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Alternative male mating tactics of the endemic Red Sea parrotfish *Scarus ferrugineus*

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The present study shows that small non-territorial terminal-phase males of the rusty parrotfish *Scarus ferrugineus* are reproductively active and are comparable with initial-phase males in behaviour, rates of participation during group-spawning and success in streaking into pair spawning. Large territorial terminal-phase males defend contiguous territories for several hours during the morning where they pair spawn with initial-phase females.

Key words: alternative male mating tactics; leks; parrotfish; protogyny; sex-change; territoriality.

In teleosts, protogyny is closely associated with systems that promote the monopolization of mating by large territorial terminal-phase males (TTP) (Warner, 1984). In many parrotfish species, however, small non-territorial terminal-phase males (STP) may be common. These are considered to have either very low reproductive output or to be reproductively inactive (Hoffman *et al.*, 1985; van Rooij *et al.*, 1996*b*). Although the reproductive hiatus is an appealing hypothesis, more field data on spawning success of the different male categories is needed to test it. In this study field observations and histological analysis were used to compare the mating success of initial-phase males (IP male) and STPs of Red Sea parrotfish *Scarus ferrugineus* Forsskål 1775.

Behavioural observations and sample collections were conducted at the fringing reef of Sheikh Said Island (15° 35′ N; 39° 29′ E), Massawa, Eritrea. Between January 2006 and May 2007 experienced divers collected *S. ferrugineus* samples by spearing them through the head causing instant death and minimal damage to the internal organs.

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TABLE I. Mean fork length (L_F) and sample sizes (n) of *Scarus ferrugineus* sampled for different life-phase categories

	Total sample		Sub-sample for histology	
Category	n	L_F cm (S.E.)	n	L_F cm (S.E.)
Initial phase				
Females	117 (95%)	23·10 (0·18)	57	23·55 (0·21)
Males	6 (5%)	21·31 (1·07)	4	23·00 (0·55)
Terminal phase	102	30·89 (0·38)	43	31·66 (0·41)

Samples were kept at −30° C prior to processing. The gonads were extracted and preserved in a 4% formalin seawater solution. Gonads were weighed and characterized as male or female based on external appearance and from observations of histological sections. Four social and sexual categories were identified: IP females, IP males (coloured as females), TTPs and STPs.

Field observations were conducted from August 2007 to June 2008. During the daily spawning period (Afeworki, 2014), two observers using scuba gear haphazardly selected two TTPs and recorded spawning behaviour. Observers estimated the size of the TTPs (for details see Afeworki *et al.*, 2013*b*) and recorded the incidences of spawning and chasing.

Since TTPs were typically >30 cm in fork length (L_F) (Afeworki, 2014), terminal-phase non-territorial males <30 cm in L_F were considered as STPs. Each spawning event was described by the type of participants: pair spawning between a TTP and an IP female (TTP–IP); pair spawning between an IP male and an IP female (IP male–IP); pair spawning between a STP and an IP female (STP–IP); group spawning defined as those spawning events that involved at least one female and more than one male. Group spawning was further described based on the number and identity of participants (IP, STP, TTP). For each TTP–IP pair spawning event, whether there was streaking or not was recorded and whether an IP, a STP or a TTP did the streaking.

TTPs with distinct natural markings such as cuts, white–black spots on the dorsal or caudal fins or unique colouration, were monitored at their spawning territories for at least 4 days a month to determine site fidelity and residency. For these TTPs, the day of first encounter and the exact location of the territory were recorded as well as the last time that a particular TTP was observed occupying that territory. Density of IPs, STPs and TTPs at the deep fore reef was determined by visual census of three replicate fixed 50 m × 5 m transects during spawning and non-spawning periods.

Behavioural results reported here are from over 200 h of underwater observations. All observed TTPs ($n = 140$) were >30 cm L_F, with the 33–35 cm size range being the most frequent. IP males represented 5% of the total IP population (Table I). Compared with the largest TTPs, IP males and STPs had a higher relative testis mass (ANCOVA $F_{3,109} = 6{\cdot}388$; $P < 0{\cdot}05$) (Fig. 1). All sexual categories of *S. ferrugineus* forage in loose groups on the reef crest and parts of the reef flat (Afeworki *et al.,* 2013*a*). In the deep fore-reef zone (6–15 m depth), foraging activity was minimal and the abundance of this species was low during non-spawning periods (Fig. 2; Afeworki *et al.,* 2013*a*). During the spawning period, all social categories of *S. ferrugineus* aggregated at the deep fore

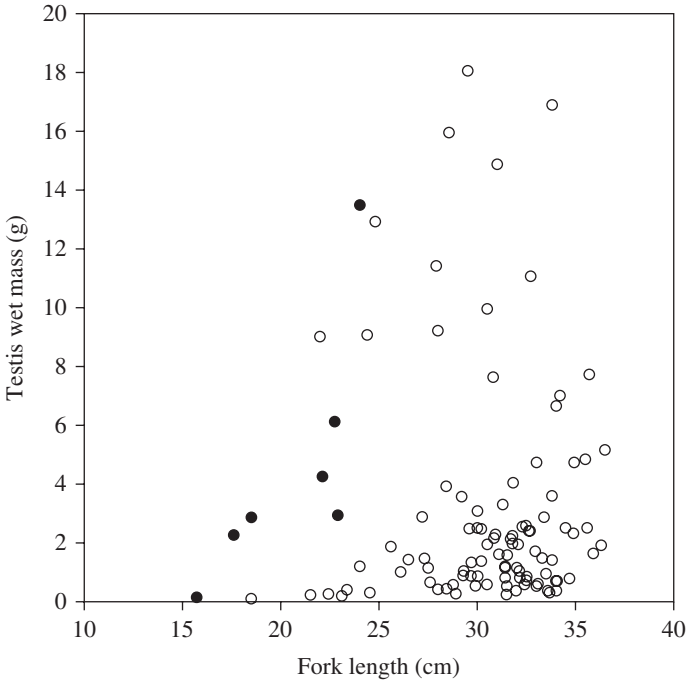

FIG. 1. Wet testis mass in relation to fork length (L_F) in *Scarus ferrugineus*. ○, terminal phase; ●, initial phase males.

reef causing the abundance in this zone to increase more than twofold (ANOVA, TTP $F_{1,4} = 12{\cdot}04$, $P < 0{\cdot}01$; IP $F_{1,4} = 32{\cdot}99$, $P < 0{\cdot}01$; STP $F_{1,4} = 16{\cdot}62$, $P < 0{\cdot}05$) (Fig. 2). The spawning period typically occurred in the morning and commenced when TTPs move to the deep fore reef where they occupied a temporary spawning territory. Territories were contiguous and ran parallel to the reef. TTPs patrolled and defended their territories against neighbouring TTPs, STPs and IP males. Intruding IPs (presumably males) and STPs were immediately chased beyond the boundaries of the territory. The frequency of chasing by TTPs was higher for IP males than for STPs, although the former were rarer in the population ($\chi^2 = 12\,790{\cdot}7$, d.f. $= 2$, $P < 0{\cdot}01$). Outright chasing between neighbouring TTPs was rare (Table II); usually TTPs engaged in broadside view, *i.e.* stretched all their fins and swam in mutual lateral movements at their common boundary and rarely engaged in aggression.

During each spawning period, which may last for 1–3 h (Afeworki, 2014), a TTP was observed to pair spawn with a minimum of 0 and a maximum of 16 IPs, with an average daily rate of 6 ($n = 79$). At the end of the spawning period, TTPs abandoned their territories and moved to the shallow reef zones to forage with conspecifics. This was ascertained by following identifiable TTPs and further confirmed by the low density of all phases of *S. ferrugineus* at this reef zone outside of the daily spawning periods (Fig. 2). Once they were at the shallow reef zones, the TTPs no longer show agonistic interactions to either IPs or smaller TPs. The above observations essentially suggest that *S. ferrugineus* is a lekking species. Monitoring of TTPs with recognizable markings indicated that they have high site fidelity and residency. Four TTPs were observed

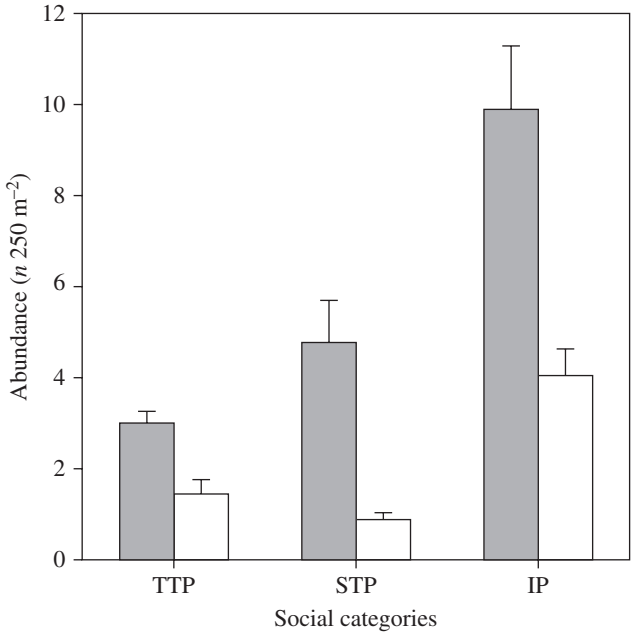

FIG. 2. Abundance (mean + S.E.) of the different *Scarus ferrugineus* social categories in the deep fore reef zone during spawning (■) and non-spawning (□) periods. IP, initial phase; STP, small non-territorial terminal-phase males; TTP, territorial terminal-phase males.

occupying the same territory for at least 150 days. Five resident TTPs ceased coming to their respective territories after they were recorded between 111 and 267 days. Since the study was continued for several months after the disappearance of these TTPs and as they have not been seen at the study site after that, it is assumed that they died.

Mating tactics differed among the male types. Large TTPs typically engaged in pair spawning with IP females ($n = 327$, 92·9% of total spawning events). IP males and STPs

TABLE II. Summary of the incidence of chasing by territorial terminal phase (TTP) male *Scarus ferrugineus* on intruding initial-phase (IP), small non-territorial terminal-phase (STP) and neighbouring TTP males

Target	Estimated percentage of the population	Number of chases elicited (%)
STP	15	2395 (35·5%)
IP	3·5	3231 (47·9%)
TTP	15	386 (5·7%)
Unclear target		736 (10·1%)
Total		6748 (100%)

*The percentage occurrence of each category in the population was estimated based on the percentage of IP (70%) and TP (30%) individuals, and the percentage of IP males among IPs (*i.e.* 5%). TP < 30 cm fork length make up *c.* 50% of the TPs and are here considered non-territorial (Afeworki, 2014).
†The targets of these chases were not recorded.

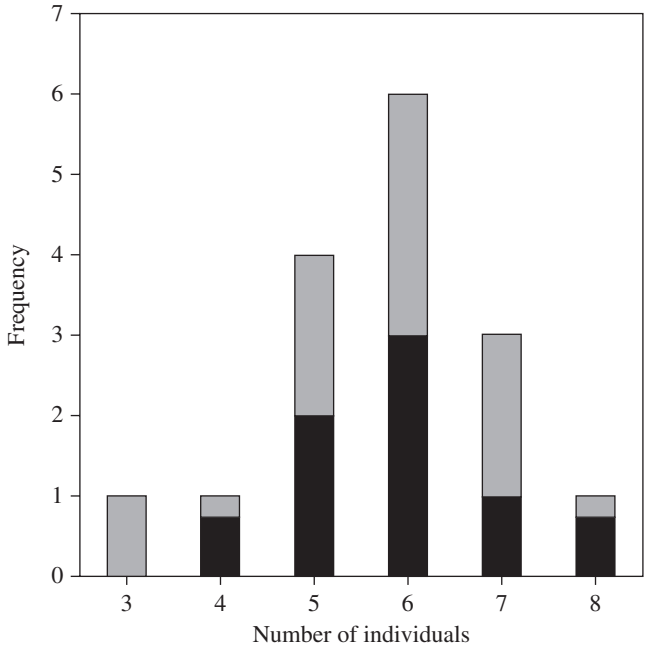

FIG. 3. Frequency distribution of *Scarus ferrugineus* group sizes during group-spawning events. The mean number of initial-phase (▒) and terminal-phase (■) individuals involved in each category are indicated.

either spawned in groups or streaked into TTP–IP pair spawning. Group spawning accounted for 6·8% ($n = 24$) of the observed spawning events. Only one instance (0·3% of total spawning events) in which a pair spawning involved two IPs was recorded, one of which was assumed to be an IP male. Streaking occurred in about 37·6% ($n = 123$) of all the TTP–IP pair spawning. Most of the streaking was by IP males (11·6%, $n = 38$), STPs (11·9%, $n = 39$) or both (3·7%, $n = 12$). Occasionally TTPs streaked into a pair spawning of a neighbouring TTP ($n = 9$). In 25 (7·6% of the total spawning events) of the streaking events the colour phase of the intruders could not be determined. The number of individuals participating in group spawning ranged from three to eight with a mode of six individuals (Fig. 3). IP males and STPs were equally involved in group-spawning events (Fig. 3).

The streaking frequency in *S. ferrugineus* was high but within the range of values reported for scarids (Robertson & Warner, 1978; Clavijo, 1983; Kuwamura *et al.,* 2009). In general, the incidence of group-spawning and streaking tends to be high in larger populations (Warner & Hoffman, 1980; Kuwamura *et al.*, 2009) or in more complex habitats (Robertson & Warner, 1978; van Rooij *et al.,* 1996*a*). The high density of the species at the study site (Afeworki *et al.,* 2013*a*), may explain the observed prevalence of streaking in this population.

Small non-territorial TPs in the population studied were abundant and their size range overlapped with that of the IP (Afeworki, 2014). These STPs are essentially a third social category of males and behavioural observations indicated that they adopt the same alternative mating tactics of streaking and group-spawning as IP males. Kuwamura *et al.* (2009) made similar observations in *Scarus rivulatus* Valenciennes 1840

on a Japanese fringing reef where STPs actively participated in group spawning. Previously, small non-territorial TPs were called bachelors and were considered reproductively inactive (Robertson & Warner, 1978; van Rooij *et al.*, 1996*b*). The existence of bachelors was explained as a strategy to channel resources to growth in order to become large enough to occupy a territory of their own (Hoffman *et al.*, 1985; van Rooij *et al.*, 1995). This is valid if reproduction reduces growth or increases mortality of the STPs (Iwasa, 1991). The present study, however, shows that transitional individuals and STPs have the fastest growth in *S. ferrugineus* (Afeworki *et al.*, 2014) suggesting that their reproductive activity does not affect their growth negatively. This is plausible since STPs do not spend energy for territorial defence. Their primary reproductive cost is sperm production which is known to constitute a small percentage of the basal metabolic cost of animals (Hayward & Gillooly, 2011).

In the *S. ferrugineus* population studied here, IP males and STPs were similar in three essential ways. Both tended to have larger testis for their size, a trait that is inherently associated with breeding tactics that involve strong sperm competition, such as group-spawning and streaking (Taborsky, 1998). IP males and STPs were equally successful in streaking and in their participation in the group-spawning events. Interestingly, the rate of chasing by TTPs was much higher for IP males despite their lower frequency in the population (Table II). Apparently, behavioural or chemical cues seem to give away the identity of the IP male resulting in an immediate chase (Warner & Robertson, 1978). These observations suggest that the female looks of the IP males of *S. ferrugineus* does not lead to higher success in streaking or group-spawning, or in interloping into a TTP territory. This further suggests that, at least in *S. ferrugineus*, IP males and STP males are functionally equivalent. It is possible, however, that other advantages such as reduced predation rate (due to their drab colouration) may accrue fitness of IP males. Indeed demographic analysis shows that STP males suffer higher mortality than IP individuals in this population (Afeworki, 2014). Clearly, further research is needed to understand the adaptive value of being an IP male compared with a STP. Early colour change and non-territorial status of STPs is not necessarily associated with a reproductive hiatus as formerly reported. These STPs actively engage in reproduction and still manage to grow fast to reach large sizes that enable them to acquire a breeding territory in the future.

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References

Afeworki, Y. (2014). Population ecology of the rusty parrotfish *Scarus ferrugineus*, a dominant grazer on a seasonal coral reef. PhD Thesis, University of Groningen, The Netherlands. Available at http://www.rug.nl/research/portal/publications/pub(aa52a38c-bf8a-4126-a05f-5f028025d78c).html/

Afeworki, Y., Videler, J. J. & Bruggemann, J. H. (2013*a*). Seasonally changing habitat use patterns among roving herbivorous fishes in the southern Red Sea: the role of temperature and algal community structure. *Coral Reefs* **32,** 475–485.

Afeworki, Y., Zekeria, Z. A., Videler, J. J. & Bruggemann, J. H. (2013*b*). Food intake by the parrotfish *Scarus ferrugineus* varies seasonally and is determined by temperature, size and territoriality. *Marine Ecology Progress Series* **489,** 213–224.

Afeworki, Y., Videler, J. J., Berhane, Y. H. & Bruggemann, J. H. (2014). Seasonal and life-phase related differences in growth in *Scarus ferrugineus* on a southern Red Sea fringing reef. *Journal of Fish Biology* **84,** 1422–1438.

Clavijo, I. E. (1983). Pair spawning and formation of a lek like mating system in the parrotfish *Scarus vetula*. *Copeia* **1983,** 253–256.

Hayward, A. & Gillooly, J. F. (2011). The cost of sex: quantifying energetic investment in gamete production by males and females. *PLoS One* **6,** e16557.

Hoffman, S. G., Schildhauer, M. P. & Warner, R. R. (1985). The costs of changing sex and ontogeny of males under contest competition for mates. *Evolution* **39,** 915–927.

Iwasa, Y. (1991). Sex change evolution and cost of reproduction. *Behavioral Ecology* **2,** 56–68.

Kuwamura, T., Sagawa, T. & Suzuki, S. (2009). Interspecific variation in spawning time and male mating tactics of the parrotfishes on a fringing coral reef at Iriomote Island, Okinawa. *Ichthyological Research* **56,** 354–362.

Robertson, D. R. & Warner, R. R. (1978). Sexual patterns in the labroid fishes of the western Caribbean, II: the parrotfishes (Scaridae). *Smithsonian Contributions to Zoology* **255,** 1–26.

van Rooij, J. M., Bruggemann, J. H., Videler, J. J. & Breeman, A. M. (1995). Plastic growth of the herbivorous reef fish *Sparisoma viride*: field evidence for a trade-off between growth and reproduction. *Marine Ecology Progress Series* **122,** 93–105.

van Rooij, J. M., Kok, J. P. & Videler, J. J. (1996*a*). Local variability in population structure and density of the protogynous reef herbivore *Sparisoma viride*. *Environmental Biology of Fishes* **47,** 65–80.

van Rooij, J. M., Kroon, F. J. & Videler, J. J. (1996*b*). The social and mating system of the herbivorous reef fish *Sparisoma viride*: one-male versus multi-male groups. *Environmental Biology of Fishes* **47,** 353–378.

Taborsky, M. (1998). Sperm competition in fish: 'bourgeois' males and parasitic spawning. *Trends in Ecology & Evolution* **13,** 222–227.

Warner, R. R. (1984). Mating behavior and hermaphroditism in coral reef fishes. *American Scientist* **72,** 128.

Warner, R. R. & Hoffman, S. G. (1980). Population density and the economics of territorial defense in a coral reef fish. *Ecology* **61,** 772–780.

Warner, R. R. & Robertson, D. R. (1978). Sexual patterns in the labroid fishes of the western Caribbean, I: the wrasses (Labridae). *Smithsonian Contributions to Zoology* **254,** 1–27.

