Females increase current reproductive effort when future access to males is uncertain

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Trade-offs between current and future repro-
duction shape life histories of organisms, e.g.
increased mortality selects for earlier repro-
ductive effort, and mate limitation has been
shown to shape male life histories. Here, we
show that female life histories respond adap-
tively to mate limitation. Female common
gobies (*Pomatoschistus microps*) respond to a
female-biased operational sex ratio by strongly
increasing the size of their first clutch. The
plastic response is predicted by a model that
assumes that females use the current competi-
tive situation to predict future difficulties of
securing a mating. Because female clutch size
decisions are much more closely linked to
population dynamics than male life-history
traits, plastic responses to mate-finding limi-
tations may be an underappreciated force in
population dynamics.

1. INTRODUCTION

Mate availability is usually not assumed to limit
female reproduction, yet there is mounting evidence
that this generalization often fails (Wedell *et al.* 2002;
Kokko & Mappes 2005; Smith & Reichard 2005). In
particular, species with male parental care (Borg *et al.*
2002; Forsgren *et al.* 2004) or significant male
nutritional investment in the eggs (Simmons &
Kvarnemo 2006) often show female–female compe-
tition for access to male parental investment. When
parental investment differs little between the two
sexes, sex roles can rapidly change in response to the
availability of the opposite sex, expressed as the
operational sex ratio (OSR; Borg *et al.* 2002; Forsgren
et al. 2004; Simmons & Kvarnemo 2006).

The consequences of limited access to males (or
sperm) for females are usually studied in the context
of female–female competition (Bro-Jørgensen 2007),

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choosiness (Kokko & Mappes 2005 and references
therein) or fertilization success (e.g. Levitan 2004;
Evans & Marshall 2005; Harris & Moore 2005). An
aspect of life history that has received scant attention
in this context is female reproductive effort. Life-
history theory predicts that when prospects of future
reproduction diminish, current reproductive effort
should increase (Gadgil & Bossert 1970; Stearns
1992; Cichon 2001). In the context of mortality, this
effect has strong experimental support (e.g. Stearns
et al. 2000), and it can have dramatic consequences
for the management of populations: for example, the
total biomass diminishes if fish mature earlier as a
response to increased fishing mortality (Ernande
et al. 2004).

Mortality, however, is not the only factor that can
favour early reproduction by making individuals
unable to breed later in life. Since difficulties of
finding a mate are equally detrimental to breeding
success, one should expect an increased early repro-
ductive effort in situations where future access to
mates is uncertain. In contrast to the elevated
mortality which can be hard for the individuals to
assess, the competitive social situation can often be
easily perceived by the individuals; this is often
equivalent to being able to observe the OSR. Thus,
while the response to extrinsic mortality may require
several generations to evolve (Stearns *et al.* 2000),
species that often experience fluctuations in the OSR
can be expected to possess reaction norms that
immediately relate current reproductive effort to the
OSR. However, experimental evidence for such a
response is lacking.

Here, we experimentally manipulated the OSR of
common gobies (*Pomatoschistus microps*) to test
whether females respond to a scarcity of males by
increasing their early reproductive effort. The life-
history predictions are analogous to those derived for
mortality patterns (Stearns *et al.* 2000 and references
therein). The predictions of the model are presented
in the electronic supplementary material and state
that regardless of the exact reason why females
should *a priori* lay their eggs in several clutches, the
first clutch (of those females who are able to mate)
should become larger in a situation in which the
OSR is female biased and future access to mates is
therefore uncertain.

2. MATERIAL AND METHODS

The common goby is a small short-lived coastal fish. It has a
resource defence mating system and paternal care. On shallow soft
bottoms, males build and defend nests under mussel shells and
rocks (Nyman 1953).

The experiment was carried out at Tvärminne Zoological
Station (Finland) throughout the 2005 mating season, using a
population with a high seasonal variation in OSR (K. Heubel 2005,
personal observation). Fish were kept in artificial outdoor pools in
which the OSR was maintained as either female-biased (three
females, one male), male-biased (one female, three males) or
neutral (without potential intra-sexual competition: one female, one
male). All females were gravid. The sex-biased trials were carried
out in seven large (80×80 cm) pools, while the neutral treatment
was conducted in seven smaller (50×60 cm) pools, in order to
minimize density differences across treatments.

We studied focal female and male reproduction in two separate
lines. The access to potential mates was held constant; a focal
female that had spawned was moved into a new tank where a male
(or males, depending on the treatment) had nests without eggs.
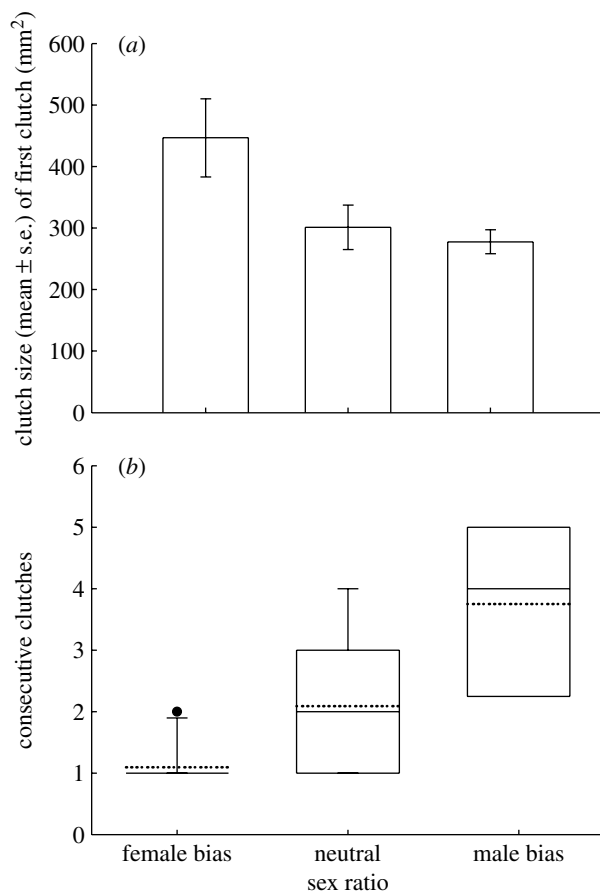Similarly, focal males got access to new females ready to spawn as

Figure 1. (*a*) Mean size (±s.e.) of female's first clutches and (*b*) median (the box encloses the inter-quartile range and the whiskers show maximum and minimum values; dotted line is the mean) number of consecutive clutches laid by females under different OSR treatments.

soon as the previous female had spawned. The replacements ensured that the OSR remained stable over time.

Each pool had a continuous flow-through of brackish seawater. Water quality, light conditions and temperature followed natural conditions. The non-transparent sides of the pools prevented interaction between pools. Under natural conditions, nest sites are scarce; hence, we provided just one nest per male using flower pot halves (4.5 cm diameter) on a 2–4 cm sand layer. Each pot had a removable piece of a transparent plastic sheet fit on the inside onto which the females attached their eggs in a single layer when spawning. All fish were wild-caught using a hand trawl and sexes kept in separate stock tanks for a few days before they entered the experiment. Fish were fed twice daily ad libitum with frozen chironomid larvae. Males entering an experimental pool were confined overnight to their allocated nests, isolated in clear cylinders (20 cm diameter), to allow undisturbed nest building. Fish were weighed and measured (total length) before they entered the experiment, and females were additionally weighed when they were transferred into another tank, e.g. after spawning. After the experiment, the fish were released back to their natural habitat.

All fish were individually marked with two colour marks (injected subcutaneously on the dorsal surface of the body to the left and the right of the dorsal fin) using visible implant elastomer tags (Northwest Marine Technology, USA).

All tanks were checked three times daily and identity, state, location and activity of each visible fish were observed as well as the state of each nest. Nests were lifted once daily to record brood-related changes inside the nest. Nest checks included identifying the nest owner, appearance of new eggs, assessment of egg development, hatching and cannibalism. In female-biased tanks, new eggs sometimes appeared without observing the spawning. In most cases, the identity of the spawned female was clear as its body shape suddenly changed from tadpole-like to slim. In the remaining uncertain cases, all females from the tank were weighed to determine the spawner. If uncertainty still remained, all females were replaced by new females.

Digital images of egg clutches were analysed using ImageJ (ImageJ v. 1.43s public domain software Wayne Rasband, NIH, USA). We analysed clutch area (mm²) and, for a subset of randomly picked clutches, counted the eggs. The number of eggs is strongly linearly related to the clutch area ($n = 29$, $r^2 = 0.838$; $F_{1,27} = 145.932$, $p < 0.000$). Graphical analysis confirmed that clutch area and the number of eggs were normally distributed. The number of consecutive clutches were analysed non-parametrically. Statistical analyses were done using Systat v. 10 (SPSS, Inc., 2000). The experiments yielded 22 (out of 39) focal males and 47 (first clutch) or 25 (all clutches) focal females (out of 69). We conducted 13 female-biased, 19 neutral and 15 male-biased replicates. Consecutive clutches were on average 9 days apart. Clutches per female ranged between 0 and 5, all laid between 12 June and 25 July 2005.

3. RESULTS

The size of the first clutch laid varied significantly across the OSR treatments (figure 1*a*; $F_{2,42} = 4.61$, $p = 0.016$), while body size and season had no effect on the size of the first clutch ($F_{1,42} = 0.853$, $p = 0.361$; $F_{1,42} = 0.081$, $p = 0.777$). A Bonferroni *post hoc* analysis revealed that the first clutches were larger in the female-biased treatment when compared with the two others (female-bias versus neutral LSM $= -145.51$, $p = 0.049$; female-bias versus male-bias LSM $= -169.09$, $p = 0.026$; MSE $= 26\,256.96$ with d.f. $= 44$).

Under female-biased conditions, focal females laid fewer clutches (Kruskal–Wallis test: $\chi_2^2 = 11.416$, $p = 0.003$, $n = 25$; figure 1*b*). Thus, females in the female-biased treatment spawned most of their eggs in their first spawning, while the increase in cumulative egg numbers was gradual and reached higher total egg counts in the other treatments (figure 2*a*,*b*). There was no significant difference in the cumulative clutch size among the three OSR treatments ($F_{2,22} = 2.219$, $p = 0.133$). However, a direct comparison between the female-biased and male-biased treatments revealed significantly lower egg numbers under female-biased conditions ($F_{1,10} = 5.768$, $p = 0.037$); size and season had no effect on accumulated clutch sizes ($F_{1,10} = 0.767$, $p = 0.402$; $F_{1,10} = 0.255$, $p = 0.624$).

For individual males, it was the male-biased treatment, and not the female-biased treatment, which lead to fewer consecutive clutches ($F_{2,19} = 27.518$, $p < 0.001$) and cumulative numbers of eggs received ($F_{2,19} = 19.874$, $p < 0.001$).

4. DISCUSSION

Numerous examples show that reproductive behaviour as a whole can be sensitive to the number and the sex of conspecifics (review: Kokko & Rankin 2006). Nevertheless, to our knowledge our experiment is the first demonstration that females increase their current reproductive effort (clutch size) as a response to perceived difficulties in competing for access to mates in the future. Females have been shown to adjust clutch size according to the social situation in other contexts, for example, in response to conspecific brood parasitism (Lyon 1998) or the attractiveness or parenting ability of the male (Sheldon 2000; Kolm 2001). In our situation, the reaction occurs as a response to the presence of competitor females rather than the identity of the male (see also Berglund 1991). Competitor females are expected to diminish the chances of an individual
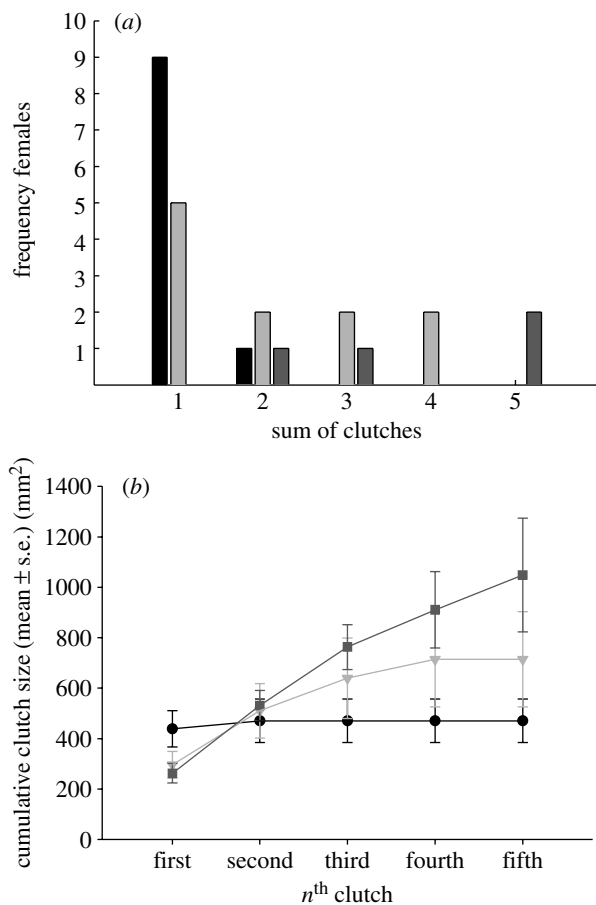
Figure 2. (*a*) Distribution of the sum of clutches laid by females and (*b*) cumulative clutch sizes (mean ± s.e.) yielded over one to five consecutive spawnings for females under different OSR treatments. Black, female bias; light grey, equal; dark grey, male bias.

female to gain future access to mates. Thus, the life-history setting is characterized by the conditions in the electronic supplementary material, where the first mating is guaranteed (the spawning female has already acquired a mate) but the second is not.

Both male and female life histories are shaped by a trade-off between current and future reproductive opportunities. The need to adjust life history to challenges of mate limitation has been amply documented in males (e.g. Badyaev & Qvarnström 2002) yet in our study the measured life-history trait, number of eggs laid, is under female rather than male control. Because this trait is much more directly linked to population-wide reproductive output than many male life-history traits, plasticity in female life histories with respect to mate-finding limitations may be an underappreciated force in population dynamics. It is also notable that females, despite their plastic increase of reproductive effort, did not compensate completely for the lack of mating opportunities: in the female-biased treatments the total number of eggs laid per focal female fell short of the maximum found in the other treatments. Our study therefore highlights the importance of considering both sexes in population dynamics (Rankin & Kokko 2007).

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