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An Evolutionary Model of Parental Care in St. Peter's Fish

SIGAL BALSHINE-EARN†,‡ AND DAVID J. D. EARN§

† *L.A.R.G., Department of Zoology, Downing Street, Cambridge, CB2 3EJ, U.K. and* § *Racah Institute of Physics, The Hebrew University, Jerusalem* 91904, *Israel*

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Galilee St. Peter's fish shows unusual lability in caring patterns; male-only, female-only and biparental care all occur in the same population. We present a game-theoretical model and investigate the evolutionary stability of the care frequencies observed. Using mean values for each of the model's parameters (estimated previously for the Lake Kinneret population of St. Peter's fish) we find that the current care frequencies are unstable and male-only care is the only evolutionarily stable parental care strategy. However, two key model parameters have significant dispersions: the operational sex ratio (OSR) varies both temporally and spatially, and the advantage of biparental care relative to uniparental care depends critically on clutch size, which can vary dramatically. Within the full ranges of observed OSRs and clutch sizes, there are regions in which each of male-only, female-only and biparental care is an evolutionarily stable strategy; there is also a region where no evolutionarily stable strategy exists. Thus natural variations in OSR and clutch size may account for the observed care frequencies.

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1. Introduction

Galilee St. Peter's fish, *Sarotherodon galilaeus*, is a mouth brooding cichlid in which parental care may be provided by either sex alone or by both parents (Fishelson & Heinrich, 1963; Fryer & Iles, 1972). This flexibility of caring behaviour presents an unusual opportunity to examine which factors select for male-only, female-only and biparental care, and to investigate care evolution in general. The aim of this study was to modify an existing game theoretical model to suit St. Peter's fish and to determine whether the frequencies of care observed in the wild (Lake Kinneret, northern Israel) can be explained using this model.

St. Peter's fish are found in rivers and lakes throughout Africa and Asia minor (Trewavas, 1983). They mate monogamously during the production of a single clutch (Johnson, 1974) laying green eggs into a shallow depression in the substrate, which both parents dig together (Ben Tuvia, 1959). The female deposits batches of 20–40 eggs in the nest and the male glides over them, fertilizing each batch as it is deposited. This procedure is repeated until the entire clutch is laid. The clutch remains on the ground for approximately 15 minutes before the male, the female or both pick up the eggs for oral incubation (Schwanck & Rana, 1991). Although both parents may be involved in mouth brooding the pair bond dissolves after egg collection (Apfelbach, 1969). The eggs hatch after about 4 days but the fry continue to develop inside the parent's mouth until the yolk sac is absorbed. Inside the parents' mouths, the eggs and later the fry are well protected and supplied with oxygen. The parents do not feed while brooding (Fagade, 1982).

In this species the outcome of any spawning event is one of four possible discrete care states: biparental care (BC), female-only care (FC), male-only care (MC), or no care (NC). The frequencies of male and female care in the wild are known (Balshine-Earn, 1996a). The costs and benefits of care for each sex

‡ Author to whom correspondence should be addressed. Current address: KLIVV, Savoyenstrasse 1a, A-1160, Vienna, Austria. E-mail: sigal@klivv.oeaw.ac.at.

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TABLE 1
Model parameters for St. Peter's fish in Lake Kinneret

Parameter	Meaning	Mean value for *S. galilaeus*	Reference
OSR: $\frac{M}{F+M}$	The proportion of males in the reproductively capable part of the population at a given time and place.	0.62 ($\pm$0.03)	a
T	The (fixed) caring time invested by a parent that cares.	13.7 ($\pm$0.4) days	b
T_{fC}	The time required by caring females to prepare for the next breeding after completing one brood.	24.1($\pm$1.6) days	b
T_{fNC}	The time required by non-caring (deserting) females to prepare for the next breeding after completing one brood.	13 ($\pm$0.9) days	b
T_{mC}	The equivalent of T_{fC} for males.	12.3 ($\pm$1.7) days	b
T_{mNC}	The equivalent of T_{fNC} for males.	4.9 ($\pm$0.8) days	b
P_0	Surviving offspring in the absence of care (NC).	0 fry	c
P_1	Surviving offspring under uniparental care (FC or MC).	650 fry (median)	c
P_2	Surviving offspring under biparental care (BC).	1059 fry (median)	c

Standard errors are given for each value. Note that the "recovery" times (T_{fC}, T_{fNC}, T_{mC} and T_{mNC}) include the time required for pair bonding and nest building before the next spawn. P_1 and P_2 are crude estimates based on number of offspring that complete larval development rather than number of offspring that reach sexual maturity. Data from: a, Balshine-Earn, 1996a; b, Balshine-Earn, 1995a; c, Balshine-Earn 1996b.

have also been measured empirically (Balshine-Earn, 1995a, 1996b).

Since an individual's fitness depends on its mate's behaviour, game theory is well suited to the study of parental care allocation. Here we present a game-theoretical model that quantifies the pay-offs of each care state for males and females and permits an evolutionary stability analysis using the data collected.

2. The Model

We model the parental care conflict as a game between two different types of players, females and males. Each individual seeks to maximize its own return or "pay-off" which depends on the strategies adopted by each of the two players. Here, the payoff is fitness, which we estimate using reproductive rates (offspring produced per unit time). We base our model on nine biological parameters for which values are known for St. Peter's fish (Table 1). Using the data in Table 1 we obtain the payoffs for the four care states (Tables 2a and 2b).

The simple analysis given in Tables 2a and 2b reveals that both males and females do best when they desert, provided their partner cares. However, if both sexes desert then neither realizes any reproductive success. Biparental care gives both sexes substantial fitness but is not an optimal strategy for either sex.

Such a static analysis of payoffs is valid for a species that breeds once or perhaps twice a year or season, but it is unrealistic for a continuous breeder like St. Peter's fish. In Lake Kinneret, breeding is essentially continuous because the long breeding season (March to September) allows sufficient time for an individual to mate several times (Ben-Tuvia, 1978). Throughout most of St. Peter's fish's range there is no distinct breeding season so breeding is certainly continuous in other lakes and rivers (Trewavas, 1983). Thus, the pay-offs should depend on the probability of remating, which itself depends on the operational sex ratio.

Maynard Smith (1977) suggested a game-theoretical model for evolution of parental care under continuous breeding (his Model 3). However, his model is inappropriate for St. Peter's fish because it assumes that the number of offspring surviving depends on how long parents spend caring. In St. Peter's fish, the caring time, T, is determined by water temperature and egg size, and does not vary between the sexes. Therefore, the appropriate evolutionary variables in this system are the probabilities, f and m,

TABLE 2a
Male pay-offs

Male pay-offs	Male cares	Male deserts
Female cares	$\frac{P_2}{T+T_{mC}} = 41$	$\frac{P_1}{T_{mNC}} = 133$
Female deserts	$\frac{P_1}{T+T_{mC}} = 25$	$\frac{P_0}{T_{mNC}} = 0$

Pay-offs are expressed in number of fry produced per day. Mating partners are assumed to be available at all times.

TABLE 2b
Female pay-offs

Female pay-offs	Male cares	Male deserts
Female cares	$\frac{P_2}{T+T_{fC}} = 29$	$\frac{P_1}{T+T_{fC}} = 17$
Female deserts	$\frac{P_1}{T_{fNC}} = 50$	$\frac{P_0}{T_{fNC}} = 0$

Again, pay-offs are expressed in number of fry produced per day and mating partners are assumed to be available at all times.

that females and males provide care after spawning. Recently, Yamamura & Tsuji (1993) have developed a model for this situation; we adapt their approach to suit St. Peter's fish.

Caring and desertion are not static tactics in St. Peter's fish; an individual fish will sometimes care and at other times desert (S. Balshine-Earn, personal observation). For simplicity, we assume that females and males decide independently whether to care or desert after a given spawn, i.e. a given fish is not influenced by its partner's decision. We also assume that all females in the population provide care with the same probability, f, and that all males in the population provide care with the same probability, m.

The Yamamura & Tsuji (1993) model needs to be generalized because the time required by females and males to prepare for the next breeding (after completing the previous brood) depends on whether or not they provided care in the previous brood. Moreover, Yamamura & Tsuji (1993) discussed only the cases of pure BC, FC, MC or NC, whereas St. Peter's fish is an example of a mixed care system (BC, FC and MC all occur). Below we show how, given values for the parameters listed in Table 1, evolutionarily stable values for f and m can be determined, if they exist.

In the first entry of Table 1, F and M denote the number of available reproductively capable females and males, respectively, in the population at a given time. Only the operational sex ratio ($\mathrm{OSR} = M/(F + M)$) is required for the analysis. The OSR was measured from a large collection of fish samples so its mean value is reliable. Later (in Section 3) we explore the full range of observed OSR values. The values assigned to P_1 and P_2 (surviving offspring under different care conditions) are medians because the sample sizes in the case of uniparental care are small (11 cases each of FC and MC). For such small samples the median gives a better estimate of the central tendency. The small sample for P_1 implies a large uncertainty in the ratio P_2/P_1; a further uncertainty arises because we are using rate of fry released to estimate survival rates. We return to this point later and examine a wide range of P_2/P_1.

Our two evolutionary variables, the probabilities f and m, cannot be measured directly, but they can be inferred from the known frequencies of each care state in the population. The probability that a female will desert is $1 - f$ and the probability that a male will desert is $1 - m$. It follows that the probability of FC is $f(1 - m)$, the probability of MC is $(1 - f)m$, the probability of BC is fm and the probability of NC is $(1 - f)(1 - m)$. From observations in Lake Kinneret and pond enclosures (Balshine-Earn, 1996b) we know the relative frequency of BC is 0.77 ($\pm$0.03); of FC is 0.15 ($\pm$0.02); and that of MC is 0.07 ($\pm$0.01); the errors are estimated from the difference between the measured values in the lake and in pond enclosures. Therefore, the probability of FC is:

$$f = fm + f(1 - m) = (0.77 \pm 0.03) + (0.15 \pm 0.02) = 0.92 \pm 0.04, \quad (1a)$$

and the probability of MC is:

$$m = fm + (1 - f)m = 0.84 \pm 0.03, \quad (1b)$$

where we have added the errors in quadrature. It follows that the probability of NC is $(1 - f)(1 - m) = 1 - f - m + fm = 0.01 \pm 0.06$, consistent with the observed NC frequency of zero (Balshine-Earn, 1996b).

For caring females, the duration of a breeding cycle is $T + T_{\mathrm{fC}}$, while for deserting females it is T_{fNC}. Therefore the maximum rate at which females become available to start a new breeding cycle is:

$$F\left(\frac{f}{T + T_{\mathrm{fC}}} + \frac{1 - f}{T_{\mathrm{fNC}}}\right). \quad (2)$$

This assumes that when a female is ready to mate there is always a male available to mate with her. Similarly the maximum rate at which males enter a new breeding cycle is:

$$M\left(\frac{m}{T + T_{\mathrm{mC}}} + \frac{1 - m}{T_{\mathrm{mNC}}}\right). \quad (3)$$

However, unless the maximum rates are identical one of the two sexes will typically have to wait a certain time after recovering from the previous reproductive attempt before mating again. The values given in Table 1 and the probabilities in eqns (1a) and (1b) imply the following inequality:

$$M\left(\frac{m}{T + T_{\mathrm{mC}}} + \frac{1 - m}{T_{\mathrm{mNC}}}\right) > F\left(\frac{f}{T + T_{\mathrm{fC}}} + \frac{1 - f}{T_{\mathrm{fNC}}}\right). \quad (4)$$

Thus before females become available, males will have a waiting time T_{mw}. As noted above, the duration of a breeding cycle is $T + T_{\mathrm{fC}}$ for a caring female and T_{fNC} for a deserting female; in contrast, it is $T + T_{\mathrm{mC}} + T_{\mathrm{mw}}$ for a caring male and $T_{\mathrm{mNC}} + T_{\mathrm{mw}}$ for a deserting male. Since the number of females and

males entering a new breeding cycle (i.e. mating) at a given time must be the same, it follows that:

$$\frac{m}{T + T_{\mathrm{mC}} + T_{\mathrm{mw}}} + \frac{1-m}{T_{\mathrm{mNC}} + T_{\mathrm{mw}}} = \frac{F}{M}\left(\frac{f}{T + T_{\mathrm{fC}}} + \frac{1-f}{T_{\mathrm{fNC}}}\right). \quad (5)$$

If, for convenience, we define:

$$\alpha(f) = \frac{F}{M}\left(\frac{f}{T + T_{\mathrm{fC}}} + \frac{1-f}{T_{\mathrm{fNC}}}\right), \quad (6a)$$

$$\beta(f) = -\frac{1}{2}\left(T + T_{\mathrm{mC}} + T_{\mathrm{mNC}} - \frac{1}{\alpha(f)}\right), \quad (6b)$$

$$\gamma(f, m) = \frac{1}{\alpha(f)}[mT_{\mathrm{mNC}} + (1-m)(T + T_{\mathrm{mC}})] - (T + T_{\mathrm{mC}})T_{\mathrm{mNC}}, \quad (6c)$$

then eqn (5) can be rewritten in the quadratic form:

$$T_{\mathrm{mw}}^2 - 2\beta T_{\mathrm{mw}} - \gamma = 0. \quad (7)$$

Solving this equation for T_{mw} we find:

$$T_{\mathrm{mw}}(f, m) = \begin{cases} \beta + \sqrt{\beta^2 + \gamma} & \text{if inequality (4) holds,} \\ 0 & \text{otherwise.} \end{cases} \quad (8)$$

In this formula the positive sign before the square root is dictated by the requirement that T_{mw} is positive if inequality (4) holds. For values of f and m for which the inequality (4) goes the other way, it is females rather than males who suffer a waiting time $T_{\mathrm{fw}}(f, m)$. The resulting formula for female waiting time is identical to that derived for males, but with the female and male caring probabilities and sex dependent parameters exchanged. Note that the ratio F/M, which appears in the above equations, is simply related to our definition of the OSR: with $\mathrm{OSR} = M/(F + M)$, $F/M = (1 - \mathrm{OSR})/\mathrm{OSR}$.

Here we estimate the fitness of a female in the population with her reproductive rate (the number of offspring produced per day). We are interested in the average reproductive rate over the entire reproductive lifetime of the animal. [The average of the instantaneous rates under each care form, used in eqns (2) and (3), is different; this distinction is the source of a controversy in optimal foraging theory (e.g. Stephens & Krebs 1986, p.16).] The number of offspring that reach sexual maturity would be a better estimate of fitness but applicable data is not available. The average reproductive rate of an ordinary female (R_{f}) is the ratio of her mean reproductive success per spawn to her mean interspawn interval:

$$R_{\mathrm{f}} = \frac{(1-f)(1-m)P_0 + (f + m - 2fm)P_1 + fmP_2}{f[T + T_{\mathrm{fC}} + T_{\mathrm{fw}}(f, m)] + (1-f)[T_{\mathrm{fNC}} + T_{\mathrm{fw}}(f, m)]}. \quad (9)$$

(Note in this equation that $(f + m - 2fm) = [f(1-m) + (1-f)m]$, i.e. the sum of the probabilities of FC and MC. Similarly an ordinary male has fitness:

$$R_{\mathrm{m}} = \frac{(1-f)(1-m)P_0 + (f + m - 2fm)P_1 + fmP_2}{m[T + T_{\mathrm{mC}} + T_{\mathrm{mw}}(f, m)] + (1-m)[T_{\mathrm{mNC}} + T_{\mathrm{mw}}(f, m)]}. \quad (10)$$

Inserting the mean parameter values from Table 1 and the values of f and m from eqns (1a) and (1b), we find that for St. Peter's fish from Lake Kinneret:

$$T_{\mathrm{fw}} = 0 \text{ days}, \quad (11a)$$

$$T_{\mathrm{mw}} = 32.4 \text{ days}. \quad (11b)$$

We also find:

$$R_{\mathrm{f}} = 31.9 \text{ fry per day}, \quad (12a)$$

$$R_{\mathrm{m}} = 20.8 \text{ fry per day}. \quad (12b)$$

To examine whether the current frequencies of male and female care are stable, consider a mutant female who, rather than providing care with probability f, never cares ($f' = 0$). If males who breed with her do not increase their caring frequency as a result of her desertion then her fitness is:

$$R_{\mathrm{f'NC}} = \frac{(1-m)P_0 + mP_1}{T_{\mathrm{fNC}} + T_{\mathrm{fw}}(f, m)} = 42.0 \text{ fry per day} = 1.31R_{\mathrm{f}}, \quad (13)$$

an increase of 31% relative to normal females. If a mutant female instead always cares ($f' = 1$) and the caring frequency of males who breed with her is unchanged, then her fitness is:

$$R_{\mathrm{f'C}} = \frac{(1-m)P_1 + mP_2}{T + T_{\mathrm{fC}} + T_{\mathrm{fw}}(f, m)} = 31.6 \text{ fry per day} = 0.99R_{\mathrm{f}}, \quad (14)$$

a decrease of 1% relative to normal females. Females would apparently be better off if they deserted more often.

Now consider an invading male who never cares ($m' = 0$). Since an ordinary female in the population

provides care with probability f, this mutant male's fitness is:

$$R_{m'NC} = \frac{(1-f)P_0 + fP_1}{T_{mNC} + T_{mw}(f,m)} = 16.1 \text{ fry per day} = 0.77R_m, \quad (15)$$

Another mutant male might adopt an always-care strategy ($m' = 1$). Assuming females make their caring decision independently, this mutant male's fitness is:

$$R_{m'C} = \frac{(1-m)P_1 + fP_2}{T + T_{mC} + T_{mw}(f,m)} = 21.4 \text{ fry per day} = 1.03R_m. \quad (16)$$

Males should apparently care more often.

3. Is there an evolutionarily stable state for St. Peter's fish?

Natural selection is expected to lead to an evolutionarily stable strategy (ESS), i.e. a strategy that is stable against "cheating" (Maynard Smith & Price, 1973). In the present model a strategy has the form "if female, care with probability f; otherwise, care with probability m". If an ESS exists and each individual in the population adopts it then no mutant can have greater fitness than ordinary fish. We have found so far that the current male and female care frequencies do not imply an ESS for the system: a never-caring female or an always-caring male could apparently invade this population.

We now establish what ESSs, if any, exist in the present model. Those who are not interested in the mathematical analysis should skip ahead and continue reading after eqn (21b).

To find all ESSs, we first obtain an expression for the fitness (reproductive rate) of a mutant female that cares with any probability f' (not necessarily 0 or 1 as considered above). This mutant female's fitness is:

$$R_{f'}(f',f,m) = \frac{(1-f')(1-m)P_0 + (f'+m-2f'm)P_1 + f'mP_2}{f'[T + T_{fC} + T_{fw}(f,m)] + (1-f')[T_{fNC} + T_{fw}(f,m)]}. \quad (17)$$

This expression differs from the corresponding expression [eqn (9)] for ordinary females in that f' rather than f appears in the probabilities of each care form. Note, however, that the waiting time $T_{fm}(f,m)$ depends on f and m and not f' because the presence of a single mutant will not affect the average waiting time in the population. We can usefully reorganize eqn (17) into the form:

$$R_{f'}(f',f,m) = \frac{[-(1-m)P_0 + (1-2m)P_1 + mP_2]f' + [(1-m)P_0 + mP_1]}{[T + T_{fC} - T_{fNC}]f' + [T_{fNC} + T_{fw}(f,m)]} \equiv \frac{a_f f' + b_f}{c_f f' + d_f}, \quad (18)$$

where a_f, b_f, c_f and d_f are defined by this equation and are independent of f'. Since $T > 0$, $T_{fC} > T_{fNC} > 0$ and $T_{fw}(f,m) \geqslant 0$, it follows that $c_f > 0$ and $d_f > 0$, so the denominator in eqn (18) is positive for any probability f' and $R_{f'}(f',f,m)$ is always well-defined. If a mutant female does not care at all ($f' = 0$) then eqn (18) reduces to eqn (13); if she always cares ($f' = 1$) then it reduces to eqn (14).

The same reasoning applies to males. A mutant male who cares with probability m' has fitness:

$$R_{m'}(m',f,m) = \frac{[-(1-f)P_0 + (1-2f)P_1 + fP_2]m' + [(1-f)P_0 + fP_1]}{[T + T_{mC} - T_{mNC}]m' + [T_{mNC} + T_{mw}(f,m)]} \equiv \frac{a_m m' + b_f}{c_m m' + d_m}, \quad (19)$$

where the male waiting time T_{mw} is given in eqn (8). If $m' = 0$ then eqn (19) is identical to eqn (15) while if $m' = 1$ then it is the same as eqn (16).

A pair of probabilities (f,m) represents an ESS if mutant fish always have lower fitness than ordinary fish, i.e. $R_{f'}(f',f,m)$ is a maximum for $f' = f$ and $R_{m'}(m',f,m)$ is a maximum for $m' = m$. Therefore, we must examine the behaviour of $R_{f'}(f',f,m)$ as a function of f' and $R_{m'}(m',f,m)$ as a function of m'.

The rate of change of $R_{f'}(f',f,m)$ with respect to f' is:

$$\frac{\partial R_{f'}}{\partial f'} = \frac{a_f d_f - b_f c_f}{(c_f f' + d_f)^2}. \quad (20)$$

Since the denominator is always positive, the direction of change is the same for all values of f' and depends only on the sign of the numerator $a_f d_f - b_f c_f$. If this quantity is negative then $R_{f'}$ always decreases as f' increases and the mutant female is better off caring as little as possible. If $a_f d_f - b_f c_f$ is positive then $R_{f'}$ always increases as f' increases and she is better off caring as much as possible. If $a_f d_f - b_f c_f$ is zero then her fitness will be identical to ordinary females regardless of how often she cares. Thus, unless $a_f d_f - b_f c_f = 0$, she will always be best either to care all the time or never. A similar argument applied to $R_{m'}(m',f,m)$ implies that, unless $a_m d_m - b_m c_m = 0$,

the fittest mutant males will be those who care either all the time or never.

A mixed ESS can occur only if both $a_f d_f - b_f c_f$ and $a_m d_m - b_m c_m$ are zero for the same values of f and m (with $0 < f < 1$ or $0 < m < 1$ or both). However, a theorem proved by Selten (1980) guarantees that whenever this occurs the pair of probabilities (f, m) is not evolutionarily stable. Thus there can be no mixed ESS.

We see that the only possible ESSs in the present model are the extreme cases: pure BC, FC, MC or NC (in practice, NC is ruled out because $P_0 = 0$). It is therefore very simple to find ESSs in this model if any exist: given specific values for the parameters listed in Table 1 we simply insert them in eqns (18) and (19) and evaluate the signs of $a_f d_f - b_f c_f$ and $a_m d_m - b_m c_m$ for the four possible ESS strategies.

If we insert the mean parameter values given in Table 1 then we find:

$$\operatorname{sign}(a_f d_f - b_f c_f) = \begin{cases} - & \text{if } f = 1,\ m = 1 \text{ (BC)}, \\ + & \text{if } f = 1,\ m = 0 \text{ (FC)}, \\ - & \text{if } f = 0,\ m = 1 \text{ (MC)}, \\ + & \text{if } f = 0,\ m = 0 \text{ (NC)}, \end{cases} \tag{21a}$$

$$\operatorname{sign}(a_m d_m - b_m c_m) = \begin{cases} + & \text{if } f = 1,\ m = 1 \text{ (BC)}, \\ + & \text{if } f = 1,\ m = 0 \text{ (FC)}, \\ + & \text{if } f = 0,\ m = 1 \text{ (MC)}, \\ + & \text{if } f = 0,\ m = 0 \text{ (NC)}. \end{cases} \tag{21b}$$

Consider first the case of MC ($f = 0, m = 1$). The sign of $a_f d_f - b_f c_f$ is " $-$ ". Therefore, a mutant female's fitness always decreases with the frequency with which she cares, so she will do best if she adopts a never-care strategy, like the ordinary females in the population. On the other hand, a mutant male's fitness increases as his caring frequency increases, so he does best to care all the time ($m' = 1$), i.e. to adopt the same strategy as ordinary males in the population. Since mutants of both sexes are fittest if they adopt the strategy of ordinary fish in the population, MC is an ESS. Now consider the case of FC ($f = 1, m = 0$). A mutant female's fitness then increases with her caring frequency, so she does best to adopt the strategy of ordinary females in the population. However, a mutant male's fitness also increases in this case so he does best not to adopt the strategy of ordinary males. Such mutant males can invade the population and therefore FC is not an ESS. Similarly, BC is not an ESS because non-caring females can invade, and (unsurprisingly) NC is not an ESS because either caring females or caring males can invade. Thus MC is the only ESS.

The preceding discussion has assumed that the OSR = 0.62. However, due to practices of stocking St. Peter's fish in Lake Kinneret, the OSR may be artificially male-biased (Balshine-Earn, 1996a). Since the 1980s, only large fingerlings have been stocked (to improve fry survival); this may have inadvertently selected for males, which grow faster in the ponds (Johnson, 1974). Previous studies (Ben Tuvia, 1959; Shefler, 1980) found equal sex ratios in the lake but did not estimate the OSR. From 1991–1994, the sex ratio and the OSR were estimated in Lake Kinneret, and both were found to be male-biased (Balshine-Earn, 1996a). Thus it is likely that the species evolved under a lower OSR (i.e. mean OSR < 0.62). Moreover, the mean OSR does not reflect its temporal and spatial variation: in 79 samples taken at different times and in different regions of the lake, OSR values in the full range (0 to 1) were observed and the standard deviation was 0.22 (see Balshine-Earn, 1996a). Therefore in the following discussion we consider the full range of OSRs.

In addition, the important ratio P_2/P_1 is uncertain for several reasons: (1) the value of P_1 is based on a small sample, (2) the estimate of survival rates is based on number of fry incubated rather than number surviving and reproducing, and (3) P_2/P_1 depends strongly on clutch size, which varies dramatically (Balshine-Earn, 1995b). When we compared fish of similar body weights providing biparental versus uniparental care we found that P_2/P_1 varied from 1 to 3.3. Therefore we also explore a wide range of P_2/P_1.

When clutch sizes are large we expect P_2/P_1 to be large, because conditions for development may be enhanced when young are not squeezed into one mouth cavity. Rana (1986) found that too many eggs in the buccal cavity cause damage to developing embryos during the churning action of incubation. This suggests that long-term survival rates under BC will be boosted relative to FC or MC, since the brood pouch tends to be less full under BC. Deserted St. Peter's fish attempt to incubate a (20%) larger brood (Balshine-Earn, 1996b). Thus 3.3 may be an underestimate of the true upper limit of P_2/P_1.

Figure 1 shows the P_2/P_1 versus OSR plane cut through the full parameter space where the five time parameters (T, T_{fC}, T_{fNC}, T_{mC} and T_{mNC}) have the mean values given in Table 1. (The four recovery times are strongly correlated: they all decrease when more food is available.) Regions where various ESSs occur are identified in Fig. 1. At the lower limit of the horizontal axis ($P_2/P_1 = 1$) biparental care is no more effective than uniparental care, and both MC and FC

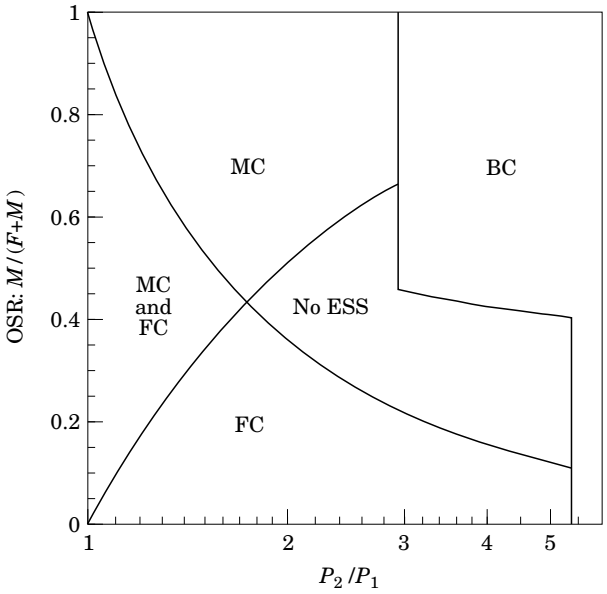

FIG. 1. The two key parameters in the model are the operational sex ratio (OSR) and the number of offspring produced under biparental care relative to uniparental care (P_2/P_1). The figure shows the regions where ESSs occur in the P_2/P_1 vs. OSR plane when all the other parameters are fixed at their mean values given in Table 1. (Note that the horizontal scale is logarithmic.) P_2/P_1 depends on clutch size, which varies between fish and between spawns. When a very small clutch is laid, one fish may be able to care for the entire clutch alone ($P_2/P_1 \simeq 1$, far left of the figure); when a large clutch is laid, many more fry may survive if both parents care ($P_2/P_1 > 2$, right half of the figure is more relevant). The full range (0 to 1) of OSRs was observed and found to vary with time and location in the lake. The significant natural variations in P_2/P_1 and the OSR suggest that each of the regions shown in the figure may be relevant at different times and places, and this may account for the observed mixed caring strategies.

are ESSs. At the other extreme ($P_2/P_1 = 6$) BC is much more effective and is always an ESS. Very similar results are obtained if the time parameters are varied throughout their observed ranges.

If we consider the full ranges of the OSR and P_2/P_1 shown in Fig. 1, then the model can account for the observed (mixed) care frequencies as follows. For a given reproductive cycle, a certain region in Fig. 1 is relevant, depending on the current, local OSR and the size of the clutch laid. Thus different strategies may be optimal for spawns that fall in different OSR and clutch size classes.

4. Discussion

Previous work has highlighted the costs of parental care in St. Peter's fish, and the existence of a biased OSR in the Lake Kinneret population (Balshine-Earn, 1995a, 1996a). The simple model described in this paper takes both these results into account. Our results emphasize that males often lose fitness by desertion and may not be able to compensate for this by remating quickly. Thus, despite the high costs of parental care for males (weight loss and longer interspawn intervals; Balshine-Earn, 1995a) they do benefit from providing care.

With parameters set at their mean values (Table 1) the model suggests that male-only care could be an ESS for St. Peter's fish in Lake Kinneret. If we accept the means as representing all biologically important information about the model parameters, then we must ask why the current population has not reached the ESS of the model (MC). Why do males sometimes desert and why do females ever care? One possible answer is that parental care evolution has simply not yet reached the ESS in this species. This is conceivable since in a closely related species, the black-chinned tilapia (*Sarotherodon melanotheron*), only males provide care (Trewavas, 1983). Another answer is that the model is too simplistic.

We have pointed out some possible systematic errors in our estimates of the means of the two key biological parameters, the OSR and P_2/P_1. We have also noted that they both have large dispersions in Lake Kinneret (due to spatio-temporal variations in the OSR, and clutch size variations leading to fluctuations in P_2/P_1). When we examine the predictions of the model for the full range of observed parameter values, we find that each of BC, FC and MC may be an ESS, or there may be no ESS, depending on the specific conditions confronting a given mating pair (see Fig. 1). [In experimental manipulations of the OSR, male St. Peter's fish desert more often in female-biased environments (Balshine-Earn, 1995b).] Thus the apparent inconsistency between the observed care frequencies and the ESS predicted by the model (using the mean parameter values given in Table 1) may simply reflect the need to take account of spatial (or temporal) structure in the OSR and fluctuations in P_2/P_1.

There are other possibly crucial factors that the present model ignores. For example: (1) in addition to the OSR and P_2/P_1, other parameters listed in Table 1 are not strictly constants but vary, e.g. with water temperature which in turn varies during the breeding season. (2) Some of the parameters listed in Table 1 may themselves be evolutionary variables. (3) Reproductive rate may not be an accurate fitness measure; offspring survival and offspring reproduction should also be considered. (4) Animals in different age or size classes may have different optimal strategies; an ESS could involve different strategies for each particular age, condition or size class of males and females. In general, variations in animal status and/or condition may be important. (5) Caring

decisions are probably not made independently; each fish's decisions are likely to be influenced by the decisions made by its partner. A better model would attempt to take some or all of these considerations into account.

Point (5) is probably the most important feature missing in the present model. After spawning, St. Peter's fish have two decisions to make: the first is whether to care or desert and the second is how many eggs to incubate if they care. (Desertion usually occurs before either sex has begun to pick up eggs for oral incubation.) Each of these decisions reflects the inherent conflict of interest between the sexes, i.e. each sex profits if its mate assumes a greater share of the parental investment (Trivers, 1972; Houston & Davies, 1985; Wright & Cuthill, 1990). This conflict is most apparent when the pair has finished spawning but has not yet begun incubating eggs. A male and female who have finished egg laying and fertilization swim in a circle above the eggs; every few minutes one parent will inspect the eggs (Schwanck & Rana, 1991). Despite the risk of brood predation the eggs may be left untouched for up to 45 minutes (Balshine-Earn, 1995b). Neither sex seems willing to pick up eggs until the other has; when one parent begins the other usually follows suit within a minute or two. In aquaria, when one fish has taken eggs but its mate has left the circle with no eggs, the brooding individual will sometimes turn on its partner (who it had just been courting) and begin to chase and butt it (S. Balshine-Earn, personal observation). Because the brooding partner's mouth is full of eggs it cannot bite and therefore does not seriously harm its partner. A chased fish sometimes ignores its partner; other times it returns to the circle, which appears to stop its mate's aggressive behaviour.

The behaviour just described resembles that expected in the war of attrition model (Maynard Smith, 1974). The battle between male and female St. Peter's fish is usually won by males. Females are usually first to pick up eggs (Balshine-Earn, 1995b), perhaps because deferring reproduction to the future is more costly for them than for males. (Compared with sperm, eggs require more energy to produce and as the season progresses food becomes increasingly limited. The asymmetry in pre-zygotic investment, coupled with seasonal changes, may explain why females care. The present simple model cannot explain why females usually pick up eggs first, but it does help explain why male care is common. The dependence of these decisions on the behaviour of partners could be included using "dynamic game theory"(e.g. Houston & McNamara, 1988). In this framework, the decision-making of two individuals and how the timing of each decision affects the other player could be considered.

In conclusion, we emphasize that the principal contribution of this paper is to apply a theoretical model to the parental care behaviour of a specific animal. Data collected in Lake Kinneret have allowed us to expose the strengths and weaknesses of a simple model applied to St. Peter's fish, and to propose that dynamic game theory be used in a more elaborate analysis. It may be that with more sophisticated modelling techniques the care frequencies observed for St. Peter's fish in Lake Kinneret will prove to be evolutionarily stable.

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