Social structure and reproductive behavior of the callionymid fish
Callionymus bairdi (Gobiesociformes: Callionymidae): with notes on male alternative reproductive tactics

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Abstract
Despite the abundance and diversity of callionymids in marine environments, information on the social structure and mating systems of the group are rare. Most research has suggested that callionymids are non-territorial, polygynous spawners where male mating opportunities are controlled by dominance hierarchies, which in turn, are governed by body size. Here, we investigate the social structure and reproductive behavior of Callionymus bairdi through observations of wild and captive fish. Males greater than 8 cm SL held territories ranging in size from 6.81-10.9 m², within which, females maintained territories of 0.182-1.41 m². Subordinate males were found to move freely through the territories of larger males and compete for mating opportunities with females. The number of subordinate males and females living within territorial boundaries correlated strongly with the size of the territory. Male alternative reproductive tactics, including female mimicry and saboteur males, are discussed.

Zusammenfassung

Résumé
Malgré l’abondance et la diversité des Callionymidés en milieu marin, nous manquons d’information sur la structure sociale et les systèmes de reproduction de ce groupe. La plupart des recherches suggèrent que les Callionymidés ne sont pas territoriaux, s’accouplent avec plusieurs femelles quand les occasions des mâles reproducteurs sont contrôlées par la dominance hiérarchique, qui, de son côté, est induite par la taille du corps. Ici, nous étudions la structure sociale et le comportement reproducteur de Callionymus bairdi par des observations sur des poissons sauvages et captifs. Les mâles de plus de 8 cm de LS occupent des territoires qui vont de 6,81 à 10,9 m² où les femelles ont des territoires de 0,182 à 1,41 m². Des mâles dominés ont été observés traversant librement les territoires de mâles plus grands et entrant en concurrence pour d’éventuels accouplements avec les femelles. Le nombre de mâles dominés et de femelles vivant dans les limites territoriales est en relation étroite avec la taille du territoire. Les tactiques de reproduction des mâles, comprenant le mimétisme femelle et les saboteurs mâles, sont discutées.

Sommario
Nonostante l’abondanza e la diversità dei callionimidi negli ambienti marini, ci sono pochi dati sulla struttura sociale e sui sistemi di accoppiamento del gruppo. Gran parte delle ricerche suggerisce che i callionimidi siano non territoriali e poligami, dove le opportunità di accoppiamento del sesso maschile sono controllate da gerarchie di dominanza, che a loro volta, sono regolate in base alle dimensioni dell’individuo. In questo lavoro, si è indagata la struttura sociale e il comportamento riproduttivo di Callionymus bairdi attraverso osservazioni su esemplari selvatici e in cattività.
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INTRODUCTION

More than 180 species of callionymids (Gobioidea: Callionymidae) are recognized worldwide (Fricke 2002). They occupy a diversity of habitats from shallow sand and mud flats to coastal rubble fields, seagrass beds, and coral reefs. Their larvae are often the most abundant representatives of inshore ichthyoplankton surveys; highlighting the ecological importance of this family in marine systems (Houde & Lovda 1984). Despite their prevalence, information relating to the social structure and mating systems of callionymids are rare. Most research has suggested that callionymids are non-territorial, polygynous spawners where mating opportunities are controlled by dominance hierarchies, which in turn, are governed by body size (Awata et al. 2010; Rasotto et al. 2010). Observations, however, suggest that the reproductive strategies of callionymids may be more complex than previously thought. Takita et al. (1983) observed interruption of spawning ascents by subordinate males of *Callionymus mus* and Treshrer (1984) references potential sneaker males in *Diplogrammus* Interruption of courtship and spawning behavior by subordinate males was recently observed in the lancer dragonet, *Callionymus bairdi* (Jordan 1888) from the West Atlantic (pers. obs.), warranting further investigation into the social structure and mating system of the species.

Male alternative reproductive tactics of fishes have been well documented in recent years with a broad diversity of strategies being observed across multiple families (e.g. Kodric-Brown 1986, Oliveira et al. 2001). Evolutionary studies are recognizing the importance of alternative mating strategies to understand how and why social interactions give rise to phenotypic alternatives (Dominey 1984, Gross 1984, 1996). The ability to detect the presence and diversity of alternative tactics, however, may be hindered by captive observations of specimens maintained under unnatural environmental conditions or social densities (Wilson 1978). Most courtship and spawning behavior observations within the Callionymidae stem from captive observations (Holt 1898; Wilson 1978; Takita & Okamoto 1979; Takita et al. 1983; Zhu et al. 1991; Gonzales et. al. 1996; Harrington 1997), which may have impeded the ability of researchers to observe such strategies within the family since natural behaviors may be constrained in captivity.

Here, we investigate the social structure, reproductive behavior, male alternative reproductive tactics, and reproductive success of the lancer dragonet, *Callionymus bairdi*, in the wild and in the laboratory. *Callionymus bairdi* (Jordan 1888) is one of two shallow water callionymids from the West Atlantic, distributed from Bermuda, southern Florida and the Gulf of Mexico, and the Bahamas to northern South America (Scott & Scott 1988). Virtually nothing is known about the life history of *C. bairdi*.

MATERIALS AND METHODS

Field Observations

Demographic Parameters. The present study was conducted in Lake Worth Lagoon, Riviera Beach, Florida (26°46 59.658’N, 80°2 31.813’W) in depths 2-5 m (Fig. 1). During preliminary observations we located a study area (20 m × 10 m) where *C. bairdi* appeared abundant. The habitat consisted of open sand, crushed shell, and rubble with very little vertical relief. The sea urchin, *Lytechinus variegatus* was often the only form of relief in the rubble fields. Using SCUBA, we conducted 14 separate underwater observations from 12 June to 23 September 2011 yielding 37 hours of total observations. Observations were timed with tide changes. Water temperature during observations ranged from 25-28°C.

Initial observations were conducted by locating and following large males, which were the most conspicuous in the habitat. These observations allowed us to map the home range of males, and locate neighboring males, as well as the females living within the range of respective males. *Callionymus bairdi* exhibits extreme sexual dimorphism; males have an enlarged first dorsal fin, and an overall larger body size. We followed four territory-holding males (identified as T-HM1-T-HM4) independently for up to two hours per observation. Once the females and subordinate males living within a male-dominated territory were identified, we followed each member of the group for a mini-
mum of 30 minutes on two separate observation days to determine their respective ranges within the larger territory. Subsequent observations were used to confirm ranges of individuals. Standard lengths (SL) of territory-holding males or subordinate males, and females were determined by calibrated photography (Nikon D200). To test for differences in mean standard length of territory-hold-

Fig. 1. Map illustrating the study site for Callionymus bairdi located in Riviera Beach, Florida, USA. The star represents the study site. A) Lake Worth inlet, B) Peanut Island Park, and C) Phil Foster Park.
ing males, subordinate males, and females, a one-way Brown-Forsythe corrected ANOVA was employed with an α-level of P < 0.05 and a Tukey HSD post-hoc test after 1/x transformation to meet normality requirements. To test for the associations between territory size, SL, and abundance, a series of both Spearman Rank and Pearson Correlation tests were conducted for the appropriate datasets.

Reproductive success: Four separate field observations (12 hours total) were made around sunset to quantify reproductive success of territory-holding and subordinate males. Reproductive success was determined by the number of successful matings defined as spawning ascents ending in gamete release.

Laboratory Observations: On 13 June 2011 six adults were collected from outside the study area and acclimated to a 30 × 30 × 30 cm glass aquarium to observe the reproductive success of subordinate males in detail. To facilitate these observations, a social group consisting of one territory-holding male (9.4 cm SL), one subordinate male (7.2 cm SL), and four females ranging in size from 4.2-5.8 cm SL were collected to mimic wild reproductive groups. Fish were fed two times daily with

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**Fig. 2.** Size frequency distribution of Callionymus bairdi specimens (N = 54) surveyed in this study (bottom pane) and back-transformed mean (± SE) standard length for each group (top pane). Different lower case letters denote significantly different groups after a Brown–Forsythe corrected ANOVA: F = 133.1, d.f. = 2,28.4, P < 0.001. SM = subordinate males, T-HM = territory-holding males.
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Frozen Mysis shrimp (Piscine Energetics, Canada) and maintained on a constant photo/thermal cycle (14L/10D at 26 °C) to initiate reproduction. A 30 minute dusk and dawn period was provided by use of two 24 W fluorescent bulbs (one 560 nm actinic, and one 10,000 K) with independent light timers. The actinic light was set to go on 30 minutes before, and turn off 30 minutes after, the 10,000 K light. Two blue LED lights (moon lights) were set at 24L/0D to offer subdued lighting during nocturnal observations. Substratum consisted of fine sand to facilitate burying behavior. No other substratum was provided. Daily observations were made from 20:00-22:00 from 8 July to 21 September 2011.

RESULTS

Field Observations

Territory-Holding Males: The four large territory-holding males identified in this study were greater than 8 cm SL (Fig. 2). These territory-holding males commanded territory sizes ranging from 6.81-10.9 m² (Table I, Fig. 3), and the territory size correlated strongly and significantly with the SL of the territory-holding male (Pearson’s r = 0.943, P = 0.029, Fig. 4). During most of the observation periods these territory-holding males were observed to wander haphazardly within their territorial boundaries consuming prey. Each time a territory-holding male encountered a female, he would approach her rapidly with fins and mouth outstretched, forming a “T” in front of the female (“T-configuration”). The male would wave his body in undulating motions while moving closer to the female. During daylight hours, females rejected such advances, slowly raising and lowering their dorsal fin several times before fleeing from the male. This behavior persisted until all of the females within the territory had been greeted. Soon thereafter, males tended to bury in the substratum for up to one hour, before reemerging and wandering their territory once more.

Two distinct color patterns were observed in territory-holding males that were identified as courtship and agonistic patterns. Courting males exhibited a conspicuous dark mottled body color, a yellow face with iridescent blue markings, yellow and orange dorsal fin with contrasting brown bands, and blue markings along the anal fin. When two neighboring territory-holding males encountered one another the body color in both fish turned pale with a near total loss of yellow and orange color from the body and dorsal fin. The face turned dark with distinct rows of dots under the eye, above the mouth and below the preopercular spine. During four territory-holding male encounters, both males also developed blackish bands under the eye, forward to the mouth and rearward to the insertion of the of the preopercular spine. Males would approach one another from up to one meter away with outstretched fins and mouths in a slow, hovering manner. Most territorial disputes consisted of two males circling one another with outstretched fins before aligning side by side and performing undulating body waves in the direction of the opponent. When males were substantially different in size (>20 mm), the smaller male fled without further behavior. For males of nearly equal size (<20 mm), territorial behaviors escalated to include biting the preopercular spine of their opponent, jaw locking, and biting fins and body. Territorial disputes rarely lasted more than 5 minutes and resulted in both males retreating to their respective territories.

Subordinate & Saboteur Males: Four subordinate males were found in the territory of T-H M 1, three in T-H M 2, and both T-H M 3 and T-H M 4 had two subordinate males living within their respective territories (Table I). The number of subordinate males in the territory-holding males territories had a strong, significant correlation with the size of the territory that the territory-holding male commanded (Pearson’s r = 0.956, P = 0.022, Fig. 5). The subordinate males had significantly smaller

<table>
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<th>Male</th>
<th>SL (cm)</th>
<th>Territory size (m²)</th>
<th>Number of Subordinate Males</th>
<th>Number of Females</th>
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<tr>
<td>T-H M 2</td>
<td>9.2</td>
<td>8.56</td>
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<td>7.81</td>
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<tr>
<td>T-H M 4</td>
<td>8.1</td>
<td>6.81</td>
<td>2</td>
<td>5</td>
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</tbody>
</table>

Table I. Territory size, number of subordinate males and females of Callionymus bairdi associated with territory-holding males.
mean SL than territory-holding males (Brown-Forsythe corrected ANOVA: $F = 133.1$, d.f. = 2,28.4, $P < 0.001$; Fig. 2). These males, in all cases, seemed to wander the entire territory of larger, territory-holding males, often traveling outside the territory-holding male’s range by as much as 3 m (Fig. 3). Subordinate males were inconspicuously colored and, with the exception of the dorsal fin length, resembled females. During times when the larger, territory-holding male was actively courting or greeting females some of these subordinate males attempted to chase the female away by biting and ramming the female. This behavior was observed throughout the day in all parts of the territory and did not seem confined to any particular area. The term saboteur male is introduced here to define the role of these males in the social unit.

Females: Females had significantly smaller mean SL than subordinate males with some overlap in size (Brown-Forsythe corrected ANOVA: $F = 133.1$, d.f. = 2,28.4, $P < 0.001$; Fig. 2) and maintained territory sizes of 0.18-1.41 m$^2$ located within the boundaries of the territory-holding male’s territory. The size of female territories correlated significantly, albeit moderately, with the female SL (Spearman’s = 0.645, $P < 0.001$, Fig. 6).

Fig. 3. Map illustrating the territory of the territory-holding males of Callionymus bairdi in the black outlines with the territory of each female within the territory-holding male’s territory shaded in grey. The dotted lines represent an observed haphazard wandering path of one of the subordinate males within each territory.
Thirteen females were observed in the territory of T-HM1, 11 females in T-HM2, 9 females in T-HM3, and 5 females in T-HM4 (Table I). The number of females in the territory-holding male's territory had a strong, significant correlation with the size of the territory held by the territory-holding male (Pearson's $r = 0.960$, $P = 0.020$, Fig. 5). Females spent near equal time wandering their home ranges in search of prey and exhibiting burying behavior. When two females came within 15 cm of each other they flashed their dorsal fins in an up and down and slightly rolling motion before moving on. Agonistic behavior was not observed.

**Spawning behavior:** Spawning occurred within 30 minutes of sunset in all observations. During observations where spawning was observed, the male exhibited heightened courtship activity one hour before sunset. Ovulation of females was readily observed at this time as the abdomen became well rounded and appeared pink from the stretched skin.

In the absence of saboteur males, territory-holding males approached females rapidly with outstretched fins and mouth from a perpendicular position to form a “T” in front of the female (“T-configuration”; Fig. 7A). Undulating body behavior, as observed during daylight hours, was not observed during dusk spawning periods. Instead, the male quickly positioned himself to the side of the female (Fig. 7B), inserted his pectoral fins below the female and attempted to lift her off the substratum. Prior to sunset, females rejected the advances of the male and either buried into the substratum or fled. After an unsuccessful attempt, territory-holding male's rapidly swam in search of other females. Successful spawning occurred when the male aligned himself parallel to the female with his pectoral fin below her body (Fig. 7B). The pair swam rapidly across the substratum for roughly 2 m before initiating a spawning assent (Fig. 7C). This horizontal swimming behavior was never in a straight line and always within ~7.5 cm of the substratum. Once the spawning assent was initiated (Fig. 7D) the rapid swimming stopped and the pair slowly ascended to 1.0-1.5 m above the substratum (Fig. 7E). At the peak of the spawning rise the male assumed a curved body position, while the female remained straight immediately prior to and during initial gamete release (Fig. 7F). Chains of pelagic
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**Fig. 5.** Pearson's correlation between territory size of territory-holding males of *Callionymus bairdi* with number of females (♀ $r = 0.960, P = 0.020$) and subordinate males (♂ $r = 0.956, P = 0.022$) within their territory.

**Fig. 6.** Spearman's rank correlation between standard length squared of *Callionymus bairdi* females with their territory size ($r = 0.645, P < 0.001$).
eggs were released for approximately 3 s. The pair then parted and swam rapidly to the bottom (Fig. 7G) where the male then began to search for another female and repeat the process.

**Spawning behavior and reproductive success of saboteur males:** Whenever a territory-holding male was present, saboteur males exhibited a very low profile, often with bodies and mouth pressed firmly to the substratum while displaying an inconspicuous color pattern. As the territory-holding male courted a target female, the saboteur male would rush in, bite or ram the female in an attempt to make her flee. During these encounters, saboteur males would always swim with darting motions while maintaining a low body profile. In response, the territory-holding male would position himself between the female and the saboteur male. These events often became quite chaotic with the territory-holding male circling the female, attempting to maintain his position beside the female. Of 17 successful spawning rises observed during sunset observations, saboteur males attempted to interrupt the courtship of the territory-holding male 10 times. Of these 10 attempts, saboteur males were able to interrupt the territory-holding male's courtship on four occasions. In each case, the saboteur male successfully mated with the courting female. Interruptions from saboteur males led to the territory-holding male initiating a rapid horizontal swim before prior to upward spawning assents. Four of the 10 interruptions mentioned above led to the territory-holding male eventually moving on to court other females. When the saboteur male was successful in interrupting the spawning behavior of the territory-holding male it would then display somewhat subdued yellow and orange colors on the face and dorsal fin as it courted the female and initiated a spawning assent.

**Fig. 7.** Callionymus bairdi spawning sequence showing A) Male approaching female in “T-configuration” B) Male displaying to female perpendicularly, C) Male position his pectoral fin under the female and starting to swim horizontally, just above the substratum, D) Initiation of spawning rise, E) Mid-water rise, F) Male assumes a curved body while female remains straight in immediately prior to, and during gamete release, G) Immediately post final gamete release both male and female make a sharp turn and quickly dart back for the substratum in opposite directions. ♂ = male, ♀ = female.
ascents initiated by saboteur males displayed reduced (typically less than a ¼ of the distance) horizontal swimming prior to the asent.

**Laboratory observations of reproductive success and female mimicry of subordinate males**: Under captive conditions the subordinate male did not spawn at all when either fluorescent bulb was on. During captive observations the territory-holding male exhibited agonistic and display behavior toward the subordinate male only near spawning time. The subordinate male exhibited submissive behavior, fleeing at the territory-holding male's approach.

Within minutes of the 560 nm fluorescent bulbs going out the behavior of the subordinate male changed dramatically. As the territory-holding male courted a female with extended dorsal fin (Fig. 8A-B), the subordinate male approached from behind and above. The subordinate male descended slowly directly on top of the territory-holding male, closing his extended dorsal fin (Fig. 8C), as it positioned itself between the territory-holding male and the female (Fig. 8D). From this position, the subordinate male initiated a spawning rise with the territory-holding male as the female departed (Fig. 8D). Up to 15 male-male ascents (Fig. 8E-G) were observed following the initial interruption of the territory-holding male's courtship. Male-male ascents were mostly short in duration and height. Following this behavior, which often lasted 10 minutes or more, the territory-holding male moved on to court other females or buried in the substratum. The subordinate male then courted and spawned with the target female. This behavior was observed each evening from 17 July to 21 September. The subordinate male successfully spawned with a single female each evening. Although the subordinate male attempts
to mimic the female, during the final phase the ascent (Figs 7F and 8F), the female maintains a straight posture (Fig. 9A), while the subordinate male assumes a curved posture in the mirror of the territory-holding male (Fig. 9B₁-B₂).

DISCUSSION

Male C. bairdi use different reproductive tactics to gain mating opportunities. A minimum body size appears to be a prerequisite to becoming a territory-holding male, where territory size and the number of females and subordinate males are related to body size. Subordinate and saboteur males less than 8 cm body length are likely not capable of defending a territory and attracting mates. Living within the territorial boundaries of large, territory-holding males offers mating opportunities without the energy expenditure of territorial defense. This is similar to the behavior of sneaker males, which live without the cost of territorial defense, but differ in their approach to acquiring mating opportunities. The behavior of sneaker males, darting in to deposit sperm during reproduction, might not be effective during pelagic spawning rises where egg release occurs relatively quickly. Interfering with the courtship and mating opportunities of the large male seems a successful strategy since the territory-holding male was not observed to mate with more than three females in a single night. If all females in the territory were receptive to mating, an overall decrease in fecundity would be observed without successful mating by saboteur males. The diversity and evolutionary significance of this behavior should be further addressed within the family.

Most evaluations of callionymid behavior have occurred in relatively small aquaria with unnaturally high densities. This may have impeded evaluations of territoriality and alternative mating tactics (Wilson 1978). Males of Callionymus lyra were regarded as territorial by Holt (1898) and Wilson (1978) who both observed them in aquaria. Territory size, polygyny or female territories were not mentioned. Takita et al. (1983) regarded C. enneactis as territorial, although this study too was probably impeded by the relatively small confines of the tank. Six males and 14 females were held in a round tank where spawning behavior was observed at night using a “faint” light. They report only two of the six males actively spawned, and maintained a territorial boundary in the middle of the tank. Takita et al. (1983) further mentions that the non-spawning males would strike at actively spawning pairs during ascents. This behavioral pattern of sabotage warrants further investigation into the reproductive behavior of both C. enneactis and the family at large. It is likely that male alternative mating tactics are more common than previously thought. Results of this study suggest that ontogenetic state or size attributes govern the reproductive pathway of males and that light levels influence the success of these alternative tactics.

This is the first study that documents territoriality and polygyny in callionymids. Spawning behavior of C. bairdi observed in the wild and in captivity was similar to that described for other callionymids, with the exception of horizontal pair swimming prior to the vertical spawning ascent. This is likely an adaptation to deal with saboteur males. Swimming rapidly across the substratum

Fig. 9. Callionymus bairdi positions prior to gamete release. A ventral view (A) of territory-holding male (♂ T-H) assuming a curved body position, while female (♀) remains straight. A dorsal (B₁) and ventral view (B₂) of both the territory-holding male (♂ T-H) and the saboteur male (♂ Sb) assuming a curved body position.
may offer the pair an opportunity to flee agonistic behavior of saboteur males prior to the vertical spawning ascent. Striking at the ascending pair as observed by Takita et al. (1983) may be the outcome of immediate ascents in the vicinity of such males. This horizontal swimming has not been noted elsewhere, but would likely be an indication of alternative mating tactics if observed.

Of particular interest is the probable stochastic population flux of the species. Three months after the field study we visited the study location to determine if the social structure had been maintained long term. Only one of the original males was present. During this observation we noticed several scorpionfish in the vicinity of the study site and observed predation of a small female C. bairdi by one of these ambush predators. Not surprising, predators such as the scorpionfish and recently introduced lionfish, probably contribute to the labile social structure patterns observed (Albins & Hixon 2008).

**REFERENCES**


