Alternative mating tactics in the gobiid fish, *Eviota prasina*

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Diversity of alternative reproductive phenotypes within sexes has recently been reported in various animals. Gross (1996) reviewed empirical and theoretical studies, and classified three kinds of strategy in the context of game theory: alternative, mixed and conditional strategies. Although little is known of alternative and mixed strategies, empirical evidence for conditional strategies has been accumulating. In most cases, larger males aggressively defend mating territories, while smaller males act as sneakers or satellites. Mating success of larger males is much greater than that of the smaller ones. Fishes provide many examples of conditional strategies (reviewed by Taborsky, 1994).

In this paper, we report two different tactics of male mating behavior in the goby *Eviota prasina*; *viz.* nest holder (NH), waiting for females to visit the nest, and trapper (TR), trapping wandering females. Body sizes, home ranges and female preference for each tactic are compared.

Materials and Methods

Eviota prasina is a small goby, widely distributed in shallow water around rocky or coral reefs of the Indo-Pacific Ocean (Lachner and Karnella, 1980). Under laboratory conditions (Sunobe and Nakazono, 1995; Sunobe, 1998), males occupy an artificial nest and exhibit courtship display to attract females. Eggs are spawned in a single layer on the ceiling of the nest. Following spawning, the female leaves the nest, the male guarding the eggs until they hatch after 4–5 days at 24–27°C.

The present study was conducted at Hanaze Beach, Kaimon Town, Kagoshima Prefecture, Japan (31°11′N, 130°31′E). The shore comprises of volcanic rocks, with well-developed, variously-sized tide pools. *Eviota prasina* was abundant in the study area (2 m×10 m) in one of the larger pools. Snorkeling observations were made daily from 06:00–14:00 from 25 June to 22 August 1986. Water temperature varied from 23 to 29°C.

Individuals were discriminated on the basis of different colour patterns on the head and nape; for some individuals, the upper or lower part of the caudal fin was clipped. Sex determination was straightforward as males had an elongated first dorsal spine (Lachner and Karnella, 1980). Out of 29 males (range=23–33 mm TL) and 38 females (20–33 mm TL) recorded in the study area, 13 and 18, respectively, were observed daily throughout the study period. The remainder moved to or from other sites during this time. As the swollen abdomen of females became reduced following spawning (unpublished aquarium observations), the state of abdominal swelling in each female was noted every day, and the frequency (%) of females with a swollen abdomen calculated so as to estimate the spawning cycle.

The location of each fish was recorded 1–6 times each day, in order to establish the home range. Behavioral interactions among individuals were also noted, in addition to the time, location and code numbers of participants during observations of courtship and spawning behaviour.

Results and Discussion

The reproductive season lasted from June to September in the study area. The frequency of females with a swollen abdomen increased over the first half of the lunar cycle, but decreased before the new or full moon, thereby showing a semilunar spawning cycle (Fig. 1). Spawning occurred from 07:00–12:00. Spawning sites were small rock cavities, about 3–5 mm in diameter. During egg guarding, males did not feed or move out of their nests, except for one case in which a male used its mouth to move a carnivorous gastropod (*Ergalatax contractus*) away from the nest.

The home ranges of nest holders (NHs), recorded on non-spawning days, were larger than those of the other males and females (Fig. 2). Male and female home ranges overlapped, although the extent of them

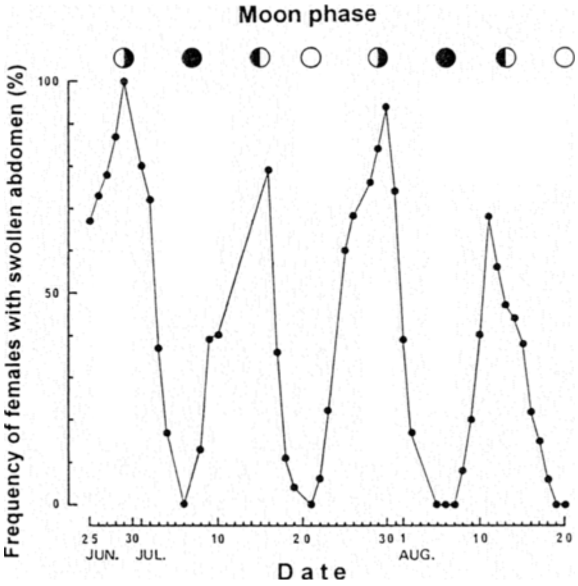


Fig. 1. Daily changes in the frequency of females with a swollen abdomen in relation to the lunar cycle.

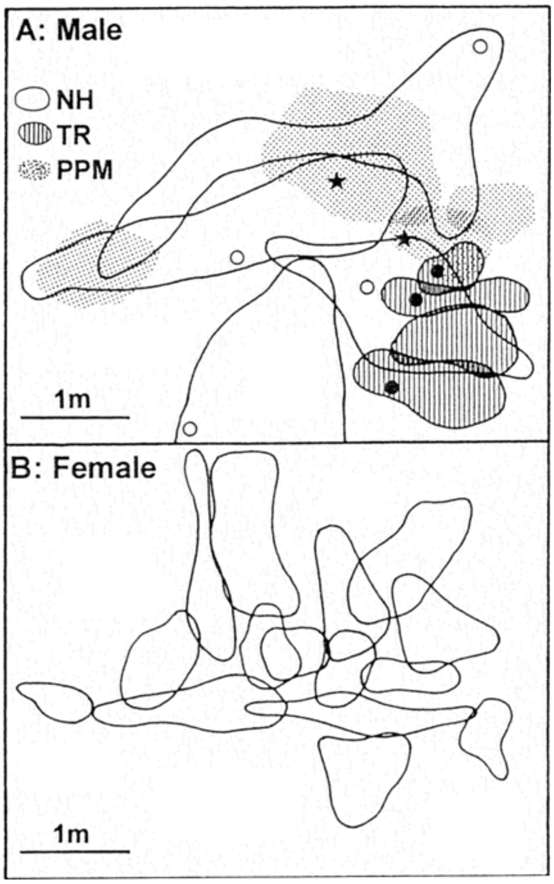


Fig. 2. Distribution of home ranges on non-spawning days, based on data from Aug. 7 to 15. Open circles, solid circles and stars indicate nest holes of nest holders (NHs), trappers (TRs) and pure peripheral males (PPMs), respectively. Nest holes of a TR and 2 PPMs unknown.

between individuals of similar status was small (Fig. 2). Aggressive interactions were not observed among any members.

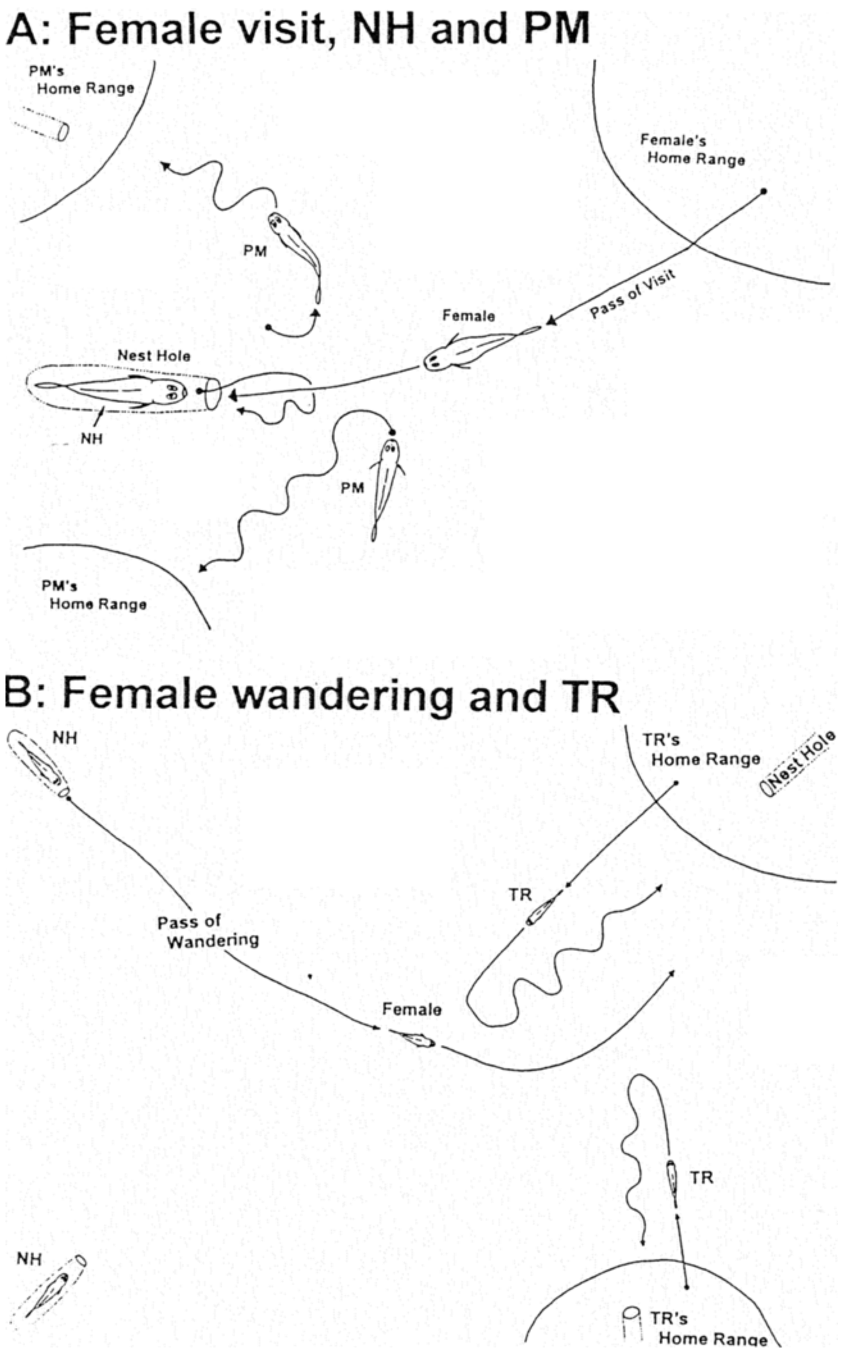
During the spawning period, nest holder (NH) males stayed in their nests to wait for females. Nine such males were apparent during the study period. Females left their home ranges and moved directly toward one of the male's nests. In most cases (26 of 27 visits), the females visited NHs which occupied overlapping home ranges. When a female approached to within 10 cm of a nest, the nest holder appeared to exhibit courtship display (Fig. 3A). The female then followed the male and entered the nest.

Females spawned on 15 of 27 visits. In the remaining cases, females entered the nests but did not spawn; three nests were empty, the owner males having disappeared. Females tended to spawn more frequently in the nests without the egg masses of the other females (12 spawnings in 14 visits) than in the nests already containing eggs (3 spawnings in 10 visits; Fisher's exact probability test, $p=0.012$). This contrasts with the many reports for fishes providing paternal care, of females selecting males caring for multiple egg masses, since this may dilute the rate of egg predation by the father (Kraak and Weissing, 1996). In the case of *Eviota prasina*, the nest hole was so small (3–5 mm in diameter) that there may not have been enough space to oviposit additional eggs, females therefore being forced to make a second choice.

After spawning ($n=15$ visits), the females soon departed the nests for their home ranges. When spawning did not occur ($n=12$ visits), 3 females visited the nest of another NH and spawned, but these remaining wandered over the site without visiting any of the other NHs (Fig. 3B).

Such wandering females were courted by trapper (TR) males (Fig. 3B). The latter, rather than remaining in a nest, actively searched for females wandering in the vicinity. Upon finding such a female, the TR dashed to court her. Subsequently, the female followed the TR to its nest for spawning. Of all 9 wandering females spawned with TRs, eight of them spawned with the first TR that courted them. In fact, when a female was following a TR, she did not respond to courtship approaches by any other TRs (Fig. 3B). Fourteen TRs appeared during the study period.

Around the nest of each NH, 1–5 males (mean ± SD=2.7 ± 1.4, $n=12$) congregated and courted the visiting females (Fig. 3A). NHs did not chase away



A: Female visit, NH and PM

B: Female wandering and TR

Fig. 3. Schematic representation of NH, TR, PM and female behavior. Wavy lines indicate courtship behavior by males. Dotted lines indicate nest hole shape. Solid circles and arrows indicate non-moving and moving status, respectively.

such males, hereafter called peripheral males (PM). Twenty-nine PMs appeared during the study period. PMs seemed to be similar to interceptors that court a passing female near a territory of a larger male (Taborsky, 1994). However, no females followed the PMs, although courtship behavior by the later was observed 48 times. Further study is needed to determine whether or not PM behavior is an alternative mating tactic.

At the conclusion of egg guarding, 6 out of 9 NHs became PMs. In addition, 5 of 14 TRs changed to PMs, when wandering females were not found. The other 18 PMs were regarded as pure (full-time) peripheral males (PPM).

TL ranges of the NHs, TRs and PPMs were 29–33 mm (mean±SD=30.7±1.4 mm, $n=9$), 25–30 mm (27.5±1.7 mm, $n=14$) and 23–28 mm (25.6±1.3 mm, $n=18$), respectively, here being significant differences among the categories (ANOVA, $F_{2,38}=36.6$, $p<0.001$; Scheffé, $p<0.001$ in NH vs. TR and in NH vs. PPM, $p<0.01$ in TR vs. PPM). Mating success, represented by the number of spawning females in a semilunar period, of NHs (range=0–2, mean±SD=1.13±0.76, $n=9$) was significantly higher than that of TRs (0–0.33, 0.21±0.16, $n=14$) (ANOVA, $F_{1,21}=19.8$, $p<0.001$).

These results suggested that male *E. prasina* may adopt a conditional strategy (for definition see Gross [1996]). TRs and PPMs may change to NHs and TRs, respectively, when they become larger. Similarly, males of the goby, *Pomatoschistus microps* change mating tactics as they grow (Magnhagen, 1992). In many fishes, which adopt a conditional strategy, smaller males attempt to join in reproduction as sneakers, so as to compete with larger territorial males (Taborsky, 1994). The smaller males of *E. prasina*, however, did not act as sneakers, because the small nest hole may have no additional space for them, in addition to allowing easy exclusion of sneakers when the NH and a female occupied the nest.

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