant interaction between sex and intruder condition, $F_{(3, 27)} = 0.98$, $P > 0.05$. Thus both male and female parents stayed near the offspring more when the intruder threat was distant compared to when the intruder threat was near, and female parents stayed near the offspring more than male parents.

This same effect of intruder condition (Fig. 3) was found when we looked at percent time the male and female parents were together near the offspring (a one-way ANOVA with four intruder location conditions), $F_{(1, 84, 16, 55)} = 8.20$, $P = 0.004$. Parents spent more time together near the offspring when intruders were distant from the offspring than when one of the intruders was near the offspring.

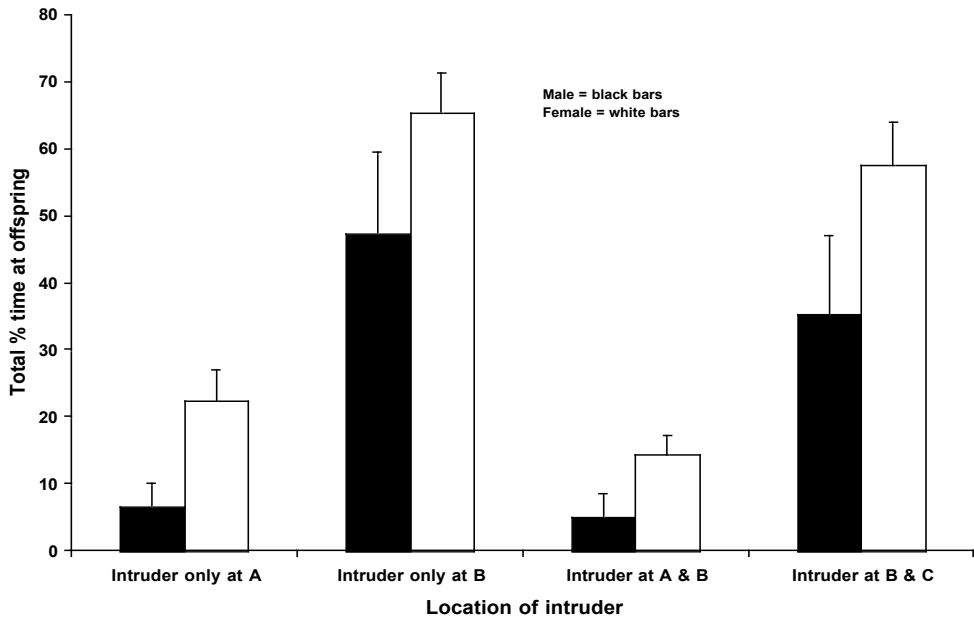


Fig. 2. — The mean percent time (out of 25 min) (with SE) that male and female parents were at the offspring (i.e., within 15 cm of the flower pot) when presented with intruders. The x-axis gives the location of intruders.

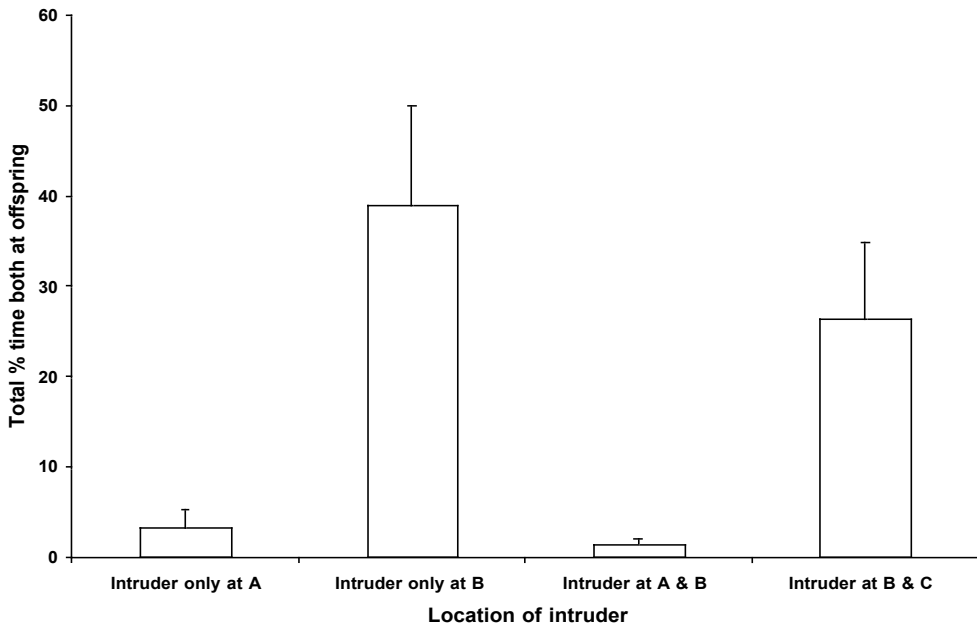


Fig. 3. — The mean percent time (with SE) that both the male and female were together at the offspring.

Time near the intruder

We analyzed the time parents spent in the intruder areas depending on how many and where the intruders were introduced (see Fig. 4). Several sub-analyses were performed to answer specific questions of interest. When a second threat (intruder) was added, we tested to see if parents divided their time between them, thus decreasing the time they were defending against each specific intruder. We also tested to see if the addition of a second intruder (increasing the total threat to the offspring) increased the total time parents spent in the intruder areas. These analyses were conditional on whether the intruders presented a greater threat by being near the offspring (site A) or presented a lesser, more distant threat (sites B and C).

To determine if parental behavior changed toward a near intruder at site A when a second distant intruder at site B was introduced, a 2 (sex) × 2 (intruder conditions) ANOVA was performed. When there was a near intruder at site A, adding a second distant intruder at site B did not change the time spent parents spent in the near intruder area, $F_{(1, 9)} = 1.58, P > 0.05$. Male parents spent significantly more time than female parents in the near intruder area, $F_{(1, 9)} = 13.66, P = 0.005$, and there was no significant interaction, $F_{(1, 9)} = 3.51, P > 0.05$. A second 2 × 2 ANOVA analyzing total time at all intruder locations showed the same pattern of results as at the near intruder only. There was no difference in total time near the intruder(s) when only the near intruder was present compared to when both a near and a distant intruder were present, $F_{(1, 9)} = 2.08, P > 0.05$. Male parents spent significantly more time than female parents in the intruder areas, $F_{(1, 9)} = 15.46, P = 0.003$, and there was no significant interaction, $F_{(1, 9)} = 2.82, P > 0.05$. Thus, when a

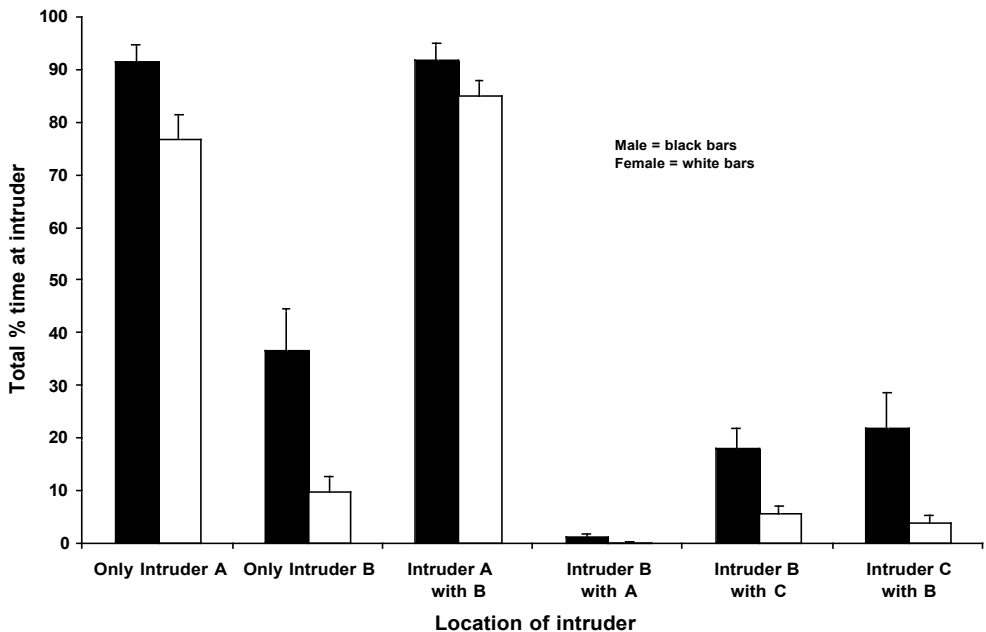


Fig. 4. — The mean percent time (with SE) that male and female parents were at an intruder box. When two intruders were present (A & B, B & C), the mean % time at each intruder is indicated.

near intruder was present, adding a distant intruder had no significant effect on the time either parent spent away from the offspring near the intruder(s).

Three different intruder location conditions included an intruder placed at distant site B: no other intruder, an additional near intruder at site A, and an additional distant intruder at site C. We performed a 2 (sex) \times 3 (intruder location conditions) ANOVA on time spent in the distant site B area. There was an overall effect of intruder locations, $F_{(1,29, 11.62)} = 17.54$, $P = 0.001$. Comparisons indicated that all three intruder locations differed significantly: less time was spent at distant intruder site B when a second intruder was added at distant site C, $F_{(1, 9)} = 6.42$, $P = 0.032$, and still less time was spent at distant intruder site B when the second intruder was added at near site A compared to far side C, $F_{(1, 9)} = 33.03$, $P < 0.001$. Male parents spent significantly more time than female parents at distant intruder site B, $F_{(1, 9)} = 21.49$, $P = 0.001$, and there was a significant interaction, $F_{(2, 18)} = 7.25$, $P = 0.004$ indicating that the intruder location effect was greater for male parents than for female parents. This interaction may only signify that female scores were constrained by being generally low (i.e., near the floor of the % time measure). A second 2 \times 3 ANOVA analyzed total time at all intruder location conditions that included distant site B. There was a significant effect of intruder locations, $F_{(2, 18)} = 130.73$, $P < 0.001$. Comparisons indicated that there was no significant effect of adding a second distant intruder at site C compared to an intruder only at distant site B, $F_{(1, 9)} = 0.08$, $P > 0.05$. However, adding a near intruder at site A dramatically increased total time in the intruder locations compared to an intruder only at distant site B, $F_{(1, 9)} = 229.16$, $P < 0.001$, and compared to two distant intruders at sites B and C, $F_{(1, 9)} = 240.49$, $P < 0.001$. For this overall measure too, male parents spent significantly more time than female parents at all intruder sites, $F_{(1, 9)} = 15.57$, $P = 0.003$, and there was a significant interaction, $F_{(1, 9)} = 3.62$, $P = 0.048$, indicating that the intruder location effect was greater for female parents than for male parents. In this case the interaction may only signify that male scores were somewhat constrained by being near the top of the scale (i.e., 93% is near the “ceiling” of the measure).

In summary, when an intruder was placed near the offspring, both the male and female spent much more time at that location, irrespective of the presence or absence of a distant intruder. With two distant intruders, males and females divided their time between the two intruders. However, overall, both parents spent similar total amounts of time at two distant intruders as they spent at a single distant intruder.

The duration the male and female were together in the intruder areas (and so away from the offspring) (Fig. 5) were also analyzed in several one-way ANOVAs. Given that the near intruder was at site A, times the parents were together at site A was not affected by the presence of a second intruder at distant site B, $F_{(1, 9)} = 1.86$, $P > 0.05$. Nor was the total time at all intruders different for intruders only at near site A versus at both near site A and distant site B, $F_{(1, 9)} = 1.87$, $P > 0.05$, again reflecting that when an intruder was near the offspring, parents rarely approached a second distant intruder. Considering the three intruder location conditions that included distant site B, no significant overall difference was found for time parents spent together in distant intruder site B, $F_{(1,10, 9.90)} = 3.86$, $P > 0.05$ (although without the correction for violation of sphericity it would have been significant). Planned comparisons indicated that less time was spent at distant site B when the second intruder was near rather than distant, $F_{(1, 9)} = 7.48$, $P = 0.023$. Though the mean time spent in site B was highest when no other intruder was present, the high variability in that condition caused comparisons with the other two conditions

to be nonsignificant. When time in all intruder areas was considered, the overall ANOVA was significant, $F_{(2, 18)} = 346.64, P < 0.001$. Both parents spent almost 80% of their time together in the intruder sites A and B (actually almost entirely in near site A), and less than 6% in distant intruder sites B and C. Comparisons confirmed that there were significant differences between the condition with intruders at sites A and B and the other two intruder location conditions, $F_{(1, 9)} = 338.76, P < 0.001$ and $F_{(1, 9)} = 448.39, P < 0.001$, but no difference between the conditions with intruders at site B versus sites B and C, $F_{(1, 9)} = 1.57, P > 0.05$. Overall, both parents spent little time together at the more distant intruders (B, B & C), irrespective of whether or not a nearby intruder was present (A).

Aggression: number of bites directed toward the intruders

The aggression scores, number of bites toward the intruder fish, were analyzed in the same fashion as time near the intruder (Fig. 6). To determine if parental aggressive behavior changed toward a near intruder at site A when a second distant intruder at site B was introduced, a 2 (sex) × 2 (intruder conditions) ANOVA was performed. When there was a near intruder at site A, adding a second distant intruder at site B did not change the number of bites parents directed toward the near intruder, $F_{(1, 9)} = 1.57, P > 0.05$. Male parents directed significantly more bites toward the near intruder than female parents, $F_{(1, 9)} = 92.06, P < 0.001$, and there was no significant interaction, $F_{(1, 9)} = 1.49, P > 0.05$. A second 2 × 2 ANOVA analyzing bites directed toward all intruders present showed the same pattern of results as bites toward the near intruder only. There was no difference in total bites when

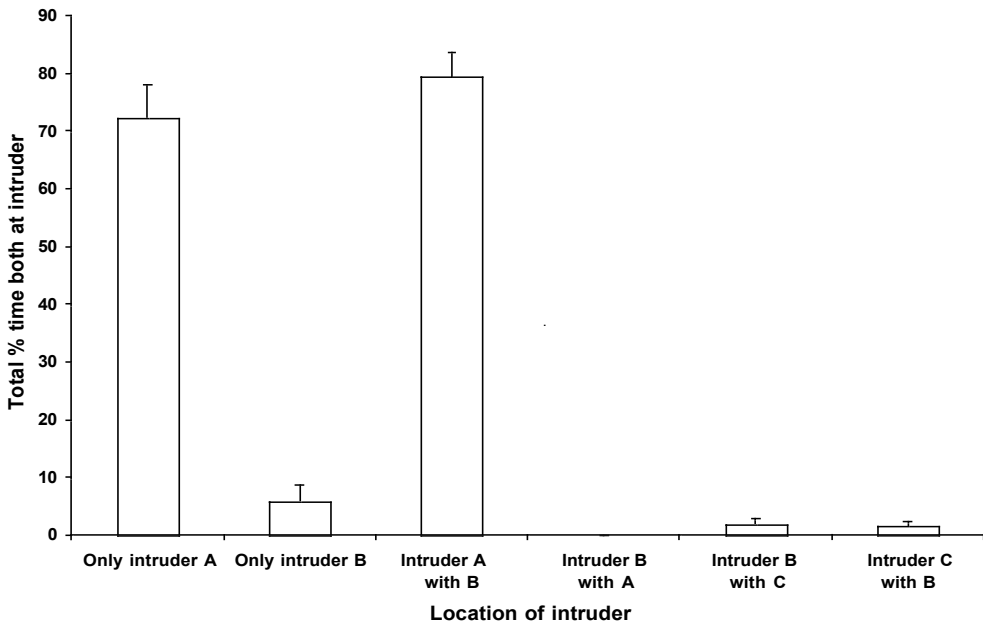


Fig. 5. — The mean percent time (with SE) both parents were at an intruder box.

only the near intruder was present compared to when both a near and a distant intruder were present, $F_{(1, 9)} = 2.04$, $P > 0.05$. Male parents directed significantly more bites toward all intruders present than female parents, $F_{(1, 9)} = 97.62$, $P < 0.001$, and there was no significant interaction, $F_{(1, 9)} = 1.25$, $P > 0.05$. Thus, when a near intruder was present, adding a distant intruder had no significant effect on the number of bites either parent directed toward the intruder(s).

We performed a 2 (sex) \times 3 (intruder location conditions) ANOVA on the number of bites directed toward an intruder at distant site B. There was an overall effect of intruder locations, $F_{(1.08, 9.74)} = 10.07$, $P = 0.009$. Comparisons indicated that fewer bites were directed at a distant intruder at site B when there was an intruder at near site A compared to either a single distant intruder at site B, $F_{(1, 9)} = 13.15$, $P = 0.006$, or two distant intruders at sites B and C, $F_{(1, 9)} = 45.47$, $P < 0.001$. Although it appeared from the means that adding a second distant intruder to one at distant site B decreased the bites toward the site B intruder, that comparison just missed significance, $F_{(1, 9)} = 4.64$, $P = 0.06$. Male parents did significantly more biting than female parents toward the intruder at site B, $F_{(1, 9)} = 20.07$, $P = 0.002$, and there was a significant interaction, $F_{(2, 18)} = 7.25$, $P = 0.004$ indicating that the intruder location effect was greater for male parents than for female parents. This interaction appears to signify only that female scores were constrained by being generally low (i.e., near the floor of zero). A second 2 \times 3 ANOVA analyzed total bites directed at all intruders for location conditions that included distant site B. There was a significant effect of intruder locations, $F_{(2, 18)} = 41.43$, $P < 0.001$. Comparisons indicated

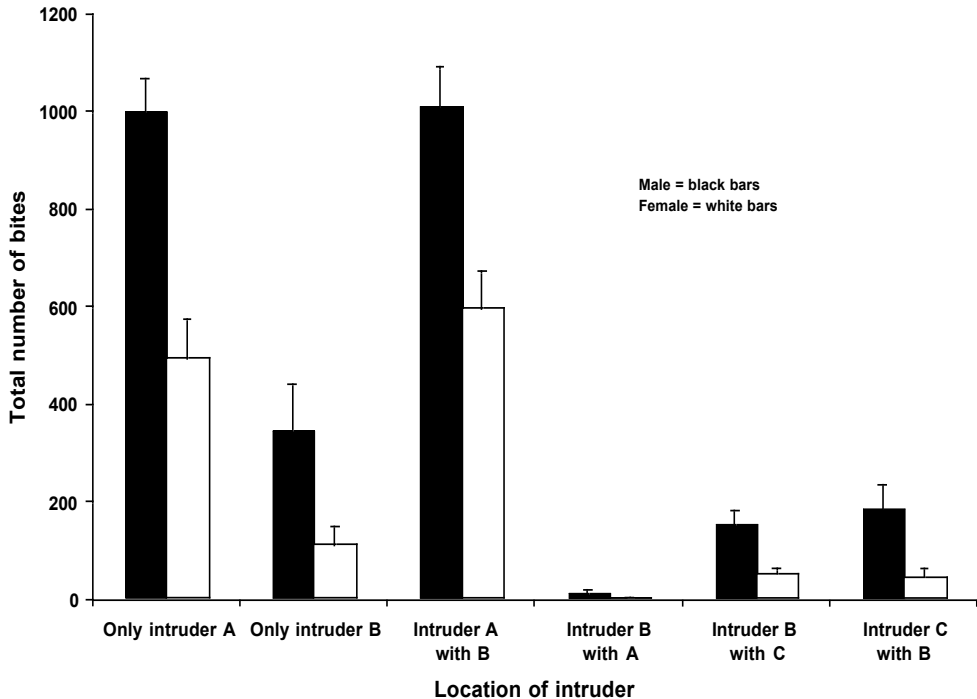


Fig. 6. — The mean number of bites (with SE) each parent directed at an intruder.

that the inclusion of a near intruder dramatically increased total bites over the number for an intruder at distant site B only, $F_{(1,9)} = 55.51, P < 0.001$, or over the number for two distant intruders at sites B and C, $F_{(1,9)} = 49.13, P < 0.001$. There was no significant effect of adding a second distant intruder at site C compared to an intruder only at distant site B, $F_{(1,9)} = 0.04, P > 0.05$.

Parents near an intruder conditional on the position of the other parent

We calculated the percentage of time each parent was near a particular intruder location depending on whether the other parent was also present near

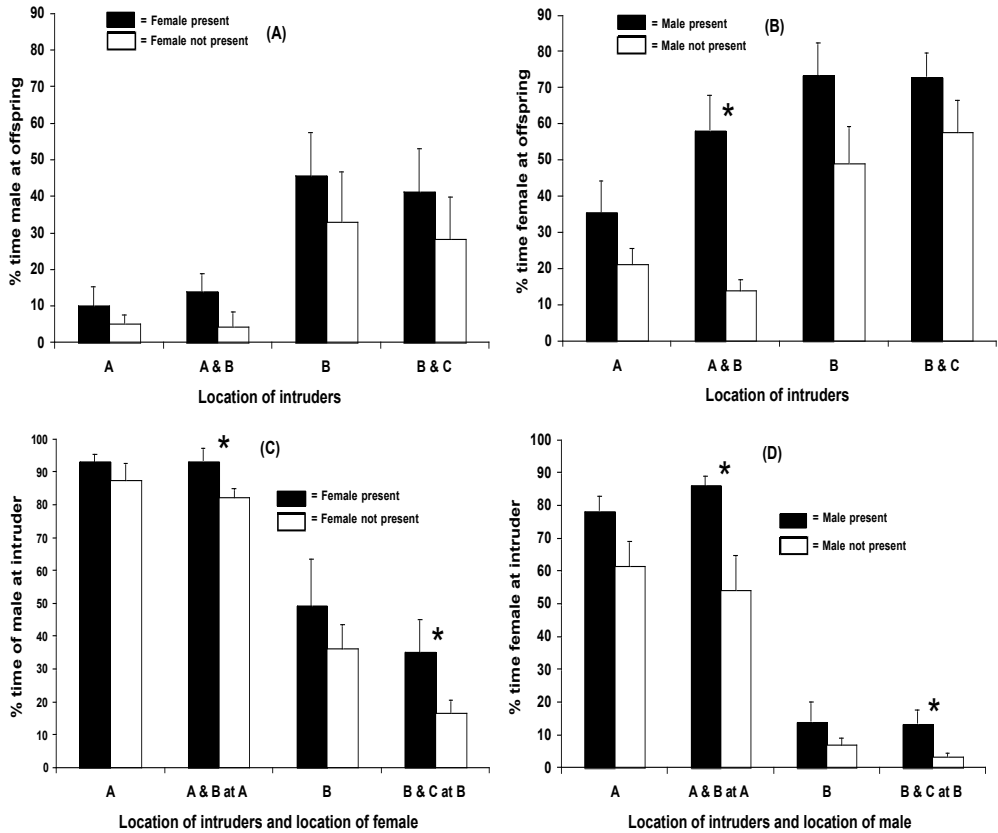


Fig. 7. — The mean percent time (with SE) the male or the female parent spent at the offspring (panels A-B) and at the intruders (panels C-D) both with (black bar) and without (white bar) the presence of the mate. The asterisks (*) indicated a significant difference (paired t-test; $P < 0.05$) between the presence and absence of the mate at that location. For panels C-D, we considered only one intruder location when two were present. For example, when intruders were present at locations A-B, we only considered location A and for intruders B-C, we considered only location B. See Results for further explanation.

that intruder or was not present. These measures provided a fairly direct index of whether or not the parents tend to show simultaneous role overlap in nurturing the offspring and/or in attacking the same intruder under the different intruder placement conditions of this experiment. The percentages were calculated for near intruder site A with and without a second distant intruder at site B, and for distant intruder site B with or without a second distant intruder at site C. If parents tend to "trade off" such that if one parent is attacking one intruder the other parent would tend to attack the other intruder, or if one parent was near the offspring the other parent would tend to attack the intruder(s), then we would expect to see that reflected in this measure. That is, one parent should spend a smaller percentage of the time at a location if the other parent was also there compared to if the other parent was not also there. Although in only five cases (Fig. 7) was the difference significant, in all 16 cases both male and female parent was more likely to be near the offspring or near a particular intruder if the mate was also at that location (overall average difference of 15.92%), indicating a tendency toward role overlap rather than role trade off in all experimental conditions.

DISCUSSION

In some species of birds, reducing the care by one parent can not be made up by the other parent (e.g., SASVARI 1986, WHITTINGHAM et al. 1994) indicating a causation for the evolutionary selection of a the parental division of labor. However, CARERE & ALLEVA (1998) suggested that the common swift (*Apus apus*) male, but not the female, reduces its parental feeding when the offspring requirements are reduced (e.g., offspring are satiated). At these times, both parents are not required to feed the offspring and this may give the male swift an opportunity to perform a different role. Here we tested whether changing the importance of a parental role would affect the parental division of roles, or even induce behavior consistent with a parental division of labor, in the convict cichlid fish.

We hypothesized that increasing the total threat to the offspring by increasing the numbers of intruders would affect the division of parental roles. Unexpectedly, the total defensive effort for both the male parent and the female parent was unaffected by the number of intruders, although, as usual, male parents allocated more total time in defensive behavior than did female parents. If one intruder was close to the offspring, a more distant intruder was almost entirely ignored and defensive behavior toward the near intruder was unchanged. If an intruder was distant from the offspring, with the addition of a second distant intruder, both sexes allocated almost equal time to attacking each intruder while the total time attacking both intruders as compared to one intruder was almost identical. In effect, each of the two distant intruders received about half the aggression from each parent in comparison to a single intruder. Thus, in terms of percent of time allocated to defensive and non-defensive behavior, increasing the threat to the offspring by adding an additional intruder did not appear to increase or decrease parental role overlap.

Although it is possible that parents evaluated two distant intruders as being no more a threat than a single distant intruder, this seems unlikely. More likely is that the parents were constrained by the context of the situation not to increase their defensive efforts against the two intruders. Under natural conditions, cryptic conspecific intruders are found dispersed through the nesting area (FRAZER &

KEENLEYSIDE 1995, WISENDEN 1995, ITZKOWITZ & SANTANGELO pers. obs) and parents spending too much time attacking distant intruders may allow other intruders easy access to the offspring. Thus, parents may allocate a minimal and fixed amount of time away from their offspring in case other intruders had penetrated the initial defensive perimeter. From this perspective, being near the offspring may play a defensive role as well as a nurturing role, and the typical pattern of the female remaining at the nest while the male patrols the perimeter may indicate that both sexes are engaged in defensive roles, not only the male.

However, our other manipulation of degree of threat to the offspring, intruder proximity to the offspring, had a dramatic effect on parental defensive behavior toward the intruder. It was not surprising that placing the intruder close to the offspring increased the aggressiveness of both the male and female. Both parents spent over 75% of their total time attacking an intruder placed near to the offspring, irrespective of whether that intruder was alone or paired with a distant intruder. With only distant intruders, both parents spent approximately 45% of their time together (at offspring + at intruder) while that increased to about 75% together, mostly near the intruder, when the intruder was placed near the offspring. Although this increase allowed the offspring to be unattended, this may have been justified by the magnitude of the threat. Also, the distance from the offspring to the near intruder was quite small and this may have minimized the risk of other intruders gaining access to the offspring while both parents engaged the intruder. Thus, increasing the magnitude of a threat by decreasing the distance between the offspring and the intruder did support the hypothesis that role overlap increases with increasing threat.

Although the female spent far less time attacking the distant intruder than the male (see also ITZKOWITZ et al. 2001 and 2005), her partitioning of her time directed at the two intruders resembled the male's behavior. Moreover, for all conditions and both sexes, parents spent a greater percentage of their time at a particular location (i.e., near the offspring, or near a specific one of the intruders) if their mate was also at that location compared to if their mate was not at that location. Tending to be together (simultaneous overlap of roles) may simply mean that both parents were responding independently of each other but were responding to the same stimuli. Alternatively, one or both parents may have been responding to the behavior of the other parent. We cannot separate these possibilities with our current experimental design in which both parents are free-swimming. However, ITZKOWITZ et al. (2003) independently manipulated the location of one of the parents by constraining them either in the offspring area or in the intruder area. They found that both parents were attracted to the location of the other parent rather than to the location not occupied by the other parent. Taken together, these data strongly suggest that parents join each other in support of both nurturing and defensive roles, and there was no support for the hypothesis that increasing the number of threatening intruders would lead to less role overlap. ITZKOWITZ et al. (2005) suggested that the role taken by one parent may provide a cue to the importance of that role and thus attract the other parent in support. ITZKOWITZ et al. (2001) suggested that the female's defensive behavior was dependent on the male's behavior and that she rarely attacked the intruder without the male also being present. In effect, the female appeared to be supporting the male's defensive effort rather than simply responding independently to the intruder. Here, also, the female was rarely alone at the intruder without the male.

In summary, changing the number of distant intruders had little effect on total defensive effort or on parental role overlap of the convict cichlid parents, although

they did attack both intruders. When one of the intruders was placed near to the offspring, the parents changed their defensive tactics by both increasing their defensive activities and ignoring the distant intruder. With one intruder near the offspring, both convict cichlids dramatically increased aggression against the near intruder and so reduced their division of roles resulting in a division of labor that was reminiscent of birds (i.e., both parents perform the same critically important activity).

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