

How Similar is the Coordination of Parental Roles Among Different Pairs? An Examination of a Monogamous Fish

M. Itzkowitz*, N. Santangelo* & M. Richter†*

*Departments of *Biological Sciences and †Psychology, Lehigh University,
Bethlehem, PA, USA*

Abstract

Although most studies on biparental care assume that parents cooperate in raising offspring, few studies have documented how parents coordinate their activities. Using the biparental convict cichlid (*Archocentrus nigrofasciatum*) we compared the parental behavior of both single ('widowed') parents and individuals within pairs during the 5 d when the offspring were in the relatively uniform and stationary wriggler stage. In particular, we were interested in the consistency of day-to-day parental activities among single individuals and among individuals within pairs. Single parents showed differences in most parental activities that were consistent from one day to the next. This day-to-day consistency remained after an intruder was added and/or the mate was present. Thus, although the social context changed (i.e., presence or absence of mate, presence or absence of an intruder), an individual's consistency remained. The male and female within pairs were significantly correlated in the time spent on most parental activities across experimental pairs. Thus, while individuals within pairs were unique in their performance of a parental activity, paired males and females managed a high degree of correlation (i.e., coordination). In general, pairs were homogeneous in the degree to which males and females were correlated across different parental activities.

Corresponding author: M. Itzkowitz, Department of Biological Sciences, 31 Williams Hall, Lehigh University, Bethlehem, PA 18015, USA. E-mail: mi00@lehigh.edu

Introduction

An obvious requirement of biparental care is that each parent supports the activities of the other parent. While such cooperation occurs in all biparental species, few studies have examined how this is achieved (Gowaty 1996). One possibility is that the individuals of a pair behave independently of each other with the offspring benefiting from the sum of their parents' activities. If so, then

we would not expect an individual to accept new parental roles when widowed. There is some evidence supporting this scenario from bird studies in which either parent was removed (e.g., Sasvari 1986) or the ability of one parent to participate in offspring care was reduced (e.g., Wright and Cuthill 1989). These manipulations revealed that both the remaining or normal parent's parental behavior was largely unchanged, except for an increase in the intensity of parental care.

In many biparental species, the two parents assume different roles. This type of role division has been observed in some birds (Kendeigh 1952) where females spend more time incubating while males emphasize territorial defense. Also, monogamous rodents may also have a division of roles in which the female may emphasize more pup care and protection than the male (e.g., Solomon 1993; Storey et al. 1994). In comparison with these studies on biparental birds and mammals, sex differences seem more pronounced in biparental cichlid fish where females spend more time near the offspring while males spend more time patrolling the territory (e.g., Smith-Grayton & Keenleyside 1978; Itzkowitz 1984; Neil 1984; Rangeley and Godin 1992). Widows in such biparental species would need to modify their roles if they were to successfully raise their offspring. In fact, the sex-typical division of parental roles seen in biparental cichlids disappears when either sex is 'widowed' (e.g., Itzkowitz 1984; Lavery & Reeb 1994). This type of role division bears some resemblance to human parental behavior in that either sex can rear the offspring, but a sex-based division of labor appears when both parents are present (e.g., Jones & Heermann 1992; Hoffman & Kloska 1995). Thus, the behavior of these biparental species appears more complex than individuals working independently to raise the same offspring.

In a previous study (Itzkowitz et al 2001), we described the division of roles in the biparental convict cichlid fish (*Archocentrus nigrofasciatum*) and determined the following: (1) as expected from previous studies on other biparental cichlids, single male and female parents behaved similarly with both sexes spending most of their time near the offspring, (2) when an intruder was present, single males spent more time near the intruder than did single female parents, (3) in the absence of intruders, paired males spent more time away from the offspring than did their mates, (4) in the presence of an intruder, both males and paired females spent more time near the intruder than did single males and females and (5) paired males spent much more time near an intruder than did their mates. We concluded that the division of roles became most pronounced with both the presence of the mate and the presence of an intruder.

The presence of a mate may have other effects beyond causing an individual to emphasize one parental role over another. Here, we further analyze the data generated from these experiments to test whether the parental roles assumed by individual males and females are more or less different than those assumed by their same-sex counterparts in other pairs. We also examine whether individual differences are influenced by the presence of the mate. We know of no study that has examined for individual differences within

monogamous pairs although such studies have been conducted on females of polygynous species. Such parental differences among primate females have been termed differences in ‘temperament’ (see review by Maestriperi 1999). Studies on parental temperament have not been conducted on fish, but Coleman and Wilson (1998) found that juvenile polygynous pumpkinseed sunfish (*Lepomis gibbosus*) show consistent individual differences in shyness or boldness when repeatedly presented with predatory models and novel food stimuli. Here we test whether such consistent individual parental differences are found within single and paired individuals of the convict cichlid fish (*Archocentrus nigrofasciatum*).

We also examined how the male and female of a pair coordinate their parental activities, that is, whether they tend to take similar or complementary parental roles to their mates. In this regard, we know of only Wynne-Edwards (1995) study on the synchronization of parental behavior between male and female Djungarian hamsters. She demonstrated that males and females tend to perform the same activities at the same time. However, convict cichlids have a sharper division of roles than Djungarian hamsters making it unclear whether males and females are positively (as in Djungarian hamsters) or negatively correlated for the same activity.

We also determined whether mates of different pairs are correlated in the same way in their performance of specific parental activities. For example, while it is possible that males in different pairs show day-to-day consistent differences for a particular activity, males and females within pairs may be able to compensate for each other’s differences in behavior such that male–female correlations in behavior are homogeneous across pairs.

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 the egg, wriggler, and free-swimming fry. The eggs hatch into wrigglers and remain at this stage for 4–6 d, until the yolk sacs have been absorbed. The young then become free-swimming fry. At the egg and wriggler stages, the female spends more time in direct care than does the male, but as the young become free-swimming fry, parental activities are shared more equally by the parents (Smith-Grayton and Keenleyside 1978); this pattern is similar to the behavior found in other types of substrate-spawning biparental cichlids (Barlow 1974; Itzkowitz and Nyby 1982; Itzkowitz 1984).

All of the fish used in these experiments were raised in our lab 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 female parents are aggressive to intruding convict cichlid males (Itzkowitz et al. 2001).

Experimental Design

Males and females were maintained separately in several 600 l stock tanks. Three males of equal size, and three females each approx. 1 cm smaller than the males, were placed in an experimental tank (470 l). 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) a 25-cm offspring area that included a flower pot, (2) a 15-cm intruder compartment at the opposite end to the offspring area formed by a sheet of clear plastic extending across the width of the tank, (3) an intruder area designated as 10 cm from the clear plastic partition, and (4) an elsewhere area encompassing the 70-cm space between the intruder and offspring areas.

At the onset of pair formation, we removed the four unpaired fish. One of the unpaired 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 and Draud 1992). For pairs left intact, the intruder was removed from the intruder compartment after eggs were laid in the flower pot ($n = 15$). For the single-parent condition, either the male ($n = 10$) or female parent ($n = 10$) was then removed. After the eggs hatched into wrigglers, we videotaped the two parents or the remaining parent of the pair for 25 min before adding an intruder and videotaping for another 25 min. Each pair or single parent was observed over the first five days of the wriggler stage. On each test day, an intruder that was approximately the same size as the male parent was randomly selected from a large stock population. After the completion of the five test days, the pair or the male or the female parent was placed in a separate stock tank to avoid using an individual more than once.

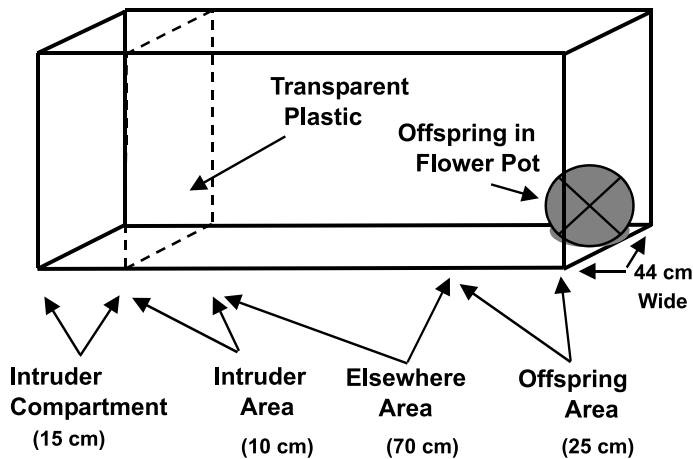


Fig. 1: A diagram of the experimental aquarium

We were alert to the possibility that the smaller size of the female, relative to both her mate and the intruder, might influence her parental role selection (i.e., she might be less inclined to attack the intruder). A current study (Itzkowitz, unpubl. data) addresses this point 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 the offspring: The total amount of time (in s) that a parent remained in the offspring area.

Time at the intruder: The total amount of time (in s) that a parent remained within the intruder area.

Bite rate: The total number of times the parent bit (i.e., mouth open) at the intruder compartment divided by the total amount of time the parent spent within the intruder area. We employed rate because the number of bites is highly correlated with the amount of 'Time at the intruder.'

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

Frontal display Rate: This behavior is similar in form to the lateral display except the parent was facing 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.

Unlike bites, neither frontal displays or lateral displays were significantly correlated to an individual's 'time at the intruder.' For the sake of brevity, we present only the rates.

Analyses

The five parental activities were examined for consistency across the five days in which the wrigglers were present. We determined the extent to which the same fish behaved consistently from one day to the next by calculating the intraclass correlation coefficient with SPSS [Statistical Package for the Social Sciences (Release 10.0.5) 1999] using a two-way ANOVA, with fish as a random factor and test session (days 1–5 of the wriggler stage) as a fixed factor. Only fish with data from all five test days were included in these analyses (from zero to three fish were excluded from each condition because of a missing datum). In addition, several more fish had to be excluded from the rate measures (i.e., bite rate, frontal display rate, and lateral display rate per minute). These behavior rates were calculated by taking the number of responses and dividing by the number of minutes near the

intruder. If any of the fish had no time near the intruder for a session this measure remained undefined and that subject was dropped from the rate analysis. Because of the large number of statistical tests ($n = 20$), one for each condition and behavior tested, to hold the overall probability of a type I error at 0.05, the Bonferroni correction was employed yielding $\alpha = 0.0025$ for each significance test.

Results

Time with the Offspring, Time at the Intruder, Bite rate

For time with the offspring, time at the intruder, and bite rate, the intraclass correlation coefficients (see Table 1) showed that a significant proportion of the variation in behavior could be attributed to differences among individuals, and that individuals were consistent in their investment in these activities over the five test sessions. This was true whether it was the male or female parent, whether the individual was tested singly or paired with its mate, and (in the case of time with the offspring) whether the intruder fish was present or not. There were only three instances where the intraclass correlation was not significant: time with the offspring for males tested in pairs with an intruder present; time at the intruder for males tested singly; and bite rate for females tested singly.

Lateral Display Rate

Single males and single females made very few lateral displays (males exhibited no lateral displays in 13 of 45 observations, and females exhibited no lateral displays in 23 of 50 observations). These data seemed inappropriate to test for consistency of response using intraclass correlation. Many more lateral displays were made by paired males, thus justifying the planned analysis. Lateral displays made by paired males were consistent across the five test sessions. For paired females, again too few lateral displays were made to justify further analysis (females failed to display in 20 of 65 observations). Because of the paucity of data, we did not include the lateral displays in Table 1.

Frontal Display Rate

Single females made very few frontal displays (no frontal displays in 21 of 50 observations) making further analysis inappropriate. The intraclass correlation coefficients were not significant in any of the remaining three test conditions.

Coordination of the Paired Male and Female

Do the male and female parents of an intact pair tend to adopt matched or complementary parental roles? To explore this question, we developed an index of coordination to measure the extent to which the male and female of a pair were

Table 1: Intraclass correlation coefficients for time at the offspring (Time/Off), time at the intruder (Time/Int), bite rate (Bite), and frontal displays (FD). Single = single parents; pair = paired parents. No intruder = intruder not present; w/Intruder = intruder present; intraclass C.C. = intraclass correlation coefficient; SE = standard errors above and below intraclass correlation coefficient; Sign. = significance level; * = $p < 0.0025$; NS not significant = $p > 0.0025$

| Behavior | Single/pair | Sex | No intruder/intruder | Intraclass C.C. | SE | F-test | Sign. |
|----------|-------------|---------|----------------------|-------------------|------|------------------|-------|
| Time/Off | Single | Males | No intruder | 0.44 | 0.15 | F(8,32) = 4.92 | * |
| Time/Off | Single | Males | w/intruder | 0.44 | 0.15 | F(8,32) = 4.96 | * |
| Time/Off | Pair | Males | No Intruder | 0.37 | 0.12 | F(13,52) = 3.90 | * |
| Time/Off | Pair | Males | w/intruder | 0.15 | 0.10 | F(12,48) = 1.90 | NS |
| Time/Off | Single | Females | No intruder | 0.58 | 0.14 | F(9,36) = 7.89 | * |
| Time/Off | Single | Females | w/Intruder | 0.36 | 0.14 | F(9,36) = 3.76 | * |
| Time/Off | Pair | Females | No intruder | 0.30 | 0.12 | F(13,52) = 3.13 | * |
| Time/Off | Pair | Females | w/Intruder | 0.83 | 0.07 | F(12,48) = 25.58 | * |
| Time/Int | Single | Males | w/Intruder | -0.06 | 0.13 | F(8,32) = 0.70 | NS |
| Time/Int | Pair | Males | w/Intruder | 0.31 | 0.12 | F(12,48) = 3.28 | * |
| Time/Int | Single | Females | w/Intruder | 0.64 | 0.13 | F(9,36) = 10.02 | * |
| Time/Int | Pair | Females | w/Intruder | 0.70 | 0.10 | F(12,48) = 12.74 | * |
| Bites | Single | Males | w/Intruder | 0.72 | 0.12 | F(8,32) = 13.91 | * |
| Bites | Pair | Males | w/Intruder | 0.61 | 0.12 | F(12,48) = 8.80 | * |
| Bites | Single | Females | w/Intruder | 0.41 | 0.17 | F(6,24) = 4.48 | NS |
| Bites | Pair | Females | w/Intruder | 0.37 | 0.13 | F(11,44) = 3.96 | * |
| FD | Single | Males | w/Intruder | 0.16 | 0.12 | F(8,32) = 1.98 | NS |
| FD | Pair | Males | w/Intruder | 0.28 | 0.12 | F(12,48) = 2.54 | NS |
| FD | Single | Females | w/Intruder | Insufficient data | | | |
| FD | Pair | Females | w/Intruder | 0.02 | 0.08 | F(11,44) = 1.09 | NS |

correlated for a particular activity over the five test sessions. For each activity, we determined the Pearson correlation coefficient between the male and female of each pair using scores from each of the five test sessions. If the male and female of a pair were coordinated such that they selected matched roles (e.g., if the male was at the intruder, the female also tended to be at the intruder) these correlations should tend to be positive. If the male and female of a pair selected complementary roles (e.g., if the male was at the intruder, the female tended to stay away from the intruder and be with the offspring) these correlations should tend to be negative. We used all 15 pairs in these analyses. For pairs with missing data, the correlations were based on four sessions rather than five.

Because the distribution of correlation coefficients departs from normal the more the correlation differs from zero, we used the Fisher r to Z transformation to normalize the data for all statistical analysis on male–female coordination (see, e.g., Zar 1996). These Z scores were taken as an index of coordination, and used as the dependent variable in subsequent analyses. The mean Z scores \pm the standard error of the mean (SE) for the six different behavioral measures (time with the offspring with and without an intruder present, time at the intruder, bite rate, frontal display rate, and lateral display rate) are presented in Fig. 2. The means for three of these behavioral activities (time with offspring with an intruder present, time at the intruder, and the number of frontal displays) were significantly different from 0 at $\alpha = 0.008$ (to hold the overall probability of a type I error at 0.05) indicating significant positive coordination of paired male and female parents for these activities, while the means for the other three were not significant. However, this outcome does not necessarily imply that males and females within pairs were more coordinated (positively correlated) for some activities than they were for others. To test this possibility, we performed a two-way repeated measures ANOVA with pair as the random factor and activity as the fixed factor, with Z score used as the dependent variable. There was no significant differences among the six mean Z values [$F(5, 70) = 1.98, p > 0.05$].

The above analyses tested for differences among behavioral activities. Here we test whether correlations between males and females for particular activities were homogeneous across pairs. To test for homogeneity of correlations among pairs, we used a χ^2 test (see Zar 1996, p. 384). Given one significance test for each of the six measures, we again used $\alpha = 0.008$ to hold the overall probability of a type I error at 0.05. For only one measure were the correlations not homogeneous. Correlations between the male and female with respect to time spent with the offspring were homogeneous across pairs both in the absence [$\chi^2(14) = 19.47, p > 0.008$] and presence of an intruder [$\chi^2(14) = 18.79, p > 0.008$]. When an intruder was present, there were significant differences among pairs in the correlation between the male and female with respect to time spent at the intruder [$\chi^2(14) = 30.59, p < 0.008$]. However, male–female correlations were homogeneous across pairs with respect to bite rate [$\chi^2(14) = 21.42, p > 0.008$], frontal display rate [$\chi^2(14) = 12.15, p > 0.008$], and lateral display rate [$\chi^2(14) = 26.30, p > 0.008$].

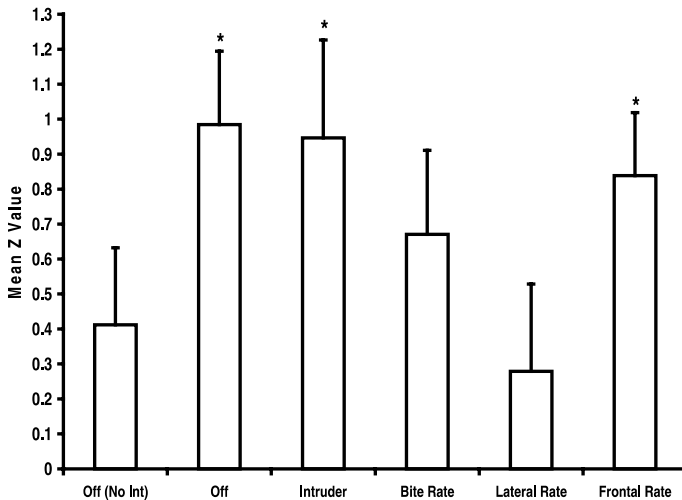


Fig. 2: The mean correlations (Z), and SE, between male and female parents for each activity. For example, the amount of time that the male spent with the offspring in each of the 5 d, when the intruder was present, was correlated with the time spent by the female. The * above a bar indicates that it deviated significantly from zero using a t -test. Off (no int.) = time at offspring and no intruder present; Off = time at offspring with intruder present, intruder = time at intruder; bite rate = number of bites per minute; lateral rate = lateral display rate per minute; frontal rate = frontal display rate per minute

Discussion

Intra-Sex Comparisons

Previous studies of biparental cichlids (Itzkowitz 1984; Lavery & Reebes 1994; Itzkowitz et al. 2001) observed that sex-typical parental roles disappeared when the mate was removed. In particular, single males and females behaved similarly by spending much of their time near the offspring. When an intruder was added, parental sex differences appeared as male parents spent more time attacking the intruder than did female parents (Itzkowitz et al. 2001). The current study illustrates that solitary males and females are similar in other ways. In near isolation-like conditions, both sexes showed a consistent, but individually unique, daily pattern.

With the presence of the mate and/or an intruder, the overall trends seen in solitary single parents (i.e., day-to-day positive correlations) persisted. That is, intraclass correlations revealed that parental behaviors remained highly consistent within individuals, even if they differed significantly among individuals. These consistencies occurred in spite of the dramatic changes in the division of roles caused by changes in social conditions (see Itzkowitz et al. 2001). For example, parental behavior remained consistent over test days although males and females spent less time with the offspring in the presence of the intruder and/or in the presence of the mate.

Each fish/pair was presented with a unique intruder on each test day. We anticipated that the different intruders would behave uniquely and thus stimulate differences in the defensive behavior (i.e., bites, frontal and lateral displays) of the parent across the five test days. However, with the exception of the single female condition, daily bite rates were significantly correlated across test sessions for single males, paired males, and paired females. Thus, the likelihood that an individual would bite was a function of the parent and not the behavior of the intruder. This was consistent with our observations that defenders would bite at stationary intruders, intruders that were swimming idly up and down the partition, and intruders biting at the defenders. However, threats produced a different response from the defenders. Under most conditions, lateral displays and frontal displays were inconsistent over the test days. Our observations indicated that parents were not likely to threaten a non-threatening intruder but were more likely to threaten in response to an intruder's threat. Thus, threat behavior (e.g., frontal and lateral displays) does appear to be dependent on the behavior of the opponent (e.g., Enquist et al. 1990).

Coordination of Individuals within Pairs

Within pairs, individuals were consistently different from each other. However, pairs were similarly coordinated. That is, each pair must have developed a unique way of partitioning their contributions across parental activities while developing similar levels of coordination for each activity. Although we found no other comparable analyses for biparental animals, human studies have revealed considerable differences in the parental division of roles among two-parent families (e.g., traditional vs non-traditional), which nonetheless retain high levels of parental coordination (e.g., Dienhart 1998).

These correlational data cannot explain how pairs achieved their coordination. However, current studies (unpubl. data) in which one or the other parent is restrained indicate that females join their mates in attacking the intruder and that males return to the offspring when the female is present. Hence, both parents appear responsible for maintaining their high degree of coordination. This positive correlation between parents is dissimilar from the most commonly described pattern observed in humans where there appears to be an inverse correlation between male and female parental activities (e.g., Cowan and Cowan 1988). Instead, convict cichlid pairs appear most similar to biparental birds in which both sexes perform the same activities, and the intensity of the activities appears related to the immediate needs of the offspring.

In summary, same-sex widows and same-sex individuals within pairs were both consistent from day to day while maintaining different intensities for the same activity. Thus, in spite of the development of a division of roles when the mate was present, individuals within pairs may not have had any additional modifications of their parental behavior that impacted on their individual temperaments. The intensity of an individual's behavior was positively correlated with its mate, and pairs were largely similar in the degree to which the male and

female were correlated for each activity. These correlations may have been caused by pair members matching their parental behavior to their mate's and/or both individuals responding to the same external conditions (e.g., behavior of the intruder).

Acknowledgements

Financial support was provided by NIH (1 R01 HD36372) awarded to MI. We also appreciate L. Schroeder for critically reading an earlier draft of this manuscript.

Literature Cited

- Barlow, G. W. 1974: Contrasts in social behavior between Central American cichlid fishes and coral-reef surgeon fishes. *Am. Zool.* **14**, 9–34.
- Coleman, K. & Wilson, D. S. 1998: Shyness and boldness in pumpkin seed sunfish: individual differences are context-specific. *Anim. Behav.* **56**, 927–936.
- Cowan, C. P. & Cowan, P.A. 1988: Who does what when partners become parents: implications for men, women, and marriage. *Marriage Family Rev.* **12**, 105–131.
- Dienhart, A. 1998: *Reshaping Fatherhood*. Sage Publications, Thousand Oaks, CA.
- Enquist, M., Leimar, O., Ljungberg, T., Mallner, Y. & Segerdahl 1990: A test of sequential assessment game: fighting in cichlid fish *Nannacara anomala*. *Anim. Behav.* **40**, 1–14.
- Gowaty, P. W. 1996: Field studies of parental care in birds. In: *Parental Care: Evolution, Mechanisms, and Adaptive Significance* (Rosenblatt, J. S. & Snowdon, C. T., eds). *Adv. Study Behav.* **25**, 477–531.
- Hoffman, L. W. & Kloska, D.D. 1995: Parents' gender-based attitudes toward marital roles and child rearing: development and validation of new measures. *Sex Roles* **32**, 273–295.
- Itzkowitz, M. 1984: Parental division of labor in a monogamous fish. *Behaviour*, **89**, 251–260.
- Itzkowitz, M. & Draud, M. J. 1992: Conspecific intruders influence pair formation in a monogamous fish. *Behav. Proc.* **28**, 59–64.
- Itzkowitz, M. & Nyby, J. 1982: Field observations on parental behavior of the Texas Cichlid *Cichlasoma cyanoguttatum*. *Am. Midl. Nat.* **108**, 364–368.
- Itzkowitz, M., Santangelo, N. & Richter, M. 2001: Parental division of labor and the shift from minimal to maximal role specializations; an examination using biparental fish. *Anim. Behav.* **61**, 1237–1245.
- Jones, C. L. & Heermann, J. A. 1992: Parental division of infant care: contextual influences and infant characteristics. *Nursing Res.* **41**, 228–234.
- Kendeigh, S. C. 1952: Parental care and its evolution in birds. *Illinois Biol. Manager.* **22**, 1–358.
- Lavery, R. J. & Reeb, S. G. 1994: Effect of mate removal on current and subsequent parental care in the convict cichlid (Pisces:Cichlidae). *Ethology* **97**, 265–277.
- Maestripieri, D. 1999: The biology of human parenting: insights from nonhuman primates. *Neurosci. Biobehav. Rev.* **23**, 411–422.
- Neil, S. J. 1984: Field studies of the behavioral ecology and agonistic behavior of *Cichlasoma meeki* (Pisces: Cichlidae). *Envir. Biol. Fishes.* **10**, 59–68.
- Rangeley, R. W. & Godin, J-G. J. 1992: The effects of a trade-off between foraging and brood defense on parental behavior in the convict cichlid fish, *Cichlasoma nigrofasciatum*. *Behaviour* **120**, 123–137.
- Sasvari, L. 1986: Reproductive effort of widowed birds. *J. Anim. Ecol.* **55**, 553–564.
- Solomon, N. G. 1993: Comparison of parental behavior in male and female prairie voles (*Microtus ochrogaster*). *Can. J. Zool.* **71**, 434–437.
- Storey, A. E., Bradbury, C. G. & Joyce, T. L. 1994: Nest attendance in male meadow voles: the role of the female in regulating male interactions with pups. *Anim. Behav.* **47**, 1037–1046.
- Smith-Grayton, P. K. & Keenleyside, M. H. A. 1978: Male-female roles in *Heterotilapia multispinosa* (Pisces: Cichlidae). *Anim. Behav.* **26**, 520–526.

- Wright, J. & Cuthill, I. 1989: Manipulation of sex differences in parental care. *Behav. Ecol. Sociobiol.* **25**, 171–181.
- Wynne-Edwards, K. E. 1995: Biparental care in Djungarian but not Siberian dwarf hamsters (*Phodopus*). *Anim. Behav.* **50**, 1571–1585.
- Zar, J. H. 1996: *Biostatistical analysis*. 3rd edn. Prentice Hall, NJ.

Received: June 25, 2001

Resubmitted: November 11, 2001

Initial acceptance: January 14, 2002

Final acceptance: March 7, 2002 (S. K. Sakaluk)