

On the evolutionary pathway of parental care in mouth-brooding cichlid fish

Sigal Balshine-Earn^{1,2*} and David J. D. Earn¹

¹Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

²Konrad Lorenz Institute for Comparative Ethology, Savoyenstrasse 1a, A-1160 Vienna, Austria

Evolutionary theory predicts that differences in parental care patterns among species arose from inter-specific differences in the costs and benefits of care for each sex. In Galilee St Peter's fish, *Sarotherodon galilaeus* (Cichlidae), male care, female care and biparental care all occur in the same population. We exploit this unusual variability to isolate conditions favouring biparental versus uniparental mouth-brooding by males or females. We first review a game-theoretic model of parental care evolution, predictions of which we test experimentally in this paper. Manipulations of the operational sex ratio show that males and females desert their offspring more frequently when the costs of care are high (in terms of lost mating opportunities). Breeding trials with males of different sizes show that small fathers desert more frequently than large fathers. We attribute this to the associated difference in the fitness benefit of biparental care relative to female-only care. Our experimental results confirm that in St Peter's fish the probability of caring is determined facultatively according to current conditions at each spawn. The experiments and model together suggest that interspecific variation in remating opportunities and clutch size may be responsible for differences in care patterns within the subfamily Tilapiini. Our results support the hypothesis that biparental mouth-brooding was the ancestral state of both male and female uniparental mouth-brooding in cichlid fishes.

Keywords: parental care; evolution; vertebrates; fish; cichlids; St Peter's fish

1. INTRODUCTION

This paper is concerned with potential causes of evolutionary transitions in parental care behaviour in cichlid fish. Cichlidae, a tropical freshwater family of fish, has a more diverse range of parental care forms than any other vertebrate family. Thus it provides one of the best opportunities for exploration of evolutionary transitions in parental care.

There is some debate about the evolutionary ancestry of existing cichlid species showing different patterns of care. Two competing theories are illustrated in figure 1: mouth-brooding is thought to have arisen from biparental substrate-guarding (Keenleyside 1991; Sodsuk & McAndrew 1991; Pouyaud & Agnese 1995), but it is not clear whether uniparental mouth-brooding evolved directly from biparental substrate-guarding or via biparental mouth-brooding (Lowe-McConnell 1959; Kraft & Peters 1963; Iles & Holden 1969). This paper describes behavioural manipulations that strongly suggest that uniparental mouth-brooding could have evolved from biparental mouth-brooding.

The costs and benefits of parental care for each sex are believed to determine the evolutionarily stable parental-care state (Maynard Smith 1977; Gross & Sargent 1985; Lazarus 1990; Yamamura & Tsuji 1993). In most species, measurements of these costs and benefits do not shed light on the evolution of the present parental care state.

Parents and offspring have typically coevolved to specific levels and types of care, and the costs and benefits of care to each sex are probably not the same now as they were when the present care state evolved. In the experiments reported below, we have circumvented these problems by using an unusual cichlid (Galilee St Peter's fish, *Sarotherodon galilaeus*), which has flexible parental care behaviour: biparental, female-only and male-only mouth-brooding all occur frequently in the same population (Fishelson & Heinrich 1963; Balshine-Earn 1997). We show that this natural variation in care pattern depends on the costs and benefits of care. It is therefore possible to draw inferences about parental care evolution in cichlid fish from our behavioural experiments with St Peter's fish.

In the next section, we review what is currently known about evolutionary transitions in fish parental care and explain where St Peter's fish fits into this picture. We then review a model that predicts what factors might influence evolutionary transitions in parental care in cichlids and motivates our experiments. In §§4 and 5 we discuss new manipulative experiments that test the theoretical predictions, and in the final section we summarize and draw some general conclusions.

2. EVOLUTIONARY TRANSITIONS IN FISH, CICHLIDS AND TILAPIINES

In fish, the absence of parental care is common (78% of all families) and thought to be the ancestral condition (Perrone & Zaret 1979; Blumer 1979; Gittleman 1981).

*Author for correspondence (sigal@klivv.oeaw.ac.at).

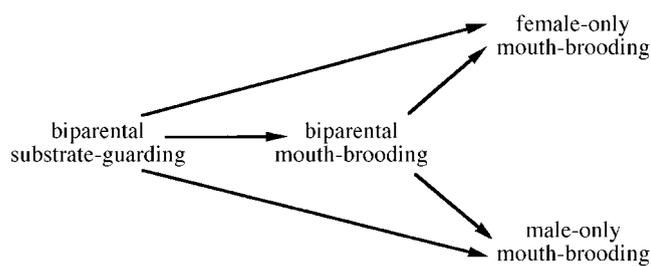


Figure 1. Two proposed pathways of evolution in tilapiine fish (Iles & Holden 1969; Kraft & Peters 1963; Lowe-McConnell 1959). Biparental mouth-brooding is believed to have evolved from biparental substrate-guarding. Uniparental mouth-brooding may have evolved either directly from biparental substrate-guarding or, as this paper suggests, via biparental mouth-brooding.

Care is believed to have evolved in males first, as an epiphenomenon associated with the advent of territoriality: the idea is that males monopolized favoured breeding grounds but once committed to defending a territory it would have paid males to protect offspring as well (Baylis 1981; Blumer 1979, 1982). From male care, biparental care is thought to have evolved when two parents were needed to effectively guard fry (Barlow 1974; Lazarus 1990), or when females could not spawn again in the same season (Blumer 1982). Finally, if changes in the operational sex ratio (OSR) increased remating opportunities for one sex (usually males), this would have favoured mate desertion; thus female care may have commonly evolved from biparental care (Gross & Sargent 1985).

In cichlid fish, parental care is ubiquitous and three care states occur (male-only care (MC), female-only care (FC) and biparental care (BC)). The wide geographical distribution of most biparental species compared to the localized distribution of uniparental species strongly suggests that biparental cichlid species are more ancient, since they have had time to spread from one location to another (Lowe-McConnell 1959; Keenleyside 1991). In addition, eggs and embryos of biparental species have morphological structures that are absent from those of the uniparental species (Kraft & Peters 1963; Peters & Berns 1978, 1982). If one assumes that the evolution of a new trait is less likely than the loss of a trait then this suggests the greater phylogenetic age of biparental species. Experiments suggest that from biparentally caring cichlids female-only and male-only care probably evolved as a consequence of either (1) reduced need for both parents to guard the clutch (Townsend & Wootton 1985*b*), or (2) greater (lost) opportunities to remate (Keenleyside 1983, 1985; Limberger 1983; Townsend & Wootton 1985*b*; Schwanck 1987).

Within cichlids, the subfamily Tilapiini contains both biparentally and uniparentally caring species. For example, in species of the genus *Tilapia* both sexes guard and aerate their eggs and fry in nests on the ground; in species of the genus *Sarotherodon*, usually both sexes mouth-brood young, providing aeration and protection for eggs and fry in the buccal cavity for several weeks; and in species of the genus *Oreochromis*, females alone mouth-brood (Trewavas 1983). Biparental substrate-guarding tilapiines are thought to be more primitive and

there is strong molecular support for this hypothesis (Sodsuk & McAndrew 1991; Pouyaud & Agnese 1995). Many substrate-guarding cichlids seem preadapted to mouth-brooding (Keenleyside 1991); they orally move eggs and fry from one excavated pit to another and use their mouths to retrieve stray fry and spit them back into the defended school (Keenleyside 1979). Indeed, biparental substrate-guarding parents have been known to hold young inside their mouths for up to several minutes if disturbed during transfers (Lowe-McConnell 1959).

The hypothesis that biparental mouth-brooding is an intermediate form between biparental substrate-guarding and uniparental mouth-brooding is supported by embryological and behavioural evidence from Galilee St Peter's fish, a cichlid in the subfamily Tilapiini. First, St Peter's fish lays green eggs like those of its substrate-guarding relatives, and unlike the yellow-orange eggs of its uniparental mouth-brooding relatives (Iles & Holden 1969; Trewavas 1983). Second, the size and number of eggs of the St Peter's fish are intermediate between the many, small eggs of the substrate guarding species and the few, large eggs of uniparental mouth-brooding species (Lowe-McConnell 1955). Third, the adhesive stalks on the zona radiata of the egg, highly developed on the sticky eggs of substrate-guarding species, are obvious but not fully functional in St Peter's fish, whereas they are non-functional or entirely absent in the uniparental mouth-brooding species (Kraft & Peters 1963). Finally, St Peter's fish has a lengthy, monogamous pre-spawning pairbond, as in the biparental substrate-guarding species, but this pairbond dissolves after mouth-brooding is initiated, as in its polygynous female-only mouth-brooding relatives (Lowe-McConnell 1959).

3. MODEL AND EXPERIMENTAL MOTIVATION

A game-theoretic model of parental care in St Peter's fish (Balshine-Earn & Earn 1997) predicts stable parental care strategies based on a number of parameters empirically measured (Balshine-Earn 1995*b*, 1996, 1997). The predictions are sensitive to two factors: the operational sex ratio ($OSR = M/(F + M)$, where M and F are the numbers of males and females that are ready to breed) and the fitness benefit of biparental care relative to uniparental care (P_2/P_1). Although a number of environmental factors (e.g. predation pressure) can affect P_2/P_1 , in St Peter's fish, this ratio probably depends most strongly on clutch size (if the clutch is sufficiently large then the mouth of one fish cannot accommodate all the eggs). Thus, for each sex the probability of care depends on the OSR and clutch size.

Figure 2 shows the outcomes predicted by our model. If the OSR is strongly biased towards one sex then uniparental care by that sex is most likely. If clutches are large then biparental care leads to much greater reproductive success than uniparental care ($P_2/P_1 \gg 1$), and biparental care is expected. For intermediate OSRs and P_2/P_1 values, mixed strategies are expected. The evolutionary outcomes in the region marked 'mixed' in figure 2 were not investigated in Balshine-Earn & Earn (1997), but will be discussed in detail elsewhere.

In Balshine-Earn & Earn (1997) much of our analysis concentrated on particular estimates of the OSR and

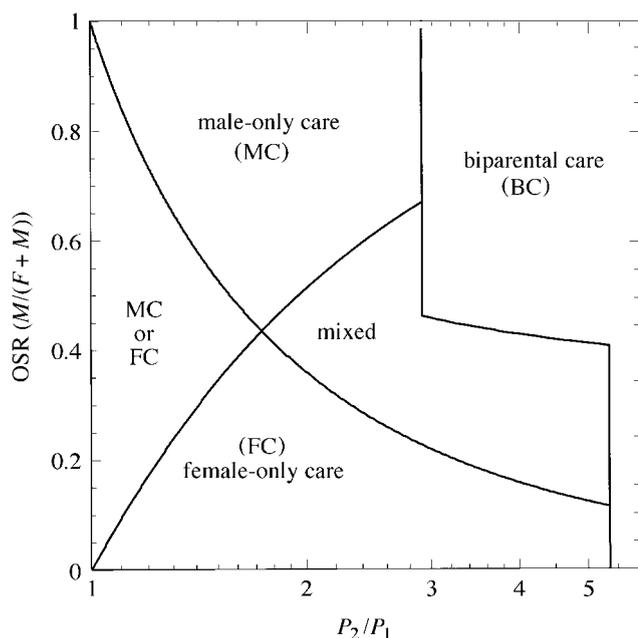


Figure 2. Our model (Balshine-Earn & Earn 1997) indicates how the frequency of care by each sex should change in response to variations in the OSR and the advantage of biparental care relative to uniparental care (P_2/P_1). The OSR is defined as the proportion of males in the reproductively capable part of the population. Mixed strategies refer to caring probabilities that are greater than 0 and less than 1.

P_2/P_1 (mean OSR $\approx 0.62 \pm 0.03$; average $P_2/P_1 \approx 1.6$). These estimates lie in the MC region of figure 2, suggesting that male-only care should be an evolutionarily stable strategy and that the observed mixed-strategy behaviour is evolutionarily unstable. However, as we discussed in Balshine-Earn & Earn (1997, p. 428), the OSR in Lake Kinneret may have been artificially male-biased by stocking practices (so the natural mean OSR may be less than 0.62). Moreover, our attempted measurement of P_2/P_1 was crude; the true mean value of P_2/P_1 is probably greater than 2 and possibly greater than 3 (see Balshine-Earn & Earn 1997, p. 428). Thus the mean OSR and mean P_2/P_1 for St Peter's fish in Lake Kinneret may lie in the 'mixed' region of figure 2. Therefore, a possible explanation of the observation of mixed care strategies is that each sex deserts with a fixed probability determined by the mean OSR and mean P_2/P_1 .

Alternatively, care decisions may be facultative: St Peter's fish may employ a decision rule based on the current OSR and clutch size at each spawn, rather than a fixed caring probability for each sex (see Balshine-Earn & Earn 1997, p. 429). This is a plausible scenario given that the OSR varies according to time and place from strongly male-biased to strongly female-biased (Balshine-Earn 1996) and clutch sizes vary considerably among females (Balshine-Earn 1995a).

In the following sections, we confirm that St Peter's fish do respond facultatively to manipulations of OSR and P_2/P_1 . Manipulating P_2/P_1 is challenging because clutch sizes cannot be altered without greatly disturbing the spawning process. Moreover, P_2/P_1 actually depends on clutch size relative to buccal cavity volume (mouth size).

Since clutch size is largely determined by body size (Balshine-Earn 1995a) we could not simultaneously control clutch size and manipulate mouth size of both parents. We therefore employed an indirect tactic: using females of the same size with males of different sizes, we attempted to control clutch size while manipulating combined buccal cavity volume. Small males were then expected to desert more often than larger males because their smaller buccal cavities corresponded to a smaller advantage of biparental care relative to uniparental (female) care.

4. EXPERIMENTAL METHODS

(a) OSR manipulation

Data were collected in three locations: the tropical aquarium of the Institute of Aquaculture, University of Stirling, Scotland (January–February 1992); the Zoological Gardens, University of Tel-Aviv, Israel (March–April 1992); and the Israeli Ministry of Agriculture's Experimental Fisheries Station at Ginosar, Israel (May–August 1993 and June–August 1994). In Stirling, the fish were third-generation laboratory stock (descended from pairs from Lake Turkana, Kenya). In Israel, the fish were wild-caught from Lake Kinneret. Greater detail of experimental conditions (tank and enclosure sizes, water temperature, pH, oxygen concentrations and light regime) can be found elsewhere (Balshine-Earn 1995a,b, 1996).

In total, 94 St Peter's fish were sexed, measured and tagged. Males and females of similar standard length and body weight were randomly assigned to one of three treatments: (1) equal sex ratio (two males and two females), (2) male-biased sex ratio (three males and one female), and (3) female-biased sex ratio (one male and three females). There was no significant difference in fish size between treatments (Kruskal–Wallis test: male size: $H(\text{corrected for ties}) = 1.68$, $p = 0.43$; female size: $H(\text{corrected for ties}) = 3.93$, $p = 0.14$).

In each trial, one male and one female pair-bonded and spawned. On the day of spawning, the form of care (BC, MC or FC) was noted. (A fish was considered to have deserted if it spawned but then did not pick up any eggs.) Broods of eggs were collected from the mouths of parents 24 h later. The eggs were then counted, weighed and measured (see Balshine-Earn (1995a) for details).

(b) Male size manipulation

This experiment was conducted at the Experimental Fisheries Station at Ginosar, Israel, during three breeding seasons: May–June 1992 (22 pairs); May–July 1993 (38 pairs) and May–July 1994 (43 pairs). Fish were collected from Lake Kinneret by using trammel nets. At capture, the fish were sexed, measured and tagged behind the dorsal fin. The mean masses of males and females were 127 ± 5.4 g and 119 ± 4.8 g, respectively. Females of the same size were used in all trials (Kruskal–Wallis test: $H = 1.54$, d.f. = 2, $p = 0.46$). Males were assigned to each of three treatments according to their size: (1) male larger than female (difference > 15 g), (2) male smaller than female (difference > 15 g), or (3) male and female of similar size (difference < 5 g). Clutch sizes were similar in all treatments (Kruskal–Wallis test: $H = 1.94$, d.f. = 2,

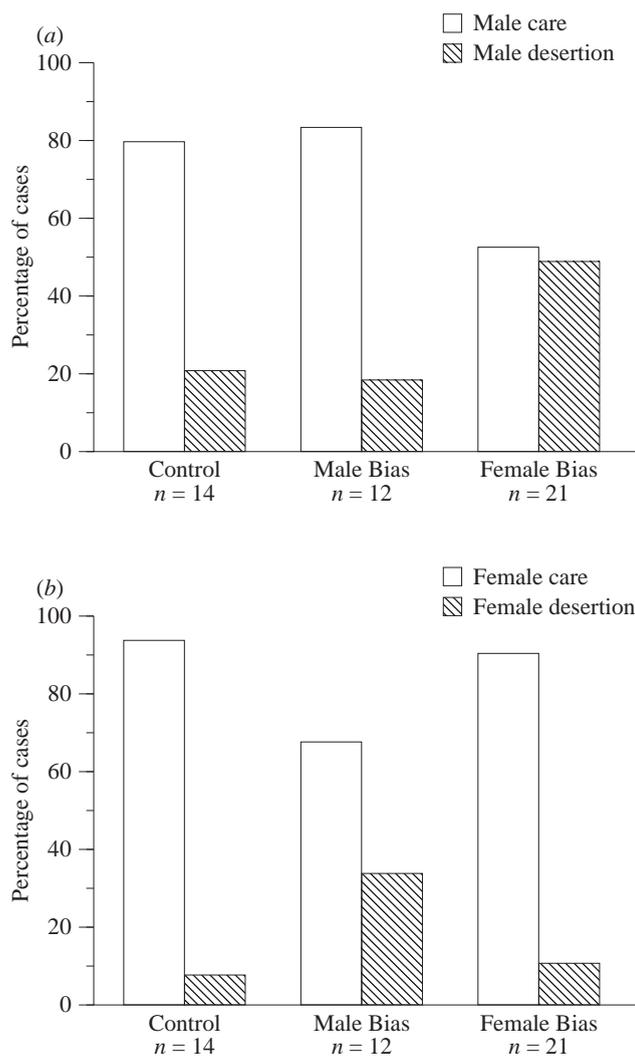


Figure 3. (a) Male caring versus desertion in three different OSR treatments. (b) Female caring versus desertion in three OSR treatments.

$p = 0.39$). Each treatment corresponded to a different value of P_2/P_1 (see § 3).

The pairs were placed in fenced enclosures in a concrete pond (for details see Balshine-Earn (1995a,b)). As in the OSR manipulation (§ 4a) pairbonds, spawning and the form of care were recorded; 24 h after spawning, broods were collected and examined.

5. EXPERIMENTAL RESULTS

(a) OSR manipulation

Male desertion rates were similar in the control and male-biased treatments (G -test; $G = 0.093$, $p = 0.85$). Compared with the combination of these two treatments, male desertion in the female-biased treatment was significantly more frequent (figure 3a) ($G = 4.3$, d.f. = 1, $p < 0.04$). Female desertion rates were similar in the control and female-biased treatments ($G = 0.062$, d.f. = 1, $p = 0.81$) but increased in the male-biased treatment, again relative to the combination of the other two treatments (figure 3b; $G = 3.8$, d.f. = 1, $p = 0.05$).

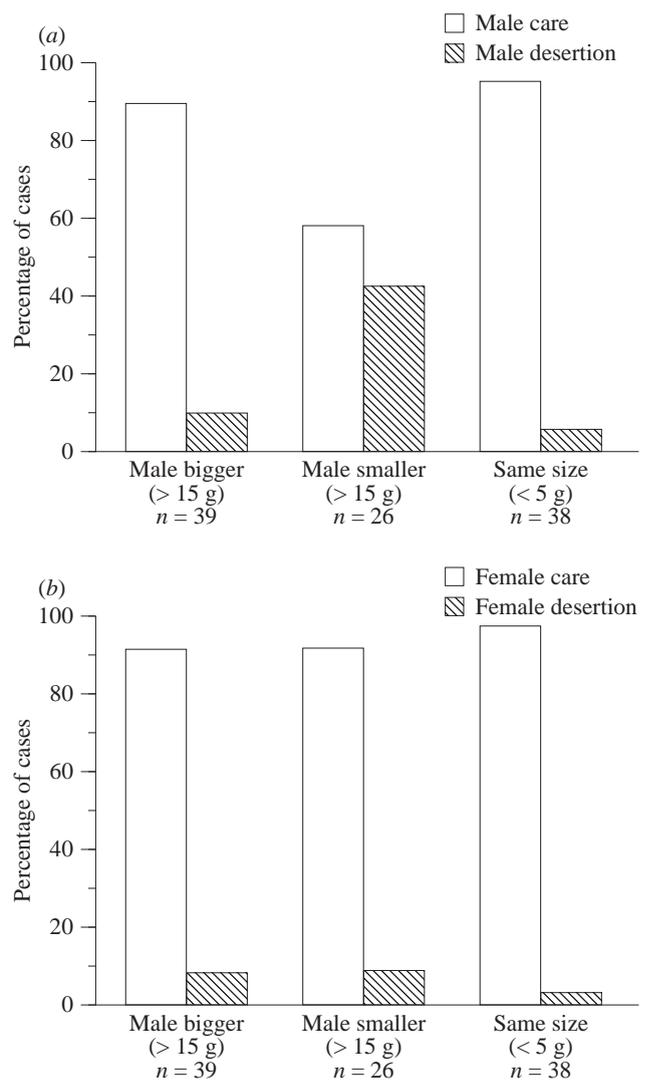


Figure 4. (a) Male desertion rates in three male-size treatments. (b) Female desertion rates in the three treatments.

To be sure that these results were not influenced by other factors, we conducted a number of further tests. The proportion of biparental, male-only and female-only care did not differ among years (1992, 1993, 1994) or between countries (Scotland versus Israel) (year: $G = 1.5$, d.f. = 4, $p > 0.80$; country: $G = 1.9$, d.f. = 2, $p > 0.40$). There were also no differences in the time before spawning between treatments (mean number of days prior to spawning: controls = 6.4, male-biased treatment = 7.1, female-biased treatment = 5.8; Kruskal–Wallis test: $H = 1.03$, d.f. = 2, $p = 0.60$).

(b) Male size manipulation

Small males deserted significantly more often than larger males, suggesting that P_2/P_1 (see § 3) affects whether or not males care (figure 4a) ($G = 15.39$, d.f. = 2, $p < 0.001$). In the 'male-smaller' treatment, males incubated a smaller proportion of the total clutch (average 26% of the eggs) compared with other treatments (average 49% of the eggs; Kruskal–Wallis test: $H = 18.4$, d.f. = 2, $p = 0.0001$). We presume this was because these smaller males had smaller buccal cavities. Note that large males have been shown to be more

successful at remating owing to female choice (Balshine-Earn 1996); this increases the benefits of deserting for large males, but large males stayed nevertheless. The frequency of desertion by females did not differ among the three treatments (figure 4b) ($G = 1.26$, d.f. = 2, $p > 0.60$).

We could not manipulate clutch size (see §3) and clutch sizes did not differ between treatments. However, if we pool all three treatments then we find that overall males were more likely to desert a small clutch (mean clutch size of caring males: 1138 ± 51 eggs, deserting males: 548.3 ± 62 eggs; Mann–Whitney U -test, $z = -4.53$, $p = 0.0001$). This further supports the hypothesis that P_2/P_1 influences male parental-care decisions. There was a weak trend for females to desert smaller clutches (all three treatments pooled; mean clutch size of caring females: 1077 ± 51 eggs, deserting females: 755 ± 84 eggs; Mann–Whitney U -test, $z = -1.67$, $p = 0.10$).

There was no difference in the caring pattern among years ($G = 2.46$, d.f. = 4, $p > 0.60$), nor was there any difference among treatments in the number of days before spawning ('male-bigger' treatment, 12 ± 1 d, $n = 39$; 'male-smaller' treatment, 9 ± 1 d, $n = 26$; 'same-size' treatment, 12 ± 1 d, $n = 38$; Kruskal–Wallis $H = 1.9$, d.f. = 2, $p = 0.39$).

6. DISCUSSION

In this study, female-biased OSRs influenced male St Peter's fish to desert and vice versa. When paired with females of a given size, small males deserted more often than large males. (This result is consistent with our suggestion in §3 that smaller males yield a smaller advantage of biparental care relative to uniparental female care because of their smaller buccal cavities.) In addition, fish were more likely to desert a smaller clutch. All these results support the hypothesis that care decisions of St Peter's fish are influenced by current OSR and the relative advantage of two versus one caring parent, P_2/P_1 (see §3).

Our results support our suggestion that St Peter's fish make care decisions facultatively according to an evolutionarily stable decision rule. Other cichlids may be subject to ranges of OSR and clutch size that our model predicts will give rise to a fixed pure strategy (see figure 2). Because environmental changes can influence OSR and clutch size (see below), our model and experiments together suggest possible evolutionary pathways between different parental care states in cichlids, and in particular show that evolution from biparental care to male-only or female-only care is possible in mouth-brooders.

Iles & Holden (1969) first proposed that biparental mouth-brooders were intermediate forms between ancestral biparental substrate-guarders and advanced uniparental mouth-brooders. This study provides the first empirical evidence for the transition from biparental to uniparental mouth-brooding. Several previous cichlid studies have found that males tended to desert under female-biased OSRs, but all of these species are substrate-guarders: *Herotilapia multispinosa* (Keenleyside 1983), *Aequidens caeruleopunctatus* (Barlow 1974), *Lamprologus brichardi* (Limberger 1983), *Cichlasoma panamense* (Townsend & Wootton 1985b), *C. nigrofasciatum*

(Keenleyside *et al.* 1985), *Tilapia mariae* (Schwanck 1987) and *C. tetraodon* (Keenleyside 1991).

Biased OSRs may arise as a consequence of primary sex ratio bias, sex-biased mortality or differences in reproductive rates (Clutton-Brock & Parker 1992). In some fish, primary sex ratio may be controlled by water temperature, which may fluctuate from year to year (see, for example, Craig *et al.* 1996). Strongly sex-biased mortality could arise because males court more actively than females (Balshine-Earn 1995a), which may be risky (Magurran & Seghers 1990; Godin 1995). Alternatively, females may be less likely to survive the food-limited winters, as they lose more energy reserves during the breeding season (Balshine-Earn 1995b).

What naturally occurring factors could have shifted the relative advantage of biparental compared with uniparental care? Changes in climate can cause large-scale changes in food availability (Zabel & Taggart 1989); these can cause females to lay small clutches (Balshine-Earn 1995a; Townsend & Wootton 1984, 1985a). Climatic changes could also lead to predator extinctions or promote colonization of new habitats with fewer predators and/or safer nursery grounds. Any or all of these could have reduced the profitability of biparental care (Barlow 1974; Erckmann 1983; but, see Reynolds & Székely 1997). Thus, in ancestral tilapiine species, particular environmental conditions may have changed the costs and benefits of parental care, favouring evolution of uniparental care from biparental care.

Our experiments were motivated by our model, but our model implicitly assumes that each partner is an equally effective carer and this was not the case when we manipulated male size. A more detailed model would separately consider the benefits of uniparental female care and uniparental male care. If the male is smaller than the female then our model underestimates his probability of desertion because (1) his mouth is smaller so the benefit of uniparental care by him is less than uniparental care by his partner, and (2) he stands to gain more from increased growth. Deserting males continue to grow while caring males lose weight (Balshine-Earn 1995b), and large males are preferred in mate choice experiments (Balshine-Earn 1996). Thus a small male that cares may greatly reduce his probability of remating soon, which increases his caring costs relative to large males. Both factors (1) and (2) amplify the probability of desertion by males—decreasing the value of biparental care relative to uniparental female care—but further work is needed to determine the relative importance of each.

In conclusion, manipulation of a present-day biparentally caring species has shown that changes in OSR and the relative advantage of biparental care can select for uniparental care from biparental care. This supports one of the two proposed phylogenetic pathways for parental care evolution in fish (see figure 1). Comparative work examining evolutionary pathways of parental-care in the family Cichlidae as a whole is currently under way (Goodwin *et al.* 1998).

S.B.E. is supported by a Royal Society postdoctoral research fellowship. D.J.D.E. is supported by a Wellcome Trust postdoctoral research fellowship. Fieldwork was funded with the help of the Lady Davis Fellowship Trust, ASAB, FSBI, the Worts Travelling Scholars Fund and the Weis Fogh Fund. We thank

Chaim Agoni, Dror Vinikur, Ze'ev Dafni and Ehud Nebo (Israeli Ministry of Fisheries Station at Ginosar) for pond facilities; Lev Fishelson and Nissim Sharon (Tel Aviv University), and Brendan McAndrew and Keith Ranson (University of Stirling) for aquarium facilities; Tim Clutton-Brock, John Reynolds and Nick Davies for useful discussions; and Nick Goodwin, Tamás Székely, Charlotta Kvarnemo, Ingrid Ahnesjö and three anonymous referees for helpful comments.

REFERENCES

- Balshine-Earn, S. 1995a *The evolution of parental care in cichlid fishes*. PhD thesis, University of Cambridge.
- Balshine-Earn, S. 1995b The costs of parental care in Galilee St. Peter's fish *Sarotherodon galilaeus*. *Anim. Behav.* **50**, 1–7.
- Balshine-Earn, S. 1996 Reproductive rates, the operational sex ratio and mate choice in St. Peter's fish. *Behav. Ecol. Sociobiol.* **39**, 107–116.
- Balshine-Earn, S. 1997 The benefits of uniparental versus biparental mouth-brooding in Galilee St. Peter's fish. *J. Fish Biol.* **50**, 371–381.
- Balshine-Earn, S. & Earn, D. J. D. 1997 An evolutionary model of parental care in St. Peter's fish. *J. Theor. Biol.* **184**, 423–431.
- Barlow, G. W. 1974 Contrasts in social behavior between Central American cichlid fishes and coral-reef surgeon fishes. *Am. Zool.* **14**, 9–34.
- Baylis, J. R. 1981 The evolution of parental care in fishes, with reference to Darwin's rule of male sexual selection. *Environ. Biol. Fish.* **6**, 223–251.
- Blumer, L. S. 1979 Male parental care in the bony fishes. *Q. Rev. Biol.* **54**, 149–161.
- Blumer, L. S. 1982 A bibliography and categorization of bony fishes exhibiting parental care. *Zool. J. Linn. Soc.* **76**, 1–22.
- Clutton-Brock, T. H. & Parker, G. A. 1992 Potential reproductive rates and the operation of sexual selection. *Q. Rev. Biol.* **67**, 437–456.
- Craig, J. K., Foote, C. J. & Wood, C. C. 1996 Evidence for temperature-dependent sex determination in sockeye-salmon (*Oncorhynchus nerka*). *Can. J. Fish. Aquat. Sci.* **53**, 141–147.
- Erckmann, W. J. 1983 The evolution of polyandry in shorebirds: an evaluation of hypotheses. In *Social behavior of female vertebrates* (ed. S. K. Wasser), pp. 113–168. New York: Academic Press.
- Fishelson, L. & Heinrich, W. 1963 Some observations on the mouth-breeding *Tilapia galilaea* L. (Pisces: Cichlidae). *Ann. Mag. Nat. Hist.* **6**, 507–508.
- Gittleman, J. L. 1981 The phylogeny of parental care in fishes. *Anim. Behav.* **29**, 936–941.
- Godin, J.-G. 1995 Predation risk and alternative mating tactics in male Trinidadian guppies (*Poecilia reticulata*). *Oecologia* **103**, 224–229.
- Goodwin, N. B., Balshine-Earn, S. & Reynolds, J. D. 1998 Evolutionary transitions in parental care in cichlid fishes. *Proc. R. Soc. Lond. B*. (In the press.)
- Gross, M. R. & Sargent, R. C. 1985 The evolution of male and female parental care in fishes. *Am. Zool.* **25**, 807–822.
- Iles, T. D. & Holden, M. J. 1969 Bi-parental mouth-brooding in *Tilapia galilaea*. *J. Zool.* **158**, 327–333.
- Keenleyside, M. H. A. 1979 *Diversity and adaptation in fish behaviour*. Berlin: Springer.
- Keenleyside, M. H. A. 1983 Mate desertion in relation to adult sex ratio in the biparental cichlid fish *Herotilapia multispinosa*. *Anim. Behav.* **31**, 683–688.
- Keenleyside, M. H. A. 1985 Bigamy and mate choice in the biparental cichlid fish *Cichlasoma nigrofasciatum*. *Behav. Ecol. Sociobiol.* **17**, 285–290.
- Keenleyside, M. H. A. 1991 *Cichlid fishes: behaviour, ecology and evolution*. (Fish and Fisheries Series 2.) London: Chapman & Hall.
- Keenleyside, M. H. A., Rangeley, R. W. & Koppers, B. U. 1985 Female mate choice and male parental defense behaviour in the cichlid fish, *Cichlasoma nigrofasciatum*. *Can. J. Zool.* **63**, 2489–2493.
- Kraft, A. & Peters, H. M. 1963 Vergleichende Studien über der Oogenese in der Gattung *Tilapia*. *Z. Zellforsch.* **61**, 435–485.
- Lazarus, J. 1990 The logic of mate desertion. *Anim. Behav.* **39**, 672–684.
- Limberger, D. 1983 Pairs and harems in a cichlid fish, *Lamprologus brichardi*. *Z. Tierpsychol.* **62**, 115–144.
- Lowe-McConnell, R. H. 1955 The fecundity of *Tilapia* species. *E. Afr. Agric. J.* **11**, 45–52.
- Lowe-McConnell, R. H. 1959 Breeding behaviour patterns and ecological differences between *Tilapia* species and their significance for evolution within the genus *Tilapia* (Pisces: Cichlidae). *Proc. Zool. Soc. Lond.* **132**, 1–30.
- Magurran, A. E. & Seghers, B. E. 1990 Risk sensitive courtship in the guppy (*Poecilia reticulata*). *Behaviour* **112**, 194–201.
- Maynard Smith, J. 1977 Parental investment: a prospective analysis. *Anim. Behav.* **25**, 1–9.
- Perrone, M. & Zaret, T. M. 1979 Parental care patterns in fishes. *Am. Nat.* **113**, 351–361.
- Peters, H. M. & Berns, S. 1978 Über die Vorgeschichte der maubrutenden Cichliden. *Aquar. Mag. Stuttga.* **7**, 324–331.
- Peters, H. M. & Berns, S. 1982 Die Maubrutpflege der Cichliden. Untersuchungen zur Evolution eines Verhaltensmusters. *Z. Zool. Syst. Evol.-Forsch.* **20**, 18–52.
- Pouyaud, L. & Agnese, J. F. 1995 Phylogenetic relationships between 21 species of three tilapiine genera *Tilapia*, *Sarotherodon* and *Oreochromis* using allozyme data. *J. Fish Biol.* **47**, 26–38.
- Reynolds, J. D. & Székely, T. 1997 The evolution of parental care in shorebirds: life histories, ecology and sexual selection. *Behav. Ecol.* **8**, 126–134.
- Schwann, E. 1987 *Reproductive behaviour of a monogamous cichlid fish Tilapia mariae*. PhD thesis, University of Stockholm, Sweden.
- Sodsuk, P. & McAndrew, B. J. 1991 Molecular systematics of three tilapiine genera *Tilapia*, *Sarotherodon* and *Oreochromis* using allozyme data. *J. Fish Biol.* **39** (Suppl. A), 301–308.
- Townsend, T. J. & Wootton, R. J. 1984 Effects of food supply on the reproduction of the convict cichlid, *Cichlasoma nigrofasciatum*. *J. Fish Biol.* **23**, 91–104.
- Townsend, T. J. & Wootton, R. J. 1985a Adjusting parental investment to changing environmental conditions: the effect of food ration on parental behaviour of the convict cichlid, *Cichlasoma nigrofasciatum*. *Anim. Behav.* **33**, 494–501.
- Townsend, T. J. & Wootton, R. J. 1985b Variation in the mating system of a biparental cichlid fish, *Cichlasoma panamense*. *Behaviour* **95**, 181–197.
- Trewavas, E. 1983 *Tilapiine fishes of the genera Sarotherodon, Oreochromis and Danakilia*. London: British Museum (Natural History).
- Yamamura, N. & Tsuji, N. 1993 Parental care as a game. *J. Evol. Biol.* **6**, 103–127.
- Zabel, C. J. & Taggart, S. J. 1989 Shift in red fox, *Vulpes vulpes*, mating system associated with El Niño in the Bering Sea. *Anim. Behav.* **38**, 830–838.

