



Is the selection of sex-typical parental roles based on an assessment process? A test in the monogamous convict cichlid fish

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In the biparental convict cichlid fish, *Archocentrus nigrofasciatum*, males and females both spend time defending their territory and their offspring, but the typically larger male parent spends more time defending the territory and the female spends more time with the offspring. Because size correlates with a convict cichlid's ability to win a fight, the larger male parent has a clear advantage in repelling intruders compared with his smaller female mate. We tested the hypothesis that male and female convict cichlids accept their parental roles as a result of their relative sizes, rather than inherent sex differences (e.g. females are more nurturing). We allowed pairs to form in which one member was smaller or larger than the other member, or of the same size (both small = 50–55 mm; both large = 70–75 mm), thus producing four pairing types. During the 5-day stationary larval stage, we subjected each breeding pair each day to a conspecific intruder that was either larger or smaller than one of the parents, or of the same size. Male and female parents adjusted their parental roles based on the size of their mates and/or the size of the intruder. Large parents displayed more defensive behaviour than small parents, regardless of sex. Male parents responded to increased threat (i.e. increasing intruder size) by increasing their defensive behaviour, but only until intruder size matched their own size, after which defensive effort decreased. Large female parents similarly responded to increased threat by increasing their defensive behaviour, but only to support their smaller mates (i.e. they did not independently attack the intruder). Larger females also showed a corresponding reduction in time spent near the offspring. Small males, in contrast, showed only a marginal increase in their time with the offspring. We conclude that the female has a more flexible parental role and, when her relative abilities change, she is more likely to expand her parental roles.

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Many studies on monogamy have used evolutionary-based hypotheses to examine how the flexibility in parental care relates to a parent's relative fitness (see reviews by Clutton-Brock 1991; Gowaty 1996). These kinds of studies often emphasized that the amount of parental care a parent 'invests' in its current offspring should be inversely correlated with the parent's future reproductive success (e.g. Trivers 1972). For example, when bird parents are faced with a reduction in the amount of parental assistance provided by their mate, their own parental care often increases but not enough to avoid some offspring mortality (e.g. Leffelaar & Robertson 1986; Sasvari 1986; Wright & Cuthill 1990; Whittingham

et al. 1994). Quite possibly, such parents are unable or unwilling to increase the level care of needed to rear all of their current offspring.

While evolutionary hypotheses are useful in understanding the amount of parental care provided by each parent, it remains unclear why, in some species, a sex often specializes in certain activities. For example, in monogamous cichlid fish where both parents appear essential to protect the offspring against predators, the male's parental role is performed mainly away from the offspring (e.g. territorial defence) whereas the female remains near to the offspring (e.g. Keenleyside 1985; Wisenden 1995). Although few studies have examined the division of parental roles in birds (Gowaty 1996), females often spend more time feeding their offspring than do males (e.g. Carere & Alleva 1998; Lölliker et al. 2000). In biparental rodents, males and females also seem to emphasize different roles and here again, females seem

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to spend more time with the offspring (e.g. Storey et al. 1994; Wynne-Edwards 1995). Not surprisingly, the most detailed studies of parental role divisions have been performed on humans, and while some role flexibility does occur in a small minority of parents, fathers typically spend less time with their children (e.g. Pedersen et al. 1987; Cowan & Cowan 1988; Jones & Heermann 1992; Witt 1994; Willoughby & Glidden 1995; Russell 1999). Although the above studies indicate that females place a greater emphasis on offspring care than do males, this 'preference' is not ingrained in females. For example, marmoset (*Callithrix* spp.) males often spend more time with their offspring than do females (e.g. Dunbar 1995). Besides role flexibility between species, the removal of one parent often causes the remaining parent to incorporate the roles of the missing parent (e.g. Itzkowitz 1984; Storey et al. 1994). In this case, role flexibility exists in a wide variety of biparental species, although it is often not expressed when both parents are present.

When both sexes can perform the same parental roles, neither the studies on animals nor those on humans emphasize the possibility that individuals within pairs may accept parental roles based on an assessment process, perhaps based on their relative abilities (i.e. in comparison to its mate's abilities) in performing the parental role. This differs considerably from studies on mate choice and fighting behaviour where assessment has often been used to explain changes in an individual's behaviour relative to different mates or opponents (e.g. Parker 1974; Real 1991). Similar to these studies, we use the term assessment to indicate that a parent changes its behaviour based on variations in the parental task or on the characteristics or behaviours of its mate. Perhaps the uniformity with which a sex performs a parental role is counterintuitive to the variable behaviour expected from an assessment process. However, when the ability to perform a parental role is based on a hardwired feature, such as morphology, variations based on an assessment system may be undetectable. For example, if females always mate with males larger than themselves, and when size is an important component to an individual's ability to perform a parental role, then differences in the parental behaviour may be the result of differences in size and not inherent sex differences. Thus, an immediate reversal in the relative sizes of the parents would correspond with an immediate reversal of parental roles.

Using the convict cichlid, *Archocentrus nigrofasciatum*, we examined whether the selection of a parental role is based on an assessment process. As is typical with other monogamous cichlid fish, the convict male parent is normally larger than his mate and spends more time defending the territory against intruders, whereas the female spends more time in close proximity to the offspring (e.g. Keenleyside et al. 1990; Wisenden 1995). Because large fish typically defeat small ones (Keeley & Grant 1993), the larger male convict cichlid is better able to defend the territory than is his smaller mate. If a parent's size relative to its mate, and not its sex, is important in accepting a parental role, we predicted that a small parent would be less likely to emphasize territorial defence. Thus, irrespective of the intruder's size, we

predicted that a large female paired with a smaller male would be more aggressive towards intruders than a small female paired with a larger male. Similarly, we predicted that a small male paired with a larger female would reduce his territorial defence and spend more time with his offspring than a large male paired with a smaller female.

However, the fish's decision to accept a role may be based on the immediate threat and not based on its own size relative to the size of its mate. In this case, we predicted that a small parent, irrespective of the size of its mate, would be less likely to defend against larger intruders. For example, Turner & Huntingford (1986), using single fish, observed that cichlid *Oreochromis mossambicus* males do reduce their defence when the intruder is much larger than the defender. Furthermore, in some species of cichlids, large fish, irrespective of sex, usually defeat smaller conspecifics (Itzkowitz & Draud 1992). Thus, we predicted that a small parent, irrespective of sex, may retreat from a larger intruder and allow the large parent to accept the defensive role. In addition, when both parents are larger than the intruder (i.e. can equally repel the intruder), or when the intruder is larger than both parents, we predicted that the division of parental roles would show more overlap compared with when only one parent can effectively defeat the intruder.

The relative size of a parent may influence whether it performs the role alone or in the presence of its mate. Itzkowitz et al. (2001, 2002) observed that when females are smaller than their mates, they attack an intruder in support of the male rather than attacking the intruder alone. We hypothesized that as the female becomes more similar in size to the male, and especially when she is larger than the male, she would be more likely to attack the intruder independently of the male (i.e. she becomes more male-like). Conversely, smaller males would be less likely to attack intruders without the support of the larger female. We also hypothesized that as intruders become larger, a parent would be more likely to assist its mate. Given that larger intruders are more threatening and more difficult to defeat than smaller ones, the smaller parent should be less likely to attack such intruders independently of its mate.

To test the above hypotheses (i.e. role selection based on an individual's relative size to its mate and role selection based on an individual's relative size to an intruder), we confronted four size combinations of parents (male parent larger, female parent larger, both parents small, both parents large) with five different-sized intruders. We used a large range of intruder sizes (40–85 mm) to examine whether small and large parents respond similarly to intruders that are smaller and larger than themselves, respectively.

METHODS

Study Animal

The convict cichlid is a monogamous, biparental, substrate-brooder that engages in extended care of the young (Keenleyside 1991). The young mature through three

distinct stages termed the egg, larval and free-swimming fry. The eggs hatch into larva (also termed 'wrigglers') and remain at this stage for 5–6 days, until the yolk sacs have been absorbed. The young then become free-swimming fry. At the egg and larval stage, the female spends more time in direct care, but as the young become free-swimming fry, parental activities are shared more equally by both parents (Smith-Grayton & Keenleyside 1978). This is similar to the behaviour observed in other cichlid species (Barlow 1974; Itzkowitz & Nyby 1981; Itzkowitz 1984).

The fish used were reared in our laboratory, and were descended both from wild-caught stocks and from stocks purchased at local suppliers. Intruder fish were male convict cichlids. The decision to use only male intruders was based on results of our preliminary experiments that convict cichlid parents do not differentiate between male and female conspecific intruders. Also, unlike males, females in our stock aquaria did not typically reach the largest intruder size needed for the experiment.

Experimental Groups

Fish were taken from unisex groups, containing approximately 50 individuals, housed in several large stock tanks (473 litre). Except for those fish reared in our laboratory, they were of unknown breeding experience; however, none had been used in our previous experiments. Four experimental groups of mated pairs were established based on two size categories (small: 50–55 mm; large: 70–75 mm). In homogeneous pairs (the parents were both either large or small), the maximum difference within a pair was 3 mm. In heterogeneous pairs, the larger parent was 20 mm larger than the smaller parent. We performed many preliminary experiments on individuals of similar sizes and thus were assured that the experimental individuals were sexually mature. Furthermore, pairs of convict cichlids in Costa Rican streams will breed when the male and female are about 30–40 mm long (personal observations).

Experiment

Within each experimental tank (120 × 44 cm, 284 litre) we placed a flower-pot on its side at one end (to provide a spawning surface) and a clear plastic barrier across the width of the tank 15 cm from the other end (to create a larger main compartment and a smaller intruder compartment) (Fig. 1). The barrier protected the intruder from the highly aggressive pair and maintained the intruder at a fixed distant from the offspring. We placed tape on the front bottom of the tank (out of sight of the inhabitants) to divide the main compartment into three areas: (1) the offspring area was 25 cm long and included the 15-cm width of the flower-pot; (2) the intruder area was 10 cm from the plastic barrier; and (3) the 'elsewhere' area included the area in between the offspring and intruder areas (70 cm).

Each experimental group consisted of 10 different mated pairs. To form a pair, we placed equal numbers of

males and females in a tank (usually three individuals of each sex) with each sex being of a particular size (i.e. either large, 70–75 mm, or small, 50–55 mm). Thus, to form a pair with a large male and a small female, the initial group of fish consisted of three large males and three small females. Once a pair formed, we removed the remaining unpaired fish and placed one unpaired male within the intruder compartment. Previous studies (Itzkowitz & Draud 1992) revealed that pairs are more likely to remain intact and lay eggs if another fish is also present in the aquarium. Once eggs were laid, we removed the intruder fish and left the pair undisturbed until testing (except for a daily feeding). Data collection began on the first day of the larval stage and continued through the fifth day. We tested fish during the larval stage because the egg stage was too short to allow for meaningful comparisons and because the distance between the young and the intruder changed continuously during the free-swimming fry stage. Larvae were largely immobile and remained at a fixed distance (i.e. in the flower-pot) from the intruder. At the end of a replicate, parents were retired to a separate aquarium and not used again.

On the first day of the larval stage, we added one of five different-sized intruders to the intruder compartment. When either the male or the female parent swam towards the intruder (generally within seconds), a 15-min trial began. All trials were videotaped and later scored with a computer event recorder. At the end of the trial, the intruder fish was removed and returned to a stock tank. The following data were taken: (a) amount of time each parent spent in each of the three areas of the tank, (b) number of bites each parent directed at the intruder, (c) the amount of time both members of the pair spent together either near the offspring, or within the intruder area.

Each pair received one intruder presentation per day for 5 days during the larval stage. Each day, we presented one of the five different-sized intruders to each pair until each pair experienced intruders of each size category. An intruder was either (1) smaller than a small parent (between 40–45 mm), (2) similar to a small parent (50–55 mm), (3) larger than a small parent and smaller than

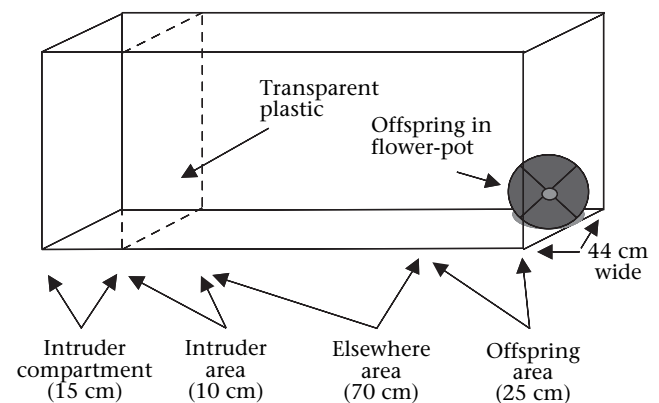


Figure 1. Sketch of the experimental aquarium.

a large parent (60–65 mm), (4) similar to a large parent (70–75 mm), or (5) larger than a large parent (80–85 mm). Our intent was to provide each of the two parent size classes with three sizes of intruders: 10 mm smaller, similar size and 10 mm larger. Presentation of intruders was randomized. For the sake of brevity, we designated parent and intruder size ranges as the lowest number in the size range (e.g. 40 mm = 40–45 mm).

A potential confound to this analysis would be if small fish behaved inherently different from large fish (perhaps as a function of age or experience) independently of the hypothesized assessment process. For example, do small males and females behave differently towards small intruders than do large males and females towards large intruders? To test this potential confound, we selected conditions for small and large parents that held size assessment constant. Thus, we compared only males and females within the two homogeneous pair types (both parents small and both parents large) in relation to intruders that were 10 mm smaller, the same size and 10 mm larger than the parents (i.e. 40, 50 and 60 mm for the small parents and 60, 70 and 80 mm for the large parents). Thus, relative to themselves, both pair types were subjected to relatively similar-sized intruders. We used a two by three ANOVA with pair sizes (both parents large, both parents small) as the between factor and the three relative intruder sizes (smaller, same size and larger than the parent) as the within factor (i.e. repeated factor). We recorded the behaviour of males and females separately, except for the time that both parents spent together near the intruder and with the offspring. We predicted that, if there were no confound, both large and small parents would show the same level of defensive behaviour (i.e. no main effect of parent size) and that both would respond to the three intruder sizes in the same way (i.e. no interaction between parent size and intruder size). None of the eight ANOVAs (i.e. percentage of time parent spent near the intruder and with offspring, separately or together, and the number of bites each parent directed towards the intruder) showed a significant size main effect or a significant interaction between parent size and intruder size. Based on these results, we concluded that the absolute size of each parent in homogeneous pair types would not influence the parental behaviour of either parent. With this foundation, we proceeded with the full analysis to examine whether changing the size of one parent affected the behaviour of the other parent in response to changing intruder sizes.

Data Analysis

These data did not differ significantly from a normal distribution and we used either a four-way or a three-way mixed ANOVA. Statistica (Statsoft 1998) was used to perform the statistical analyses. For the ANOVAs in which male and female parent were included as separate factors, we had four factors: male size, female size, parent sex and intruder size. Male and female size were the sizes of the parents and each variable had two levels that corresponded to the two parental sizes: 50 mm and 70 mm.

The parent sex variable had two levels; the behaviour of the male parent and the behaviour of female parent. Intruder size had five levels, each one corresponding to the five sizes of the intruders (i.e. 40, 50, 60, 70 and 80 mm). Since the behaviour of male and female parents (parent sex) were measured from intact pairs, all analyses considered parental pairs as the experimental units. Thus, parent sex and intruder size were treated as 'within pairs' (i.e. repeated measures) factors and male size and female size, which differed between pairs, were treated as independent factors.

To summarize, the statistical design was a two (male parent size: small versus large) by two (female parent size: small versus large) by two (sex: male versus female behaviour) by five (intruder size: 40–80 mm) ANOVA. Factors that affect the parents' relative role selections would be reflected in the size of the sex effect. For example, if small males spend less time near the intruder (relative to their female partners) than large males, this would be reflected in a male parent size*sex interaction. If females spend more time near the intruder (relative to their male partners) when the intruder is large, this would be reflected in a sex*intruder size interaction. If females spend more time near the intruder (relative to the male) when the intruder is large but only when the male partner is small, this would be reflected in a male size*sex*intruder size interaction. For the ANOVAs testing the time that the male and female parents were together near the intruder or with the offspring, we omitted the parent sex factor, yielding a three-factor design: two (male size) by two (female size) by five (intruder size).

RESULTS

Time Spent by Each Parent within the Intruder Area

To test the effects of parent size and intruder size, we used the four-factor ANOVA: two (male size) by two (female size) by two (parent sex) by five (intruder size), with the latter two factors treated as repeated measures (Table 1, Fig. 2). There was a significant main effect of sex, indicating the typical division of sex roles, with the male spending almost 60% of session time near the intruder (defensive role) and the female spending only about 13% of session time near the intruder. The significant main effect of intruder size indicates that, in general, as intruder size increased (representing increased threat), parents spent a greater percentage of time in the intruder area, although there was no apparent difference between the two largest intruder sizes (70 and 80 mm).

There were also two significant double interactions, male size*parent sex and female size*parent sex, indicating that sex role differentiation was modified by the size of the parents. When the male of the pair was large, sex role differentiation as measured by the percentage of time spent near the intruder was maximal (64.6% versus 8.5% for males and females); however, when the male was small, this sex difference was reduced to 53% versus 18.8%. Similarly, when the female of the pair was small,

Table 1. Results of four-way mixed ANOVA for time spent near the intruder

	df effect	MS effect	df error	MS error	F	P
Main effects						
1 (Male size)	1	13	36	762.44	0.02	NS
2 (Female size)	1	8	36	762.44	0.01	NS
3 (Parent sex)	1	210 089	36	711.64	295.22	<0.05
4 (Intruder size)	4	1320	144	358.19	3.67	<0.05
Interactions						
1×2	1	7	36	762.44	0.01	NS
1×3	1	10 645	36	711.64	14.96	<0.05
2×3	1	4224	36	711.64	5.94	<0.05
1×4	4	501	144	358.19	1.40	NS
2×4	4	51	144	358.19	0.14	NS
3×4	4	536	144	254.60	2.11	NS
1×2×3	1	958	36	711.64	1.35	NS
1×2×4	4	91	144	358.19	0.26	NS
1×3×4	4	1587	144	254.60	6.24	<0.05
2×3×4	4	23	144	254.60	0.09	NS
1×2×3×4	4	77	144	254.60	0.30	NS

males averaged 62% of session time near the intruder compared with 10.3% for females; when the female was large, this difference was reduced to 55.9% versus 16.6%. Thus, sex role differentiation as measured by the percentage of time spent near the intruder was maximal when large males were paired with small females, as is typical in natural environments, and reversing the typical size relationship (small male paired with a large female) modified the typical division of roles by making the behaviour of the male and female more similar.

The only significant higher-order interaction was for male size*parent sex*intruder size, indicating that the effect of male size on sex role differentiation resulted primarily from how the pairs responded to the two largest and most threatening intruders. The differences between the male and female parents were not much affected by male parent size when the intruder was relatively small (40–60 mm). However, for intruders in the 70–80-mm range, large males spent 76.0% and 68.9% of their time near the intruder compared with 13.8% and 9.8% for

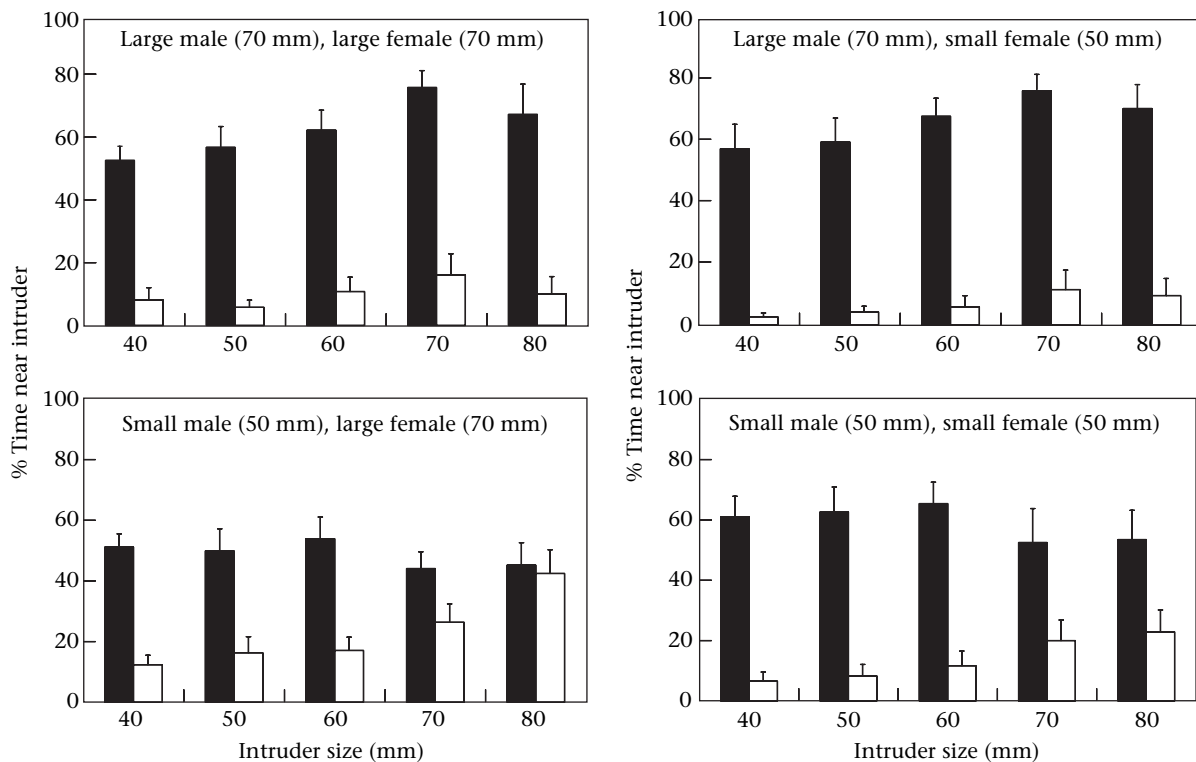


Figure 2. Percentage of time (mean \pm SE) female and male parents spent within the intruder area (total possible time = 900 s). Each panel represents one of the four pair types. X axis denotes the general size of the intruder. The actual intruder size was as much as 5 mm greater than the size indicated. \square : female; \blacksquare : male.

females. In contrast, small males spent only 48.3% and 49.4% of their time near the intruder compared with 23.2% and 32.7% for females. Thus, the difference in time each parent spent near the intruder for pairs with a small male parent was mediated both by a decrease in the time spent by male parents and an increase in the time spent by the female parents.

Time Spent by Each Parent within the Offspring Area

To test the effects of parent size and intruder size on the percentage of time a parent spent with the offspring, we used an ANOVA identical to the one used for the percentage of time spent near the intruder. Because parents spent relatively little time (roughly 15% of total session time) in the middle of the experimental tank, away from both offspring and intruder, the results are a mirror image of those for time in the intruder area (Table 2, Fig. 3). Thus, the parent sex effect showed that females spent more time near the offspring than males, and the intruder size effect showed that parents spent a greater percentage of time near the offspring when the intruder was small than when the intruder was large. The male size*parent sex interaction showed that the sex role differentiation as measured by the percentage of time with the offspring was greater when the male parent was large than when the male parent was small, and the female size*parent sex interaction showed that sex role differentiation was greater when the female parent was small than when the female parent was large. The triple interaction of male size*parent sex*intruder size showed that sex role differentiation as measured by the percentage of time with the offspring was relatively unaffected by male size for the three smallest intruders, but for the two larger intruders, and especially for the largest, sex role differentiation was reduced for pairs with small male parents compared with pairs with large male parents.

Similar to the percentage of time spent near the intruder, the percentage of time with the offspring illustrates

that large females paired with small males increased their time away from the offspring (and thus more closely resembled the behaviour of the small mate) only for the two largest intruders.

Bites Directed at Intruder by Each Parent

Bites were considered direct assaults against the intruder and thus may indicate a different level of aggressive intensity compared with simply being near an intruder. Bites directed towards the intruder were subjected to the same four-way mixed ANOVA as the time measures (Table 3, Fig. 4). For the most part, the pattern of results for number of bites, a direct measure of aggression, was parallel to the pattern for time in the intruder area. Thus, there were significantly more bites by males than by females, and number of bites increased as intruder size increased with a peak at 70 mm.

The male size*parent sex and female size*parent sex interactions again indicated that the sex difference in biting was greater for pairs with large males than for pairs with small males, and greater for pairs with small females than for pairs with large females. Similar to the time near the intruder, there was a significant and similar triple interaction for male size*parent sex*intruder size. For pairs with large males, the difference in the number of bites that each sex directed towards the intruder increased as intruder size increased, but the opposite was the case for pairs with small males. The decrease in the sex difference for pairs with small males was mediated almost entirely by a marked increase in the number of bites directed by the female of the pair as intruder size increased. The number of bites that male parents directed towards intruders increased with intruder size until the size of the intruder was equal to that of the male parent (50 and 70 mm, for small and large male parents, respectively), after which the number of bites directed by the male parent decreased. Although the number of bites by female parents towards intruders also increased with intruder size, females paired with smaller males directed significantly more bites

Table 2. Results of four-way mixed ANOVA for time spent with offspring

	df effect	MS effect	df error	MS error	F	P
Main effects						
1 (Male size)	1	663	36	1087.994	0.61	NS
2 (Female size)	1	236	36	1087.994	0.22	NS
3 (Parent sex)	1	265.513	36	985.64	269.38	<0.05
4 (Intruder size)	4	2601	144	364.350	7.14	<0.05
Interactions						
1×2	1	5	36	1087.994	0.01	NS
1×3	1	5942	36	985.645	6.03	<0.05
2×3	1	5120	36	985.645	5.19	<0.05
1×4	4	874	144	364.350	2.40	NS
2×4	4	91	144	364.350	0.25	NS
3×4	4	337	144	269.806	1.29	NS
1×2×3	1	748	36	985.645	0.756	NS
1×2×4	4	445	144	364.350	1.22	NS
1×3×4	4	1002	144	269.806	3.72	<0.05
2×3×4	4	69	144	269.806	0.26	NS
1×2×3×4	4	182	144	269.806	0.68	NS

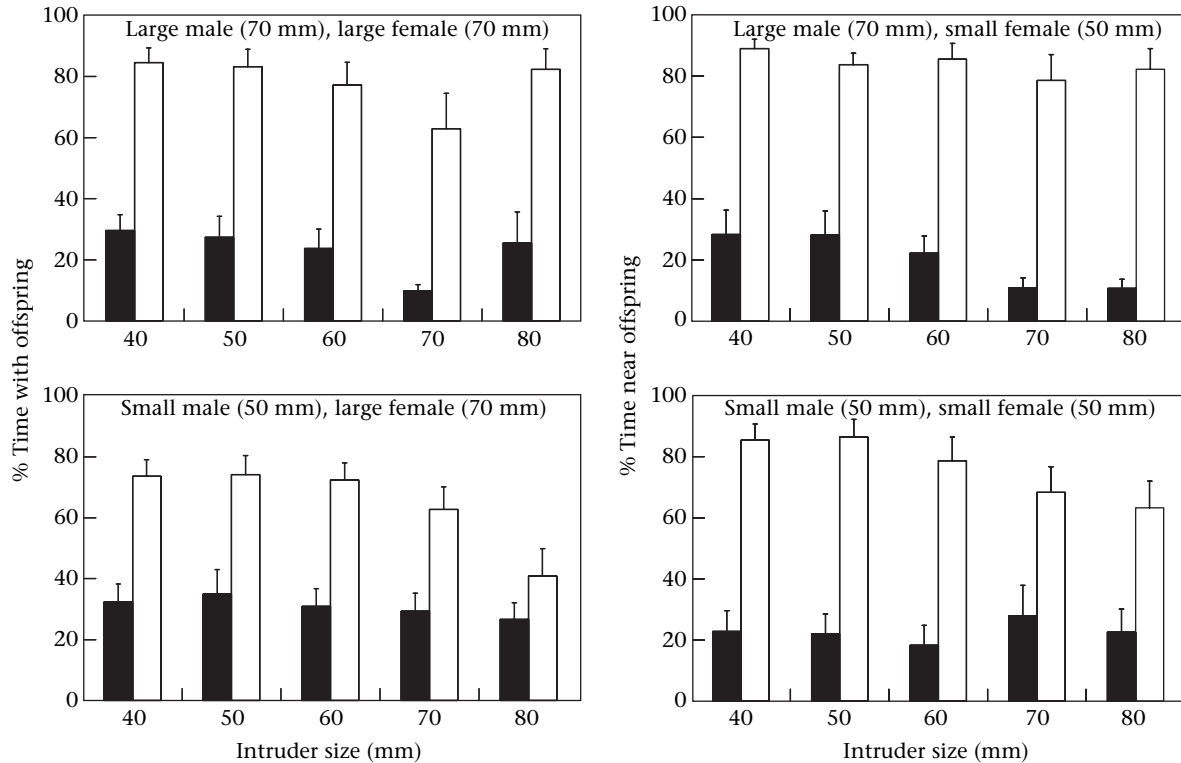


Figure 3. Percentage of time (mean \pm SE) female and male parents spent within the offspring area. See legend for Fig. 2 for more details.

towards the intruder than females paired with larger males, and they continued to increase their biting even when intruders were larger than their mates, whereas females mated to larger males did not.

There was an additional significant triple interaction for the bite measure male size*female size*parent sex that was not significant for the intruder time measure. For all four of the parental size conditions, more bites were directed at the intruder by the male parent than by the female parent; however, for pairs with a large male and small female, males directed significantly more bites than females. Thus, males were much more aggressive than

their female mates when they were larger than their mates but their behaviour was more similar to that of their mates when they were the same size or smaller than their mates.

Time Spent Together within the Intruder Area and within the Offspring Area

The percentage of time that the parental pair spent together in the intruder area was analysed with a three-way mixed ANOVA: two (male size) by two (female size) by

Table 3. Results of three-way mixed ANOVA for total bites towards the intruder

	df effect	MS effect	df error	MS error	F	P
Main effects						
1 (Male size)	1	48 952	36	104 705.0	0.4675	NS
2 (Female size)	1	6667	36	104 705.0	0.0637	NS
3 (Parent sex)	1	4 958 861	36	27 586.6	179.7561	<0.05
4 (Intruder size)	4	187 561	144	34 008.9	5.5151	<0.05
Interactions						
1 \times 2	1	380 257	36	104 705.0	3.63	NS
1 \times 3	1	394 447	36	27 586.6	14.30	<0.05
2 \times 3	1	202 455	36	27 586.6	7.33	<0.05
1 \times 4	4	75 509	144	34 008.9	2.22	NS
2 \times 4	4	4677	144	34 008.9	0.13	NS
3 \times 4	4	25 499	144	15 142.9	1.68	NS
1 \times 2 \times 3	1	128 845	36	27 586.6	4.67	<0.05
1 \times 2 \times 4	4	24 976	144	34 008.9	0.73	NS
1 \times 3 \times 4	4	79 750	144	15 142.9	5.26	<0.05.00
2 \times 3 \times 4	4	2635	144	15 142.9	0.17	NS
1 \times 2 \times 3 \times 4	4	15 320	144	15 142.9	1.01	NS

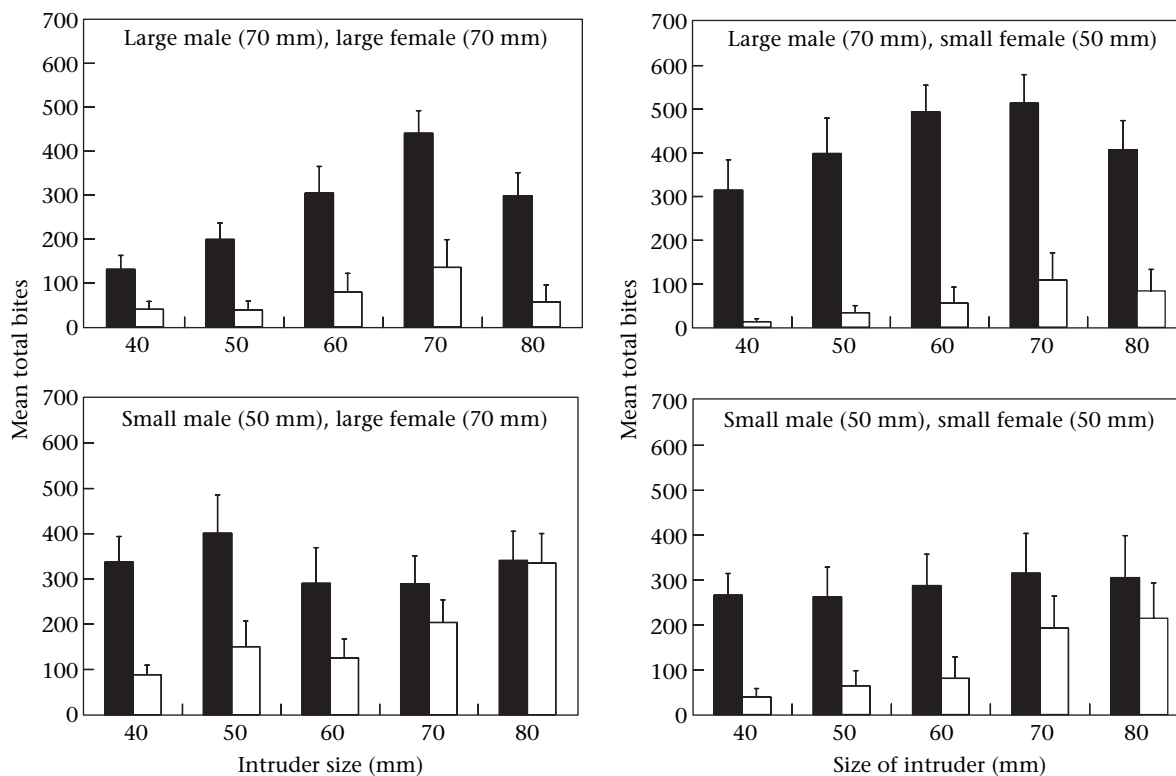


Figure 4. Mean number (\pm SE) of bites male and female parents directed at the intruder partition. See legend of Fig. 2 for more details.

five (intruder size) (Table 4, Fig. 5). There was a significant main effect of male size on time spent in the intruder area. Pairs spent significantly more time together in the intruder area when the male of the pair was small. Female size did not have a significant effect. There was also a significant intruder size effect, showing that pairs remained together in the intruder area longer when intruders were larger. There was only one significant interaction, that between male size and intruder size. Pairs remained together in the intruder area longer when the male of the pair was small compared with when the male of the pair was large regardless of intruder size, but this effect was magnified for larger intruders. In particular, for the largest intruder size, small males spent almost three times more time with the female in the intruder area compared with large males.

Table 4. Results of three-way ANOVA for percentage of time both parents were together near the intruder

	df	MS	df	MS	F	P
	effect	effect	error	error		
Main effects						
1 (Male size)	1	2673	36	466.86	5.73	<0.05
2 (Female size)	1	658	36	466.86	1.41	NS
3 (Intruder size)	4	1583	144	153.30	10.33	<0.05
Interactions						
1 \times 2	1	444	36	466.86	0.95	NS
1 \times 3	4	505	144	153.30	3.30	<0.05
2 \times 3	4	20	144	153.30	0.13	NS
1 \times 2 \times 3	4	107	144	153.30	0.70	NS

The percentage of time the parental pair remained together with the offspring was also analysed using a three-way mixed ANOVA (Table 5, Fig. 6). However, unlike the intruder and offspring time analyses for males and females separately, there were no significant main effects or interactions for the percentage of time the pair remained together with the offspring. That is, neither male nor female size nor intruder size had a significant effect on how long the pair remained together with the offspring.

DISCUSSION

Parental Role Acceptance Based on Relative and Absolute Sizes

We tested the hypothesis that parental task specialization would be driven by an assessment process in which parents would accept a defensive role or an offspring care role based on their size relative to that of their mate and/or an intruder. We expected the male to accept the defensive role when he was the larger parent because this is the sex-typical size relationship and prior studies have shown that the male specializes in territorial defence (Lavery & Reeb 1994; Wisenden 1995; Itzkowitz et al. 2001). Our present results confirm that males emphasize defence (time near intruder; number of bites towards the intruder) whereas females emphasize offspring care (time with offspring).

The hypothesis that size, irrespective of sex, determines the division of roles was partially supported. Overall, the sharp dichotomy between the male's emphasis on

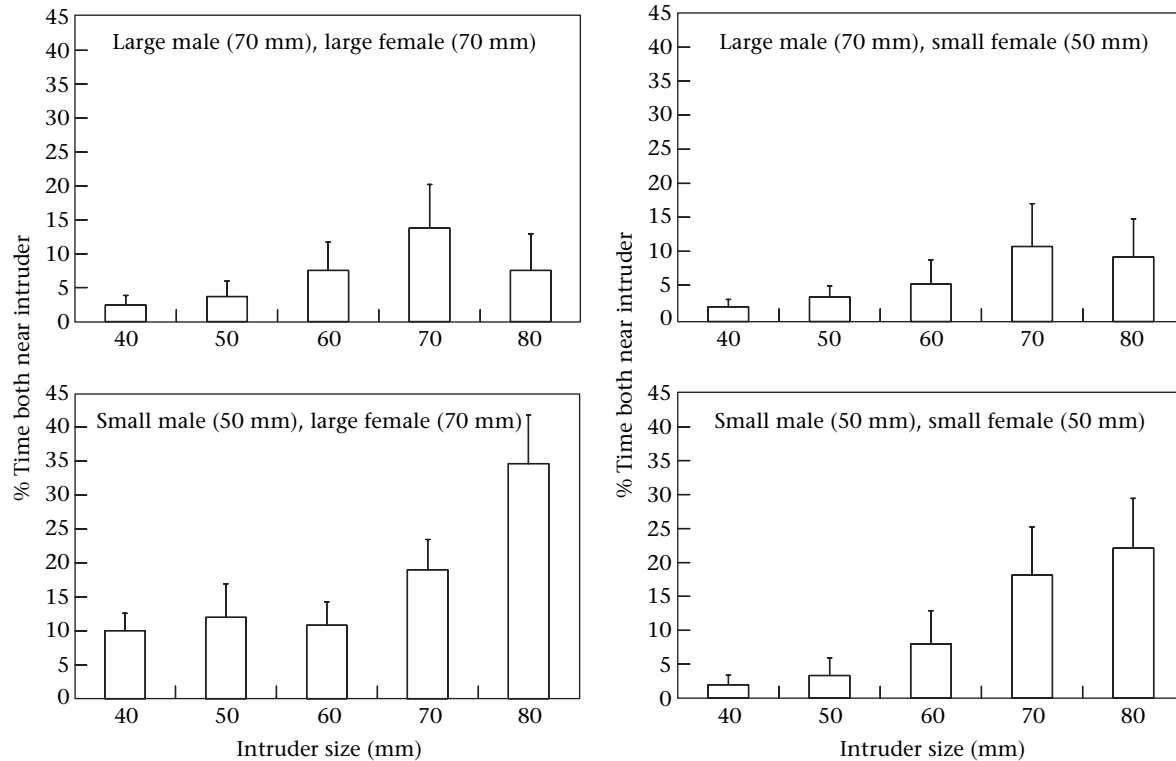


Figure 5. Percentage of time (mean \pm SE) the male and female spent together within the intruder area when confronted with the five differently sized intruders.

defensive behaviour and the female's emphasis on offspring care became less pronounced when the male was small (irrespective of the female's size). In effect, both large and small females increased their defensive effort when paired with small males, whereas small males marginally reduced their own defence. This trend was especially apparent when such pairs were faced with large intruders, indicating that females assess their mates' size relative to that of an intruder. The tendency for females to assist their smaller mates became more pronounced for large females, indicating that the females' behaviour depended on their assessment of their own size relative to that of their mate and that of the intruder. There was no support for the hypothesis that female parental roles changed independently of an immediate threat, because females (both large and small) that were paired with small

males showed the typical reluctance to defend against small intruders.

In addition to an increase in time spent near the large intruder when paired with a small male (a mean increase in total time of about 23%), large females reduced the time they spent with the offspring (decline of about 30%). Small males spent less time than large males near the largest intruder (a mean decline of about 19.5%), suggesting that females mated to small males were compensating for their mates' reduced time near the intruder (but see below). The small male's increase of about 6% in offspring time (compared with large males) did not offset the large female's sharp decline in time spent with offspring. Thus, the small male did not fully compensate for the female's reduction in offspring time. Instead, the small male spent more time in the 'elsewhere' area (between the intruder and the offspring), perhaps providing a defensive posture. Thus, when confronted by very large intruders, large females paired with small males made much larger changes in their parental behaviour than did their smaller mates. For the smaller intruders, there were only minimal differences between small and large females and between small and large males.

While the relative sizes of the male, the female and the intruder did influence the division of roles, it was clear that males and females did not reverse roles. For example, although large females increased their defensive behaviour in an amount similar to the male's decline in defensive behaviour, especially when confronted by the largest intruder, the female usually confronted the intruder only when her mate was also present. Because the total time

Table 5. Results of three-way ANOVA for percentage of time both parents were together with offspring

	df effect	MS effect	df error	MS error	F	P
Main effects						
1 (Male size)	1	135	36	519.95	0.26	NS
2 (Female size)	1	474	36	519.95	0.91	NS
3 (Intruder size)	4	515	144	241.77	2.13	NS
Interactions						
1 \times 2	1	660	36	519.95	1.27	NS
1 \times 3	4	538	144	241.77	2.20	NS
2 \times 3	4	94	144	241.77	0.39	NS
1 \times 2 \times 3	4	325	144	241.77	1.35	NS

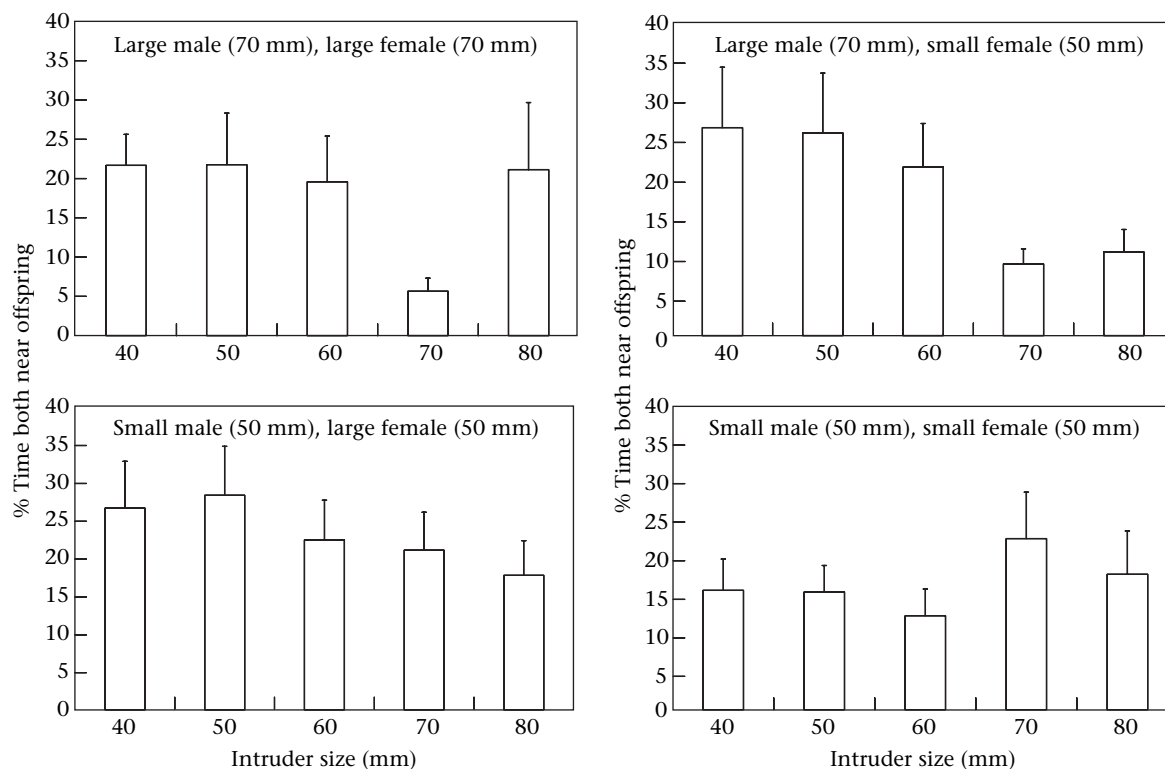


Figure 6. Percentage of time (mean \pm SE) the male and female spent together within the offspring area when confronted with the five differently sized intruders.

females spent near the intruder (Fig. 2) and the total time they spent near the intruder with their mates (Fig. 5) were similar, females did not increase independent action against the intruder, but rather increased the time they spent supporting their mates. Females attacking intruders in support of the male has been reported previously for pairs in which the male was slightly larger than the female (Itzkowitz et al. 2001). This behaviour also extends to females that were much larger than their mates and were perhaps more capable of defeating large intruders than were their small mates. Further experiments are required to determine whether the large female would have increased her time near the intruder if the male were absent.

The hypothesis that pairs are more likely to jointly attack the most threatening intruders was supported. That is, with increasing intruder size, both members of the pair increasingly attacked the intruder together. This relationship held true for all pair types, including small females paired with large males. However, it was especially obvious when the male was small and again illustrates that the female (irrespective of her size) was more likely to support a more vulnerable small mate than a large one. Although these data cannot separate whether females join males or males join females when confronting an intruder, our observations indicate that females are more likely to join males that are already in the act of attacking the intruder.

Role Flexibility

Females appear to have a more flexible parental role than males because females were more likely to assist

males in their role (defence) than the reverse (offspring care). However, Lavery & Reeb (1994) found that widowed convict cichlid males adopt the female's role of offspring care, whereas widowed females continue to stay with the offspring without increasing defensive behaviour, suggesting that the male's role is more flexible (see also Itzkowitz 1984 for Texas cichlids, *Herichthys cyanoguttatus*). Perhaps in the absence of the female, the male has no choice but to increase direct care. In our experiments, the male could rely on the female to emphasize offspring care. This is similar to Whittingham et al.'s (1994) observations on tree swallows, *Tachycineta bicolor*, that widowed birds compensate more for their mates' absence than birds whose mates are only handicapped. Qvarström (1997) also observed that female collared flycatchers, *Ficedula albicollis*, correspondingly increase their offspring feeding when they are paired with males that invest more in territorial defence. In a study of starlings, *Sturnus vulgaris*, Wright & Cuthill (1990) found that the interactions between members of a pair further influence each individual's response to external factor. Thus, the male convict cichlid may spend marginally more time with his offspring if the female reduces her time. Preliminary observations of convict cichlids in our laboratory provide evidence of one parent reacting to the actions of the other (such as the large male chasing the small female away from the intruder and back to the offspring); this behaviour also has been observed in other studies on cichlid fish (Smith-Grayton & Keenleyside 1978; Itzkowitz 1984).

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