Constraints on paternal care capacity favor a monogamous mating system in the group-living gobiid fish *Trimma marinae*

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Abstract

We examined why the group-living gobiid fish *Trimma marinae* is monogamous despite a high potential for polygamy. Our observations revealed that in 75.5% of spawning events within established pairs, females spawned before the previous clutch hatched, forcing males to care for two clutches simultaneously. Previous findings showed males can care for up to three clutches, while mating with a second female would likely require them to care for four. Our results indicate that female mate guarding is a strategy to monopolize a male's limited paternal capacity by preventing her partner from mating with additional females.

Keywords

Mating system, Monogamy, Mate guarding, paternal care, gobiid fish, *Trimma marinae*

Introduction

Monogamy is a mating system in which males and females typically mate with a single partner, often maintaining this relationship beyond one reproductive cycle; given the difficulty in defining monogamy unambiguously across animal lineages (Kvarnemo 2018; Bales et al. 2021), this study adopts the definition traditionally used in fish behavioral ecology, following Barlow (1988) and Whiteman and Côté (2004). The ecological conditions under which monogamy is evolutionarily stable have long been investigated (e.g., Emlen and Oring 1977; Shuster and Wade 2003). Even when focusing on marine fish, at least six ecological factors have been proposed to facilitate the evolution of monogamy: biparental care, habitat limitations, low population density/low mate availability/low mobility, increased reproductive efficiency, territorial defense, and the net benefit of sequestering a single mate (Whiteman and Côté 2004). Because there is a great diversity of marine fish, accumulating knowledge of the ecological features of monogamous species is expected to strengthen existing theories and generate new hypotheses.

Trimma marinae is a small (approx. 25 mm TL), group-living gobiid fish found on coral reef slopes in enclosed bays of the Western Pacific (Shibukawa 2004). The framework of Emlen and Oring (1977) predicts that species in environments with a high potential for acquiring additional and monopolizable mates will exhibit a high

environmental potential for polygamy. Based on this framework, *T. marinae* is predicted to favor the evolution of a polygamous mating system because it inhabits groups where potential mates are spatially clustered. However, contrary to this prediction, Fukuda et al. (2017a) revealed that *T. marinae* has a monogamous mating system. They reported that this mating system primarily results from intrasexual competition among females (i.e., mate guarding) and suggested that its adaptive significance lies in monopolizing the limited paternal care capacity of males. By preventing her partner from mating with other females, a female should be able to avoid sharing the male's limited parental investment, thereby increasing her reproductive success. This hypothesis is supported by occasional observations from Fukuda et al. (2017a) showing that while males could care for up to three clutches, they failed to care for all of them successfully when simultaneously guarding four clutches, with some eggs decomposing or being cannibalized. These observations suggest that the paternal care capacity of *T. marinae* males is constrained. However, that study did not quantitatively investigate whether a male's care capacity is already saturated by the reproductive output of a single female partner during continuous reproduction within typical monogamous pairs.

To address this question, the present study investigated the spawning interval of continuous pairs under laboratory conditions. Our aim was to determine the number of clutches a male must typically care for simultaneously, and thereby examine the hypothesis that females obtain benefits from mate guarding.

Materials and methods

The data used in this study were obtained from a rearing observation previously reported by Fukuda et al. (2017a). The materials and methods for specimen collection and rearing conditions, which are identical to the original report, are briefly summarized below. A single group of 25 individuals (8 males, 17 females) was collected by SCUBA at Amami Oshima, Kagoshima Prefecture, Japan, and transported to the laboratory. Each fish was subcutaneously tagged for individual identification and housed in a 120 × 45 × 45 cm tank at 25°C. Ten polyvinyl chloride pipes were halved as spawning nests. Reproductive behavior was observed between 04:00 and 12:00 for 37 consecutive days. At the rearing temperature of 25°C, the eggs of *T. marinae* hatch on the third day post-fertilization, with

hatching triggered by it becoming dark (sunset).

Following the criteria of Fukuda et al. (2017a), a male–female pair was considered an established monogamous bond if pairing behavior was observed for more than 2 days. As *T. marinae* typically reproduces in monogamous pairs, we recorded spawning intervals exclusively for females in these established pairs. To clarify representative spawning intervals, we analyzed only females that spawned at least twice and recorded the number of days between their successive spawning events.

Results

A total of 49 spawning intervals were recorded from established pairs, with a median interval of 2 days; this means that females typically spawned approximately 48 hours after the previous spawning (IQR = 1–3 days). As eggs of *T. marinae* hatch on the third day post-fertilization, this reproductive pace indicates that males may be required to care for two clutches simultaneously. The full frequency distribution of the spawning intervals, which ranged from 1 to 13 days, is shown in Fig. 1. Of the 49 total recorded intervals, 37 (75.5%) were 3 days or less (i.e., intervals of 1, 2, or 3 days); this reproductive pace requires males to care for at least two clutches simultaneously. Similarly, 26 of these intervals (53.1%) were 2 days or less (requiring care for three or more clutches), and 12 (24.5%) were just 1 day (requiring care for four clutches).

Discussion

This study demonstrated that in 75.5% of reproductive events within monogamous *T. marinae* pairs, females spawn their next clutch before the previous one hatches. This indicates that males routinely face opportunities to care for two clutches simultaneously during a typical reproductive cycle, even when paired with a single partner. This situation suggests that mating with a second female would create a high probability of the male being required to care for four clutches, a number exceeding the male's paternal care capacity. Furthermore, in 53.1% of reproductive events, the spawning pace required males to care for three clutches simultaneously, indicating that a single female's reproductive cycle is already sufficient to saturate a male's paternal care capacity. Therefore, to ensure that their own eggs receive sufficient care until hatching, it would be adaptive for a female to prevent her partner from acquiring additional mates.

This female behavior may explain the evolution of a monogamous mating system in *T. marinae,* despite their high environmental potential for polygamy. The present findings offer support for the hypothesis proposed by Fukuda et al. (2017a). This species forms aggregations in which the sex ratio is biased toward females (Fukuda et al. 2017). Such a female-biased sex ratio, and the resulting female-skewed operational sex ratio (OSR), may have led to conditions that favored the evolution of female mate guarding and subsequent monogamy in *T. marinae*. Indeed, in the monogamous pipefish, *Corythoichthys haematopterus*, which also exhibits a female-biased sex ratio, female mate guarding is suggested to contribute to the maintenance of monogamy (Matsumoto and Yanagisawa 2001). This behavior is considered to be promoted by the skewed OSR (Sogabe and Yanagisawa 2007).

One possible factor contributing to the limited paternal care capacity of *T. marinae* is that males are smaller than females (Fukuda et al. 2017a). This pattern contrasts with that of the polygynous *Trimma* species (e.g., *T. okinawae* [Sunobe and Nakazono 1990], *T. grammistes* [Fukuda et al. 2017b], *T. caudomaculatum* [Tomatsu et al. 2018]). In these species, the larger male body size likely enables the care of multiple clutches from several females simultaneously, thus leaving females with little need to compete for paternal care. Indeed, in *T. caudomaculatum*, it has been observed that three females spawned simultaneously in a single male's nest without competition (Tomatsu et al. 2018). In *T. marinae*, however, the smaller male body size likely constrains their capacity to care for the clutches produced by the relatively larger females. This constraint is thought to drive intrasexual competition among females to monopolize a male's parental care, favoring the evolution of monogamy. The case of *T. taylori*, the only other *Trimma* species reported with a similar sexual size dimorphism to *T. marinae*, lends further support to this hypothesis; it is also suggested to be monogamous due to female competition over limited paternal care (Oyama et al. 2023). This pattern suggests that a small male body size relative to females has been a potential factor in the evolution of monogamy, at least within the *Trimma* lineage. Cases suggesting that constraints on paternal care induce female mate guarding, ultimately leading to the evolution of monogamous mating systems, have been previously reported. For example, in the coral-dwelling goby *Paragobiodon xanthosomus*, female intrasexual competition driven by limitations in paternal care is suggested to be a key

factor in the establishment of its monogamous mating system (Wong et al. 2008). This process is similar to the one proposed for *T. marinae*. Given that parental care is commonly provided only by males in gobiid fishes, further studies may identify additional species exhibiting monogamy due to similar selective pressures, even in environments with a high potential for polygyny.

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Author contributions

Conceptualization, Methodology: KF, TS; Investigation: KF; Formal analysis: KK; Writing - original draft preparation: KK; Writing - review and editing: KF, TS; Funding acquisition: TS; Resources: KF, TS; Supervision: TS.

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Data availability

The datasets are available from the corresponding author on reasonable request.

Declarations

Conflict of interest

The authors declare that they have no conflicts of interest.

Ethical approval

At Tokyo University of Marine Science and Technology, there are no institutional ethical regulations for fish. Therefore, all procedures adhered to the ASAB/ABS guidelines for the treatment of animals in behavioral research.

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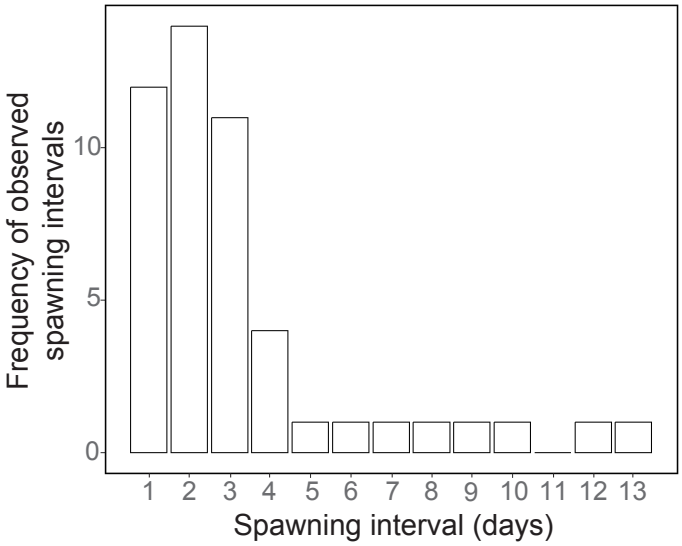
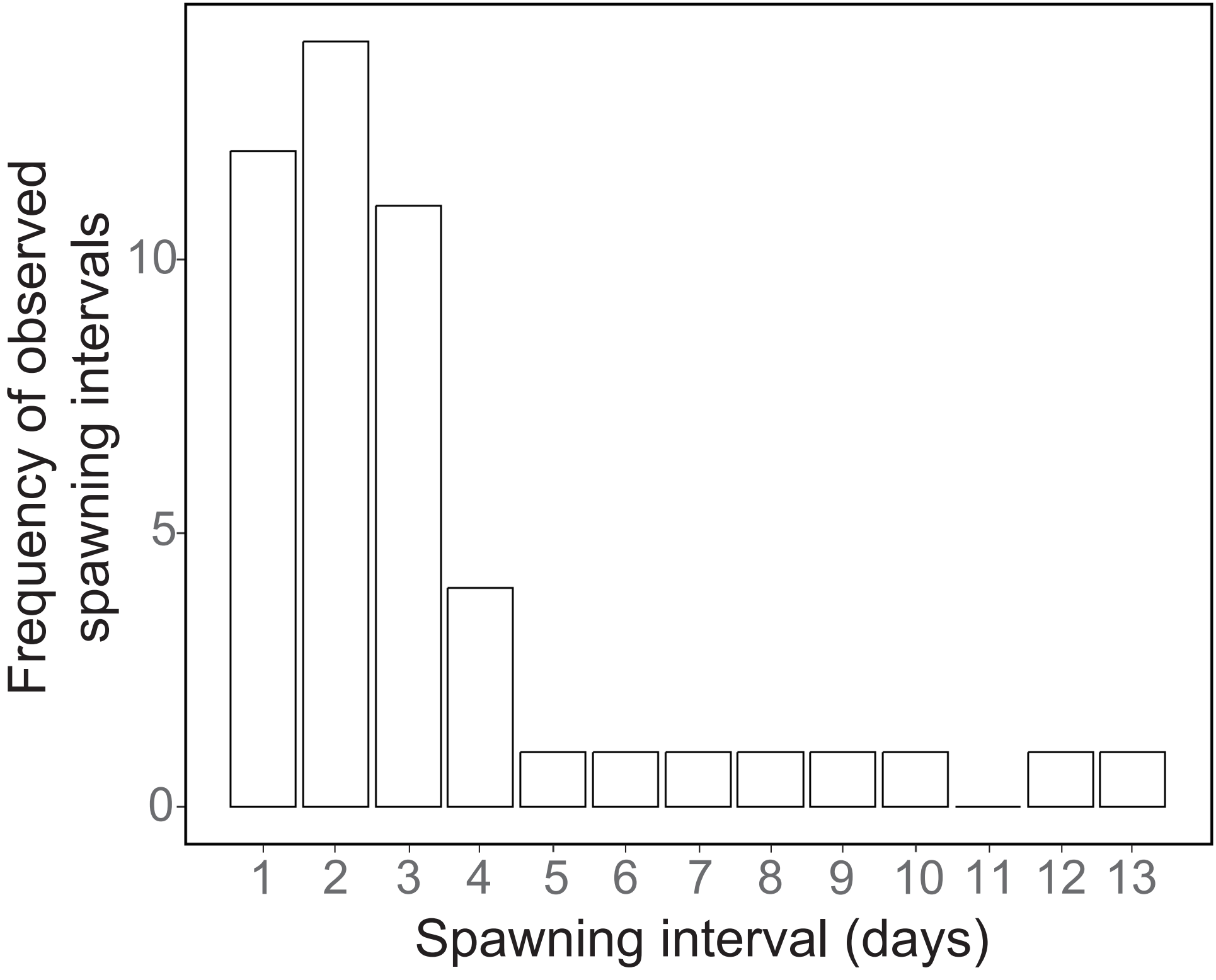


Figure legend

Fig1. Histogram of the spawning intervals distribution (days). The x-axis indicates the number of days between spawning events within monogamous pairs


Frequency of observed spawning intervals
0
5
10
1
2
3
4
5
6
7
8
9
10
11
12
13
Spawning interval (days)