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Reproductive rates, operational sex ratios and mate choice in St. Peter's fish

Abstract Operational sex ratio (OSR) theory predicts that sexual differences in potential reproductive rates (PRRs) create biases in the OSR and thus determine the relative strength of sexual selection (competition and choice) operating on each sex. Although this theory is well accepted, empirical studies that quantify it are still lacking. This paper presents such a study. I measured the natural OSR of Galilee St. Peter's fish (*Sarotherodon galilaeus*) in the field (Lake Kinneret) and examined the direction of mate choice in the laboratory. The OSR in Lake Kinneret was male biased. Both a male-biased sex ratio and higher male reproductive rates (twice as fast as females) contributed to the skew in the OSR, but the sexual differences in PRR were shown to be the main factor causing variation in the OSR. Females, the sex with the lower PRR, were more selective for mates. The faster male reproductive rate may explain why females are more selective for mates despite varying less in quality.

Introduction

Ever since Darwin (1871), biologists have sought to explain why males are usually more competitive and females more selective. Sexual differences in competi-

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tion have been linked to gender differences in size of gametes (Bateman 1948), extent of parental investment (Williams 1966; Trivers 1972), gamete cycling time (Baylis 1981) and variance in mating success (Sutherland 1987; Clutton-Brock and Vincent 1991). Current parental investment theory asserts that regardless of whether males or females provide parental care, the sex with the higher reproductive rate will be more abundant in the unmated population, bias the operational sex ratio (OSR), and compete more strongly for mates (Emlen and Oring 1977; Clutton-Brock and Vincent 1991).

The relationship between reproductive rates and mate choice is more complicated (Owens et al. 1994). Throughout the animal kingdom, the sex with the lower reproductive rate is usually more selective (Vincent et al. 1994; Owens and Thompson 1994), but the costs and benefits of choosiness must also be considered. During mate choice, individuals should aim to optimise the trade-off between the quality of mates that they obtain during each reproductive bout, and the number of such bouts they obtain. In many species, males have higher reproductive rates and therefore the OSR is often male biased. As a result the costs of male mate choice can outweigh the benefits; choosy males will mate with high quality partners but they will do so infrequently because such partners are hard to find (Owens and Thompson 1994). Thus, sexual differences in reproductive rates will *always* determine which sex will be most competitive and will *usually* determine which sex will be most choosy. When the differences in reproductive rates are small, the *benefits of choosiness* for each sex begin to determine which sex will be most selective for mates (Owens and Thompson 1994). If the differences in reproductive rates are small, the sex which is most choosy will be the one that displays the least variance in quality (Owens and Thompson 1994).

This paper examines the relationship between potential reproductive rates (PRRs), the OSR and mate choice in Galilee St. Peter's fish, a biparental mouth

brooding cichlid. Sexual differences in PRRs were used to predict from theory which sex will be most abundant in the reproductively capable portion of the population. This prediction was tested by studying the OSR in a population of St. Peter's fish in Lake Kinneret. However, sexual differences in reproductive rates are just one of three factors thought to influence the OSR. The other two are the adult sex ratio and the spatio-temporal distribution of males and females (Clutton-Brock and Parker 1992). The influence of each of these three factors on the OSR in Lake Kinneret is examined here. In addition, mate choice tests were conducted to examine how PRRs affect which sex will be most choosy in mate selection.

Methods

Estimating the OSR

I used sexual differences in PRRs to predict the OSR. I examined interspawn intervals of caring and non-caring male and female St. Peter's fish in an experiment described elsewhere (see Balshine-Earn 1995a). Here, I used these interspawn intervals to compare male and female PRRs by dividing the maximum number of fry released by the minimum (shortest) inter-spawn interval for each sex. The estimate of interspawn interval for caring females was conservatively low as the care period had been artificially shortened to 10 days (normally 14 days) to ensure that clutches could be collected.

To test the predicted OSR, the OSR was estimated directly by sampling fish twice a week with local fishermen in Lake Kinneret, northern Israel (32°45′-32°13′N and 35°38′E) during the 1992, 1993 and 1994 breeding seasons. Sampling began when the water in the littoral zone (spawning grounds) reached 18–20°C, the minimum required spawning temperature for St. Peter's fish (Ben-Tuvia et al. 1992a; Johnson 1974). I sampled from 15 April to 29 June in 1992, 5 May to 13 September in 1993, and 27 April to 23 July in 1994. Fish were examined in the boats as soon as the nets were pulled out of the water and any signs of caring or spawning were recorded (determined by the presence of eggs/fry in the mouth, the presence of a brood pouch or swollen genital papilla). In both male and female St. Peter's fish the genital papilla swells prior to spawning. The eggs are picked up by parents and are carried in the mouth; during oral incubation the buccal cavity distends downwards to form a "brood pouch".

On each sampling trip the weather (% cloud cover), time of day, water and air temperature were recorded. Using a temperature probe, water temperature (110 cm into the water column) and air temperature (off the edge of the boat, in the shade) were recorded.

Two shallow-water sampling sites were used: the Buteiha Nature Reserve (northern shore) and the shore near Kibbutz Ginosar (western shore). These shallow water samples (<5 m depth) differed in substrate. The substrate in the Buteiha plain is primarily composed of black mud (vegetation-abundant) while the substrate on the Ginosar shore is primarily small rocks and large boulders (vegetation-sparse). The shallow samples were taken with the help of two fishermen working in small boats (4 m) and trammel nets. At each shallow water site I sampled the catch taken in a 2-h period. Deep water samples (>10 m) were taken from a number of sites around the lake with the help of two crews of fishermen working on large purse seine boats. I would remain on these boats for the entire day (0700–1600 hours) and examine all St. Peter's fish collected. The fish examined were not individually marked but they were permanently removed from the population as they were placed in an iced storage tray after examination and later sold in the fish market of Tiberias, Israel.

In addition to reproductive rates and adult sex ratio, the third determinant of OSR (the distribution of males and females in space and time) was also investigated. To ensure that the resulting OSR was not simply due to sampling in one particular place or at one particular time each sample was assigned to the following categories: depth (<5 m vs. >10 m), substrate type (mud vs. gravel and boulder mix), time of day (morning vs. afternoon) and time in the season (early vs. late). The breeding season was divided into two periods, early and late according to water temperature: in May and June temperature commonly ranged from 18 to 25°C while in July and August the water temperature generally remained above 25°C. I compared the samples in these different categories to investigate how each factor (depth, substrate type, time of day and season) affect the OSR.

To check that the catching technique was not biased, I sampled fish in the areas where the trammel nets were set, using three other methods: beach seines, shore transects and underwater transects (using a mask and snorkel). Unfortunately each catching technique had its own biases. Only juvenile St. Peter's fish were caught in the beach seine. The poor underwater visibility in Lake Kinneret and the general shyness of St. Peter's fish made it difficult to sex free-swimming fish underwater. From the shore it was possible to sex free-swimming St. Peter's fish (usually monochromatic and monomorphic) only during early courtship or during spawning when the sexes have dichromatic dorsal fins. Thus, the trammel nets probably gave the best estimate of the OSR. To ensure that it was equally possible to catch males and females, I examined the size distribution of a sample of males and females caught in the trammel nets.

Measuring sex differences in behaviour

Mate choice was studied in aquaria because mating competition and choice in St. Peter's fish are difficult to study in the field. This is because (1) pair formation initially occurs while fish are still in large pelagic shoals (Ben-Tuvia 1978), and (2) the established pairs that come to the littoral zone to breed are not territorial except during a brief period while fertilised eggs are on the ground (personal observation). Body size was the variable trait in the mate choice trials. The preference for large body size (or weight) was investigated as body size has important fitness consequences for both sexes. In female St. Peter's fish and in female fish in general, fecundity increases with body weight (Balshine-Earn 1995b; Li and Owings 1978; Loiselle 1982; Wootton 1990) so males are expected to prefer large females (Sargent et al. 1986). As large size is likely to confer either superior protective capabilities (direct benefits) and/or genetic qualities (indirect benefits) it is likely that females will also prefer large males (Bisazza and Marconato 1988; Cote and Hunte 1989; Downhower and Brown 1980; Reynolds and Gross 1990).

The fish used in these experiments were third generation St. Peter's fish laboratory stock from the Tilapia Reference Collection at the Institute of Aquaculture, University of Stirling. The fish were lightly anaesthetised [with ethyl p-aminobenzoate (Benzocaine), marketed by Sigma], then sexed, measured and tagged behind the dorsal fin with a unique Carlin numbered tag (Neal Ltd, Finchley, London). The fish were sexed by examination of the urogenital opening (females have a wide T-shaped slit and males have a single hole). Ten body measurements were taken using a ruler, callipers and an electric scale (weight, total length, standard length, width, girth, head length, lower jaw length, dorsal, pectoral and pelvic fin length; see Balshine-Earn 1995b for further details).

The mate choice experiments were conducted in a test aquarium (564 l) equipped with one 300-V heater and two 10-cm-long air-stones. Water temperature was 27.5 ± 2°C and a 12:12 h light:dark regime was maintained for both experiments. The test aquarium was divided into three compartments, two small end compartments and a larger middle compartment. Each end compartment was separated from the middle by a fixed transparent barrier and a removable opaque barrier. In addition, two 60% width opaque barriers were placed in the middle compartment such that
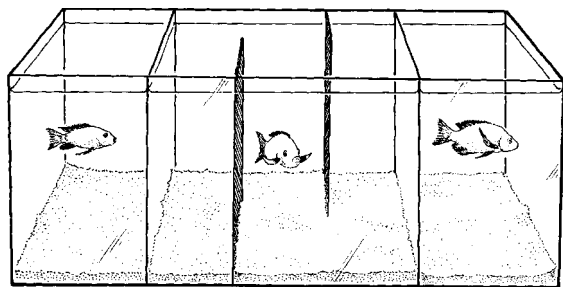
Fig. 1 A schematic diagram of the mate choice aquarium set up. See Balshine-Earn (1995c) for an additional example of this tank design

there was no direct line of sight between the end compartments (Fig. 1).

Male mate size preference was investigated by placing one large ripe female and one small ripe female in opposite end compartments of the test aquarium. Ripeness was assessed by a swelling of the lower abdomen and of the genital papilla that generally precedes oviposition. The females were given 48 h to habituate to the test aquarium, during which both the fixed transparent and removable opaque barriers were in place, preventing entry into the middle compartment. In each trial, a single male St. Peter's fish was placed in the centre compartment of the test aquarium. After four hours of habituation, the full opaque barriers were removed. A 15-minute choice trial was begun as soon as the test male had visually inspected each female once. In total, 15 males were tested and their preference for each female was recorded. Preference was quantified by measuring the time spent near and the display rate to each female. In each test, the time the male spent with each female and the display rate of each fish was noted using a Psion Organiser and video taped with a camcorder.

After all 15 males were tested, the females were switched between end compartments and the males were retested to control for preferences for particular ends of the tank. Two different sets of females were used to control for particular individual preferences. The large females weighed 647 g and 599 g and the small females weighed 415 g and 398 g respectively.

Female mate choice was investigated with an identical design but ripe females were tested and ripe males were used as end fish. The 15 females were tested for mate size preference with two sets of male pairs that varied in size. The large males weighed 602 g and 555 g and the small males weighed 410 g and 394 g, respectively.

Results

Estimating the OSR

The maximum number of mature fry observed incubated by a female was 1617. She was paired to the male incubating the greatest number of mature fry recorded, 1970. Using these values and results from experiments measuring the minimum inter-spawn interval (ISI) for caring females (15 days), non-caring females (7 days), caring and non-caring males (both 1 day) (see Table 1 and Balshine-Earn 1995a) I calculated the reproductive rates (potential and average) for males and females. Thus, a deserting female could theoretically have a potential (or maximum) reproductive rate of 1970 fry/7 days or 281 offspring per day. A deserting male's potential reproductive rate would be 1617 offspring per day which is nearly 6 times higher than the PRR of females. In addition to the maximum or potential rate, the average reproductive rate of caring males was 1.6 times higher than the average reproductive rate of caring females (Table 1). The higher male reproductive rates imply that the OSR is likely to be male-biased.

The sex ratio can also affect the OSR. The adult sex ratio was male-biased: of the 2580 fish sampled, significantly more males were caught than females (statistics presented in Table 2). In addition, in each year more samples tended to be male-biased (Table 2).

Moreover, the magnitude of the bias in the adult sex ratio was significant. The adult sex ratio was estimated by dividing the number of males caught in each sample by the total number of fish caught in each sample and then taking a mean of all these samples. The male proportion was significantly higher than 1/2 in 1993 and 1994 but not in 1992 (statistics reported in Table 3).

To examine how the third factor (the distribution of males and females) influences the OSR, the samples were taken at different depths, and times of day, in different seasons and on different substrate types. The

Table 1 Reproductive rates of caring and non-caring males and females, calculated here using the results of two experiments (one on males, the second on females) conducted to estimate reproductive costs (see Balshine-Earn 1995a)

Sex	Measures	Mouth brooding	Non-mouth brooding
Females	Mean number of fry released	600 fry	
	Range	68–1617 fry	
	Mean interspawn interval	24 days	13 days
	Range	15–42 days	7–19 days
	Maximum reproductive rate	56 offspring/day	281 offspring/day
	Average reproductive rate	16 offspring/day	49 offspring/day
Males	Mean number of fry released	642 fry	
	Range	71–1970 fry	
	Mean interspawn interval	12 days	5 days
	Range	1–33 days	1–12 days
	Maximum reproductive rate	131 offspring/day	1617 offspring/day
	Average reproductive rate	25 offspring/day	120 offspring/day

Table 2 The number of males versus females caught each year and the number of male-biased samples versus female-biased samples; *n* equals the total number of samples taken in that year. Equal sex ratio samples were ignored

	Males	Females	*G*	*P*	Male-biased samples	Female-biased samples	*G*	*P*
1992 (*n* = 20)	602	501	9.3	<0.01	14	5	3.5	>0.05
1993 (*n* = 45)	572	363	47.1	<0.001	33	6	18.9	<0.001
1994 (*n* = 25)	313	229	13.1	<0.001	18	5	6.6	<0.02

deep water samples were ultimately not included in the calculation of the OSR because two lines of evidence suggested that St. Peter's fish breed only in the shallow littoral zone of the lake. First, mouth-brooding individuals of either sex were extremely rare in the pelagic zone (deep-water). Caring fish were observed in only 3 of the 18 deep water samples (6 caring individuals were recorded). In comparison, 760 caring fish were found in 63 of the 75 shallow water samples ($G = 20.4$, $df = 1$, $P < 0.001$). Second, in shallow water males and females had heavier gonads per body weight (gonadic somatic index) confirming that the shallow littoral zone is the breeding ground of St. Peter's fish (Males: n_1 (deep water) = 40, n_2 (shallow water) = 31, $\bar{x}_1 \pm SE = 0.1 \pm 0.03$, $\bar{x}_2 \pm SE = 0.2 \pm 0.03$, Mann-Whitney *U*-test, *z* (males) = -1.9, $P = 0.06$; Females: n_1 (deep water) = 47, n_2 (shallow water) = 52, $\bar{x}_1 \pm SE = 1.0 \pm 0.2$, $\bar{x}_2 \pm SE = 2.0 \pm 0.4$, $z = -2.105$, $P = 0.04$).

The sex ratio did not vary with season (Fig. 2a, Mann-Whitney *U*-test, $z = -1.24$, $P = 0.21$), time of day (Fig. 2b, Mann-Whitney *U*-test, $z = -1.1$, $P = 0.28$) or substrate type (Fig. 2c, Mann-Whitney *U*-test, $z = -0.03$, $P = 0.98$).

In each year I counted the total number of reproductively capable males and females, *M* and *F*. The OSR is normally defined as *M/F*. However, to facilitate comparisons between years with different catches per unit effort, the OSR was calculated as the number of males available for mating divided by all individuals available for mating ($M/M + F$). This proportion is simply related to *M/F* and will be called the OSR hereafter. Defined this way, the average OSR was 0.55 in 1992, 0.66 in 1993 and 0.57 in 1994. The OSR was significantly male biased in 1993 and 1994 but was not in 1992 (Table 4a). However, these calculations of the

Table 3 The male proportion of the total fish caught in 1992, 1993 and 1994. The Wilcoxon signed ranks test was used to calculate the *z* statistic

	1992	1993	1994
Male proportion of total fish	0.55	0.61	0.58
n (samples)	20	45	25
Z (corrected)	−1.89	−3.07	−3.17
P	0.059	0.002	0.002

OSR underestimated the extent of the bias because all caring males were excluded. In an experiment
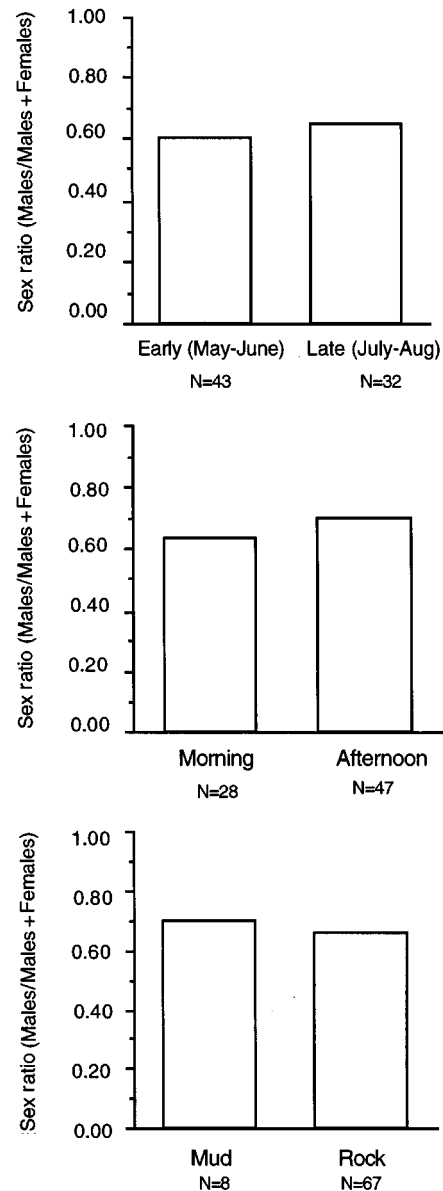

Fig. 2 a The sex ratio early versus late in the breeding season. **b** The sex ratio in the morning versus afternoon samples. **c** The sex ratio on mud versus gravel and boulders substrate (*n* is the number of samples)

Table 4 a The number of samples in 1992, 1993 and 1994 that were male-biased and female-biased. **b** The number of male biased samples versus female biased samples in 1992, 1993 and 1994 when all males (including mouth brooding males) are considered. Equal operational sex ratio (OSR) samples were ignored in both

Number of samples	Male-biased OSR	Female-biased OSR	Binomial test (2-tailed)
a 1992 ($n = 20$)	8	7	N.S.
1993 ($n = 45$)	31	7	<0.001
1994 ($n = 25$)	15	3	0.036
b 1992 ($n = 20$)	15	0	<0.001
1993 ($n = 45$)	33	5	<0.001
1994 ($n = 25$)	21	1	<0.001

conducted in 1994, males were shown to be capable of courting and spawning while mouth brooding (Balshine-Earn 1995a). When the OSR was recalculated to include all males (Fig. 3), significantly male-biased OSRs were found in all three years (Table 4b).

To ensure that the male-biased OSR was not due to sampling errors, I compared the size of males and females caught, to check that males were not bigger than females and therefore more easily caught in the trammel nets. Males and females did not differ significantly in standard length (t-test, unpaired t value = 0.197, n (males) = 100, n (females) = 99, $P = 0.85$).

To compare the effect of sex ratio and reproductive rates on the OSR, an expected OSR was calculated based on the sexual differences in average reproductive rates (Table 5a). This expected OSR was compared to the observed OSR (column 1 in Table 5b) and the OSR adjusted to account for the sex ratio bias (column 3 in Table 5b). The sex ratio (column 2 in Table 5b) was consistently less male-biased than the OSR confirming that reproductive rates have an important influence on the OSR.

Measuring sex differences in behaviour

Males showed a preference for large females. In 15 trials, 9 males spent more than half the test with the large female while 6 males spent the majority of time with small females (Fig. 4a, $G = 0.27$, $df = 1$, $P > 0.60$). There was a trend showing that the mean time males spent with large females was greater than the mean
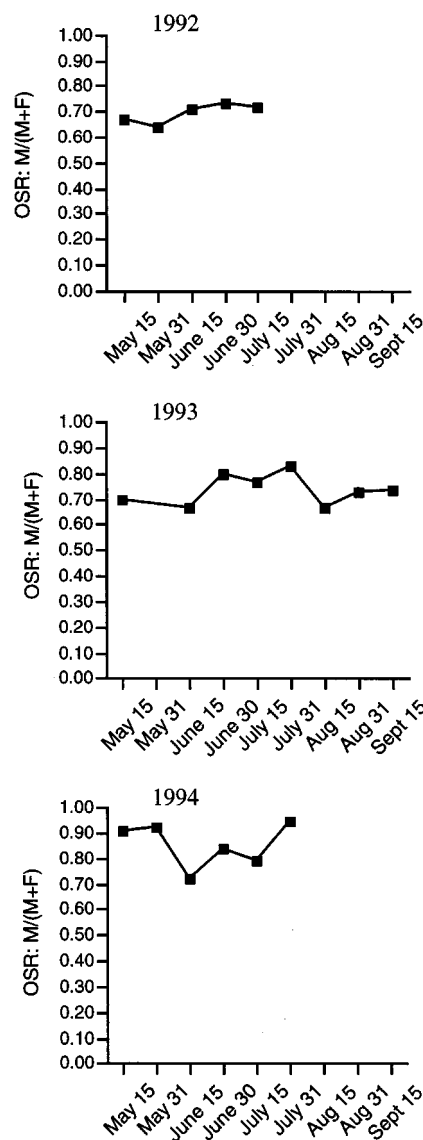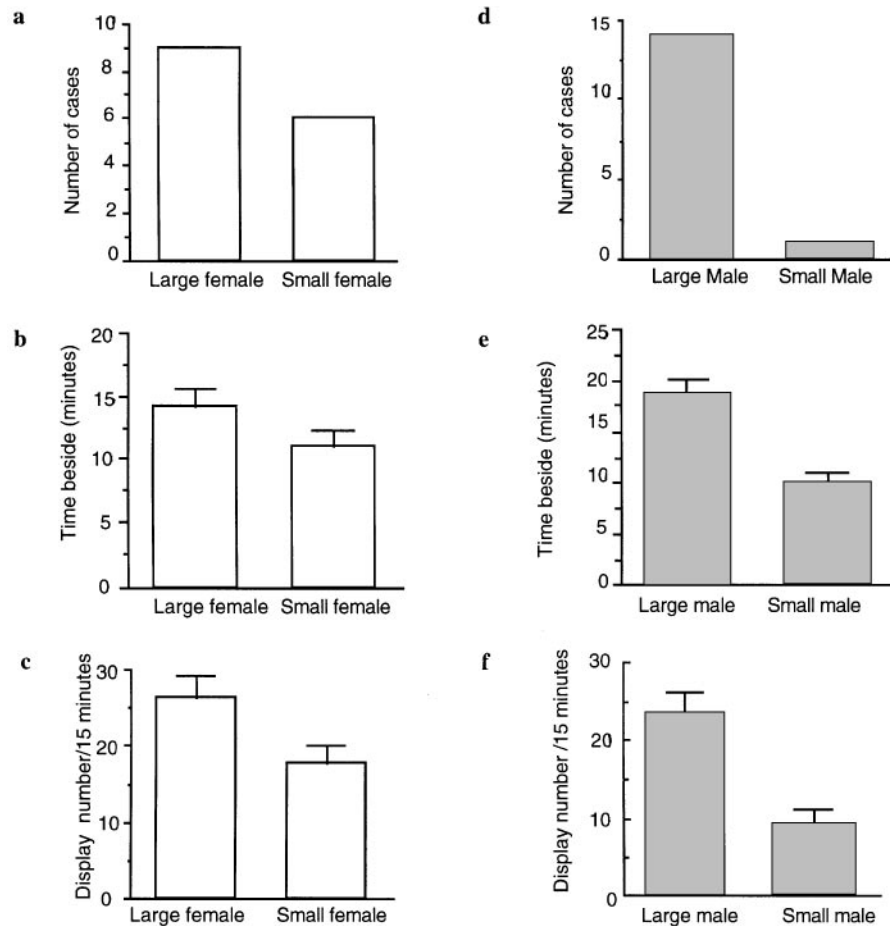
Fig. 3 The OSR in 1992–1994. The OSR is calculated by dividing all males by all males plus all non-caring females. Each *point* on the graphs represents the mean OSR from four samples (2 per week) taken during the 2 weeks preceding this date

time spent with small females (Fig. 4b, Wilcoxon signed ranks test, $z = -1.704$, $P = 0.09$). Males clearly performed more courtship displays (shakes and quivers) and at a higher rate to large females than to small

Table 5 a Predicted OSR from reproductive rates compared with **b** the actual OSR (males: reproductively capable females), the sex ratio (males:females) and the OSR minus the sex ratio in each year of the study

a	OSR predicted from PRRs
Both caring	2:1
Male deserting and female caring	8:1
Male caring and female deserting	1:2
Both deserting	2:1

b Year	OSR	Sex ratio (M:F)	OSR relative to the sex ratio
1992	1.8:1	1.2:1	1.5:1
1993	2.2:1	1.6:1	1.4:1
1994	2.0:1	1.4:1	1.4:1

Fig. 4 a The number of males that spent more than half the test with the large female versus the small female. **b** The time males spent with large females versus small females. **c** The number of displays males performed to large versus small females. **d** The number of females that spent more than half the test with the large male versus with the small male. **e** The time females spent with large males versus small males. **f** The number of displays females performed to large versus small males (bars show SEs)

females (Fig. 4c, Wilcoxon signed ranks test, male display number, $z = -2.474$, $P = 0.01$; male display rate, $z = -2.354$, $P = 0.02$).

Females strongly preferred large partners. Of 15 trials, 14 females spent more than half the test duration with the large male and only 1 female spent the majority of the test time with the small male (Fig. 4d, $G = 11.0$, $df = 1$, $P < 0.001$). In addition, the mean time females spent with large males was significantly greater than the mean time spent with small males (Fig. 4e, Wilcoxon signed ranks test, $z = -2.953$, $P = 0.003$). Females also performed more courtship displays to large males but their rate of display did not vary between males (Fig. 4f, Wilcoxon signed ranks test, female display number, $z = -3.362$, $P = 0.0008$; female display rate, $z = -1.357$, $P = 0.15$). Males and females were not simply choosing the end fish closest to their own body size (males: $n_1 = 7$, $n_2 = 8$, $\chi^2 = 0.07$, $P > 0.70$; females: $n_1 = 9$, $n_2 = 6$, $\chi^2 = 0.60$, $P > 0.30$).

End fish did not differ in their display number or rate to the choosing fish and therefore did not affect mate choice in this experiment [end females $\bar{x} \pm$ SE display number (per watch): large females $= 21.4 \pm 2.9$, small females $= 17.6 \pm 2.0$, Wilcoxon signed ranks tests, $z = -1.22$, $P = 0.22$; end males $\bar{x} \pm$ SE display number (per watch): large males $= 17.9 \pm 2.1$, small

males $= 17.9 \pm 3.5$, $z = -0.853$, $P = 0.39$; end female $\bar{x} \pm$ SE display rates (per minute): large females $= 3.9 \pm 0.8$, small females $= 2.5 \pm 0.3$, $z = -1.601$, $P = 0.11$, end males $\bar{x} \pm$ SE display rates (per minute): large males $= 2.8 \pm 0.3$, small males $= 3.2 \pm 0.5$, $z = -1.603$, $P = 0.11$].

Which sex is most choosy?

To determine which sex had the strongest preference for large individuals, I compared male and female preferences and found that females are more choosy for partner size. Females spent substantially more time near large males than males spent near large females (Mann-Whitney U-test, $z = -2.9$, $P = 0.004$). The number of males who spent more time near large females (9/15 cases) was significantly different from the number of females (14/15) who spent more time near large males ($G = 5.06$, $df = 1$, $P < 0.025$). Males and females performed roughly equal numbers of courtship displays to large individuals (Mann-Whitney U-test, $z = -1.01$, $P = 0.32$). However, males' display rate to large individuals was significantly higher than females' (Mann-Whitney U-test, $z = -2.39$, $P = 0.02$). In addition, the size variation between end males was less

substantial than between end females, yet females were still more choosy.

The benefits of choosiness for each sex are difficult to compare. For females it is not known what magnitude of increase in reproductive success is experienced by choosing a 600-g male over a 400-g male. On the other hand, a large female (600 g) will be able to lay on average 2000 eggs, whereas a small female (400 g) will usually lay about 1500 eggs (Balshine-Earn 1995b). This potential difference in fecundity between large and small females means that males will probably experience a 25% increase in number of offspring if they choose large females over small ones.

Discussion

Male St. Peter's fish can potentially reproduce faster than females and hence the OSR was expected to be male biased. This was the case in all 3 years and on all substrates, throughout the entire breeding season and at all times of day examined. The actual OSR (not accounting for the bias in adult sex ratio) was approximately two males for every female (Table 5). The male bias in the OSR did not consistently increase or decrease during the season. Both the male bias in the sex ratio, and the faster male reproductive rate influenced the OSR to be male-biased. As the OSR is thought to determine the direction of mate choice and sexual competition (Clutton-Brock and Vincent 1991; Clutton-Brock and Parker 1992; Vincent et al. 1994; and Owens and Thompson 1994), male St. Peter fish were expected to be more competitive for mates and females to be more selective. Mate choice experiments revealed that both sexes of St. Peter's fish preferred large partners but that females were more choosy.

The results raise several related questions that I will address in turn.

Why is the OSR male-biased?

Two factors were identified as causes of the skew in the OSR: (a) the PRRs of each sex, and (b) the adult sex ratio. Adult sex ratio alone could not account for all the bias in the OSR. A third potential factor mentioned in the introduction was the spatial and temporal distribution of males and females. There was little evidence that this influenced the OSR. In St. Peter's fish, there are no known sexual differences in mortality rates or life span (Johnson 1974). Similarly, there are unlikely to be sexual differences in spatial distribution. Both sexes reach the littoral zone (breeding grounds) at approximately the same time (Johnson 1974). Pairs of males and females appear rather than lone individuals or groups of fish (Ben-Tuvia 1978). Fish distribution may be influenced by food availability; early in the breeding season (April–June) large quantities of food

are found in the form of *Perridinium* blooms in the pelagic zone, but the blooms disappear late in the breeding season (July–August) (Serruya 1978). However, this seasonal change in food abundance is likely to influence the range of both sexes equally.

Why is the adult sex ratio male-biased?

The male bias in the adult sex ratio is certainly puzzling. The Ministry of Agriculture may have caused the sex ratio bias by stocking more males than females. Lake Kinneret has been artificially stocked with *Sarotherodon galilaeus* since 1951, but in the 1980s there was a significant increase in the number of *S. galilaeus* fingerlings stocked in the lake each year (from an average of 1 million to an average of 3 million) (Sarid 1979; Golani 1984; Grofit 1993). Although it has never been confirmed that the stocked fingerlings survive and breed in the lake, there have been correlations showing that stocking affects the fish catch 2–3 years onwards (Ben-Tuvia et al. 1992b). Sex determination may be affected by hatchery conditions or possibly hatchery conditions may favour the survival of male fingerlings over females. Earlier studies found equal adult sex ratios in the lake (Ben-Tuvia 1959; Shefler 1980). Experiments are now underway to examine the suggestion that more males have been stocked.

What are the consequences of biases in the OSR?

A growing number of studies have examined the consequences of biased OSRs. The southern green stink bugs, a hemipteran that produces fluids distasteful to potential predators, has been shown to undergo facultative sex ratio adjustment in response to biases in OSRs (McLain and Marsh 1990). Keenleyside (1983) showed that male *Herotilapia multispinosa* will desert their brood when the OSR is female-biased. This Central American cichlid species is a substrate brooder, and although females tend to clean and fan the eggs and larvae, both parents are capable of all brood-caring activities. However, in Keenleyside's (1983) study females did not abandon their broods in male-biased environments. Similar results have been found with a number of cichlids (Barlow 1974; Keenleyside 1985; Keenleyside et al. 1990; Limberger 1983; Schwanck 1987; Townsend and Wootton 1985). However, Rogers (1987) found that neither male nor female *Cichlasoma citrinellum,* another substrate-guarding cichlid, will desert, regardless of the sex ratio. Berglund (1994) reports that sex-role reversed male pipefish, *Syngthathus typhle,* which are usually selective for mates, mate randomly as the OSR becomes increasingly male-biased. In this species, the male receives eggs from the female which he broods on his ventral body surface. A field study of this pipefish species, showed that under a

female-biased OSR females took bigger risks and interacted with other females more frequently, suggesting that female competition increased (Vincent et al. 1994). Likewise, in Wilson's phalarope a small sex-role reversed swimming shorebird female competition for males fluctuates with seasonal changes in the OSR (Colwell and Oring 1988). An increase in male-male competition with male biased OSRs has been observed in the Japanese medaka, *Oryzias latipes* (Grant et al. 1995), the pupfish, *Cyprinodon pecosensis* (Kodric-Brown 1988) and the water strider, *Gerris remigis* (Clark 1988). In Lake Kinneret's St. Peter's fish the male biased OSR probably ensures that females are more choosy for mating partners than males.

Four potential problems have been identified with the mate choice experiments described here:

1. We cannot unequivocally rule out the possibility that males will show stronger mate choice than females based on some other trait. For example, in this study, we could not assess the possibility that both sexes base mate choice on vigour of display since end fish displayed at a similar rate.
2. Display number was measured but intensity and duration of displays were ignored because they appeared to vary little between individuals and were more difficult to quantify accurately.
3. It would be desirable to repeat the experiment with several different stimulus pairs. It remains possible in the mate choice for size experiment that both sexes were not attracted by size but by some other unknown characteristic particular to the stimulus pairs used.
4. Actual mating rather than time spent near and display rates would have been the best mate choice test. However recording of actual matings were not attempted because of the logistical difficulties involved. To use actual matings as a mate choice test, the middle fish would have had to be much smaller than the end fish, allowing it access through a small hole in the partition but not allowing the end fish out of their end chambers. This would prevent aggression between the two end fish and inhibit dominance hierarchies forming between them. Such size variation in fish was not available and furthermore male and female St. Peter's fish mate assortatively by size so such matings between dramatically different size partners would probably have been unrealistic.

Bearing these limitations in mind, it is important to address two further questions suggested by the results.

Why is large size preferred in St. Peter's fish?

In species with biparental care, we expect both sexes to select breeding partners. Mutual mate choice has been tested only in two other monogamous species, the crested auklet, *Aethia cristatella* (Jones and Hunter 1993) and the midas cichlid, *Cichlasoma citrinellum* (Rogers and Barlow 1991). In the crested auklet, both sexes preferred elongated forehead crests but female response to accentuated models was stronger than the male response. In the midas cichlid, females preferred large over small males, aggressive males over unaggressive ones and experienced males over inexperienced ones. Males showed no consistent choice among females in any of the three variables. Both male and female St. Peter's fish preferred large mates, probably because it is beneficial to mate with an individual that can provide superior protection for eggs. For example, a large mate might be in superior condition and consequently able to invest a larger absolute measure of resources in raising the brood [possibly it is less likely to desert (Balshine-Earn 1995b) or cannibalise eggs (Rohwer 1978)]. In addition, a large mate may have greater care experience because it is older: age and size are positively related in St. Peter's fish (Johnson 1974). Finally, a large mate may have fewer predators because they are more intimidating and effective at keeping potential predators away. Male St. Peter's fish have an extra reason to choose the largest available mate since female fecundity increases with female size (Balshine-Earn 1995a).

Why were females more choosy?

Since the variance in quality in terms of size is likely to be greater in females (size affects both fecundity and parental ability) than in males (size affects only parental ability) we might have predicted that males would be more selective. Reproductive rates may explain why females are the more selective sex. Although both sexes care, male St. Peter's fish can process mates faster than females. Caring males can potentially produce offspring 1.6 times faster than caring females, and caring males can respawn immediately while caring females must wait a minimum of 15 days before they can spawn again (Balshine-Earn 1995a). If the differences in reproductive rates were very small and the OSR close to parity then the variance in mate quality would probably influence which sex would be the most selective and males may have been more choosy. However, a twofold difference in reproductive rates caused a male bias in the breeding population. This male-bias in the OSR makes mate choice reproductively costly for males and these costs outweigh the benefits.

This study is among the first to examine in a single species both the OSR and sex-biases in choice in light of recent theoretical advances. The results support modern OSR theory; reproductive rates of St. Peter's fish indeed control the extent and direction of biases in the OSR which in turn influence sex differences in mating competition and choice. The results also suggest that PRRs are more important than sex ratio in determining the OSR. To further test this proposal

it would be valuable to compare Lake Kinneret's St. Peter's fish population with St. Peter's fish from Lake IIta in Nigeria where Fagade et al. (1984) have reported a female bias in the adult sex ratio of St. Peter's fish.

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