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# The Relationship Between the Presence of Satellite Males and Nest-Holders' Mating Success in the Azorean Rock-Pool Blenny *Parablennius sanguinolentus parvicornis*

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## Abstract

In the Azorean rock-pool blenny, sexually active males may adopt alternative reproductive tactics. In the present paper the relationship between the presence of satellite males and the reproductive success of nest-holders was investigated by comparing nests with and without an associated satellite male. Males with an associated satellite male suffered more conspecific intrusions but they did not display a higher frequency of attacks towards conspecifics. Nest-holder males were more aggressive towards other conspecifics than towards satellites and the tolerance of nest-holders towards satellites was inversely correlated with the time spent by the satellites in the breeding territory, which suggests control by the nest-holder male of the satellite investment in shared territorial defence. Nest-holders with an associated satellite male had higher condition factors and received more female visits and more spawnings. These results bear two possible interpretations. (1) Nest-holders benefit from the presence of a satellite male by increased attractiveness of their nests to females; satellite males are mutualists helping to defend the nest-owner's territory and to attract females, which is why they are tolerated. (2) Satellite males associate preferentially with more successful nest-holder males which have higher condition factors, and by doing so have more opportunities to achieve parasitic fertilizations. Only experiments will allow these two hypotheses to be distinguished.

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## Introduction

In many species in which male reproductive competition occurs, males of lower competitive ability can adopt alternative reproductive tactics (ART) to obtain access to mates. The terms ‘bourgeois male’ and ‘parasitic male’ have been proposed to describe, respectively, the males that actively compete for and invest in the acquisition of mates and the males that exploit the investment of bourgeois males to obtain access to females and fertilize their eggs (Taborsky 1997).

In fishes, the occurrence of male ARTs is widespread (140 species from 28 different families; Taborsky 1998). This seems to be explained in part by the fact that fishes have a high degree of indeterminate growth, and thus variance in body size among sexually active individuals can be very high (Taborsky 1999). The ARTs described so far in teleosts can be classified into two major groups: (a) males that try to monopolize females for a short period of time (e.g. nest take-over, piracy, or female interception) and (b) males that do not try to obtain exclusive access to females but release sperm in the vicinity of the female when she is spawning with a bourgeois male (e.g. sneaking) (Taborsky 1994). In the later tactic, kleptogamic males may use a number of different tactics to approach the pair during spawning: (a) rush to the spawning pair and shed sperm close to them (e.g. streaking in open water spawners with pelagic eggs, such as the snipefish *Macrorhamphosus scolopax*; Oliveira et al. 1993); (b) mimic female morphology and behaviour in order to be tolerated by the bourgeois competitor male during spawning (e.g. female mimicry in sunfish and blennies; Dominey 1981; Gonçalves et al. 1996), or (c) cooperate with the bourgeois male in order to be tolerated by him and thus obtain better access to the female when spawning occurs (e.g. satellite males in the European wrasses and in cichlids; Taborsky et al. 1987; Martin & Taborsky 1997). In the first two tactics, males using ARTs to breed are exploiting the reproductive effort of the bourgeois male (i.e. his investment in morphological, physiological and/or behavioural sexual traits), while in the later case they may be cooperating with the bourgeois male to obtain access to females, and so there are different degrees of asymmetry in the relationships. Thus, not all ARTs are necessarily parasitic on the bourgeois male.

*Parablennius sanguinolentus parvicornis* (Blenniidae) is a very abundant species in the rocky intertidal area of the Azores Islands (Santos et al. 1994). Two alternative male mating tactics have been detected in this species (Santos 1985b). Large males (average total length ≈14 cm; age ≥ 2 yr) establish parental territories, while some of the smaller males (total length 7–10 cm; age = 1 yr) remain as satellites in the parental territories (Santos 1985b). Satellite males are younger than nest-holders and the age classes of the two species do not overlap, which suggests that satellites may develop into nest-holders with age (Santos et al. 1995). Satellite males participate actively in territory defence against males of the same size and against parental neighbours and floaters. When females enter the nests to spawn, satellite males sneak inside these nests and try to steal fertilizations (Santos 1985b, 1992). Satellites have mature testes and sperm is present in their *vas deferens*, and their gonadosomatic indices are higher than those of parental males (Santos et al. 1996). The social units composed of a parental male and one or two satellites are stable over time. Both phenotypes seem to benefit from the association: the parentals because the satellites participate in the defence of the territory, and the satellites because they increase the probability that they will fertilize eggs (Santos 1985b, 1992). It was also suggested that territorial males associated with satellites obtained more spawnings than solitary parentals (Santos 1992).

In the present paper we evaluated the role of satellite males as mutualists or as parasites by analysing the costs and benefits for nest-holder males of having an associated satellite. We also investigated whether satellites prefer certain male traits when associating with a territory owner.

## Methods

### Study Site and Species

The observations were conducted in rocky intertidal pools located in a flat basaltic intertidal platform at Feteira, on the south coast of Faial Island, Azores (38°31′N, 28°27′W). The main study area comprised two large tidal pools permanently connected to the sea through channels. *P. s. parvicornis* is the dominant species in these pools (Santos et al. 1994). During the breeding season, which lasts from May to Aug. (Santos 1989), large males of this species defend a reproductive territory in which they prepare a nest in a natural crevice. Males court females by signalling the location of the nest and circling and leading the females, and spawning occurs inside the nest. The males clean the nest and guard and fan the eggs until they hatch. Thus, it is a promiscuous mating system with exclusive male parental care (Santos 1985a, 1992; Santos & Barreiros 1993).

### Data Collection

Nests were mapped and observed on a daily basis during the 2 mo of the field study. Nest-holder males were recognized individually using a combination of natural marks (e.g. scars) and relative size differences. Non-nesting individuals (e.g. satellites) were tagged with a combination of three coloured plastic beads inserted at the base of the dorsal fin following the method described by Patzner (1984), and previously used successfully in this species (Taborsky & Limberger 1980; Santos et al. 1989).

Behavioural focal observations (sensu Martin & Bateson 1993; total of 49 h) were conducted on 33 nests at low tide throughout the months of Jun. and Jul. 1999. The observations were made outside the water from the tidepool margins. At high tide strong wave action impeded observation. Thus, the results presented here are based on the assumption that the behaviour exhibited by the fish at low tide is indicative of their behaviour at high tide (i.e. a successful male at low tide would also be successful if observed at high tide). Each behavioural observation lasted for 20 min and on average three observations were made per nest on different days (mean observation time per nest of 86.5 min, with a minimum of 20 min and a maximum of 180 min). The observations were distributed over the day from 09:33 to 19:36 h. In each observation the following variables were recorded: number of visits by conspecifics and the identity of the visitor (i.e. other nest-holder, floater male, satellite male, sneaker or female; see below); details of all social interactions involving the nest-holding male, including agonistic and courtship behaviours given and received and the identity of the intervening conspecifics; activities performed by the nest-holder at the nest site [i.e. feeding; patrolling (i.e. an excursion out of the nest without feeding and without any intruder present); cleaning of the nest; egg fanning]. For a detailed description of the behavioural patterns of *P. s. parvicornis*, see Santos & Barreiros (1993).

The males were classified into different types according to the following criteria: (a) nest-holder male – medium to very large male seen guarding a nest for at least 3 d; (b) floater – medium to very large male with secondary sex characters but not seen guarding a nest; (c) satellite – small to medium male lacking secondary sex characters observed in the same breeding territory for at least 3 d; (d) sneaker – small to medium male lacking secondary sex characters never seen associated with a breeding territory. Sneakers were distinguished from females on the basis of head and belly profiles (i.e. sneakers have higher head heights than females and non-swallow bellies).

We used scanning observations to record fish present in the area around the nest (approximate diameter of 60 cm) every 1 min during 20 min of observation.

To study the patterns of association of satellite males with different nest-holders, male size and nest characteristics were measured as follows. Nest-holder body size was not directly measured since their capture from inside the nests would require the use of an anaesthetic (e.g. quinaldine), which could affect the survival of the brood. Thus, males were classified by consensus among the observers into four size classes: extra-large (XL), large (L), medium (M) and small (S). This classification was validated a posteriori by capturing a number of males previously allocated to one of the above-mentioned size classes and measuring their standard lengths [Kruskal–Wallis ANOVA: $H_{3,22} = 15.7$, $p = 0.001$; arithmetic x ± SD (n): XL = 12.7 ± 0.6 (6); L = 11.6 ± 1.0 (9); M = 9.3 ± 0.8 (6); no small nest-holders were found; Dunn's multiple comparisons test ($p < 0.05$): XL > L > M]. Maximum nest width and height were measured to the nearest millimetre with a ruler. The product of nest width by nest height was used as an indicator of nest opening area. Nest size was assessed by a measure of nest inner depth, which was taken by probing the nest with a flexible metal rod and measuring the maximum length of string inserted inside the nest. Distance to the nearest neighbour was measured with a meter tape to the nearest centimetre as the shortest line between the focal nest opening and its closest nest opening. Territory size was calculated as the average patrolling distance (i.e. the mean of the maximum distances that the nest-holder male moved away from the nest during patrolling excursions). The number of patrolling excursions, on which the territory size estimate was based, varied from zero (in nest-holder males that were never seen to leave their nests; territory size of zero) to 20 ($\bar{x}$= 2.46).

The presence of a satellite male in the vicinity of the nests was recorded by daily scan observations. Nests with which smaller individuals were consistently associated were classified as having a satellite male. Individual tagging of small and medium-sized non-nesting individuals allowed the detection of the same individual associated with a given nest on consecutive days.

To investigate the relationship between the presence of the satellite male and the nest-holder's mating success we recorded the spawning rate (i.e. number of observed female spawnings per observation time).

### Data Analysis

To investigate the association of satellite males with nest-holders of different size classes, we used simulation statistics applied to the analysis of contingency tables to avoid the problem of increasing type I errors (ACTUS; Estabrook & Estabrook 1989). To investigate the preference of satellite males for particular nest characteristics we compared nest characteristics between nests with and without an associated satellite.

We also compared the number of territorial intrusions, female visits and female spawnings and the agonistic and courtship behaviours of the nest-holders with and without an associated satellite male, to assess the relationship between the presence of the satellite male and the success of the nest-holder in mating and in territorial defence. The relationship between the presence of the satellite male and the physical condition of the nest-holders was assessed by comparing the relative condition factors $K_{ab} = W/aL^b$, where $W$ = body weight and $L$ = standstandard length (Bolger & Connolly 1989). The values of a and b, derived from the length/weight relationship, were $a = 0.00699$ and $b = 2.90$ ($n = 14$).

All the statistical procedures, except the ACTUS test, were run on the software package STATISTICA v.5.0 A (Statsoft Inc., Tulsa, OK, USA).

## Results

### Selective Association of Satellite Males with Nest-holder Males: Effects of Male Size and Nest Characteristics

The association of satellite males with nests of males of different size classes was not random (Table 1). Eighty-three per cent of the XL males had a satellite male associated with their nests, while only 38% of L males and 12.5% of M males had an associated satellite male. Satellite males were preferentially associated with bigger nests but showed no preference for nests with wider openings (Table 2). The number of openings of a nest was another factor to

*Table 1:* Relationship between male body size and the presence of satellite males in *P. s. parvicornis*

| | Nest-holding male body size | | | |
|---|---|---|---|---|
| Presence of satellite male | XL | L | M | ACTUS |
| Present | 5 | 7 | 1 | $X^2_2 = 7.2$ |
| Absent | 1 | 11 | 7 | $p = 0.03$ |

which satellites also seem to be sensitive when associating with a nest. All the nests with two entries had a satellite male ($n = 5$) while only 9 out of 28 nests with a single opening had an associated satellite male (Fisher exact probability test, $p = 0.008$).

### Relationship Between the Presence of Satellite Males and Nest-Holder Male Fitness

Nest-holding males with an associated satellite male had higher body condition factors than nesting males without satellites (Mann–Whitney U-test: $z = 2.07$, $p = 0.04$; see Fig. 1). Nest-holder males with satellite males suffered more intrusions from other conspecific territorial males. However, they did not show a higher rate of attacks directed towards conspecific males (Table 2). The two nests without satellites in which spawnings occurred suffered a very high rate of sneaking attempts by other conspecific males (i.e. sneakers and floaters) on both occasions (i.e. 100% of spawnings, $n = 2$). In comparison, six out of the eight spawnings in nests with satellites suffered sneaking attempts (75% of spawnings, $n = 8$). In nests with associated satellite males, in 62.5% of the spawnings ($n = 8$) the satellite male tried to parasitize fertilizations. Overall, other male conspecifics performed significantly more sneaking attempts than satellite males did (Wilcoxon matched pairs test: $n = 14$, $z = 2.20$, $p = 0.027$). Nest-holding males tolerated the presence of satellite males more readily than the presence of other conspecific males. In fact, although satellite males spent on average approx. 50% of the observation time in the nest-holder's territories ($n = 14$, $x \pm SD = 46.4 \pm 17.3\%$ of observation time) they experienced a lower rate of attack from nesting males than did other conspecific males (i.e. nest-holders from other nests, floaters and sneakers) which only briefly intruded into the nest-holder's territory (Wilcoxon matched pairs test: $n = 14$, $z = 3.64$, $p < 0.001$; see Fig. 2). This tolerance towards satellites correlated with the time the satellite spent in the territory of the nesting male (Spearman rank order correlation between the proportion of observation time that the satellite male was seen in the nesting territory and the rate of attacks received by the satellite male: $r_s = -0.53$, $n = 14$, $p = 0.05$). For the nest-holder males with an associated satellite male, there was no significant correlation between the rate of attacks on satellites and the rate of attacks on other male conspecifics ($r_s = 0.13$, $n = 14$, $p = 0.70$).

*Table 2:* Differences in behavioural variables and nest site characteristics between nest-holding males with and without an associated satellite male

| Variable | Z | p | Median (min–max) | |
|---|---|---|---|---|
| | | | with satellite | without satellite |
| Nest opening area ($mm^2$) | − 0.57 | 0.57 | 57 (15–608) | 66.5 (24–196) |
| Nest inner depth (mm) | − 3.1 | 0.002 | 14 (8–20) | 9 (4–20) |
| Distance to the nearest neighbour (cm) | − 0.68 | 0.49 | 43 (14–81) | 33 (6–87) |
| Territory size (radius, cm) | − 0.69 | 0.49 | 15 (0–47) | 20 (0–40) |
| Female visits (acts/h) | − 2.8 | 0.006 | 3 (0–9) | 0 (0–11) |
| Female courtship (acts/h) | − 2.9 | 0.002 | 0.5 (0–2.5) | 0 (0–0.5) |
| Female spawnings (acts/h) | − 3.1 | 0.004 | 0.55 (0–1) | 0 (0–0.5) |
| Male courtship (acts/h) | − 1.2 | 0.22 | 0 (0–3) | 0 (0–2.5) |
| Male conspecific intrusions (acts/h) | − 3.8 | 0.0002 | 20.6 (12.5–48) | 11 (0–22) |
| Sneaking attempts[a] (acts/h) | − 1.5 | 0.13 | 0.25 (0–6) | 0 (0–5) |
| Attacks towards conspecifics[b] (acts/h) | − 0.38 | 0.70 | 8.75 (1.5–15.3) | 4.5 (0–12) |
| Egg fanning (acts/h) | − 0.69 | 0.49 | 1.95 (0–34.5) | 0 (0–32) |
| Nest cleaning (acts/h) | − 2.13 | 0.03 | 0 (0–20) | 0 (0–3) |
| Proportion of attacks towards heterospecific intrusions | − 0.61 | 0.54 | 0.04 (0–0.18) | 0.08 (0–0.18) |

Statistical values refer to Mann–Whitney U-tests. Sample sizes were 14 for nest-holders with an associated satellite and 19 for nest-holders without, except in the case of nest measurements, for which $n = 18$.

[a] Including fertilization attempts by satellite male.

[b] Excluding attacks directed towards satellite male.

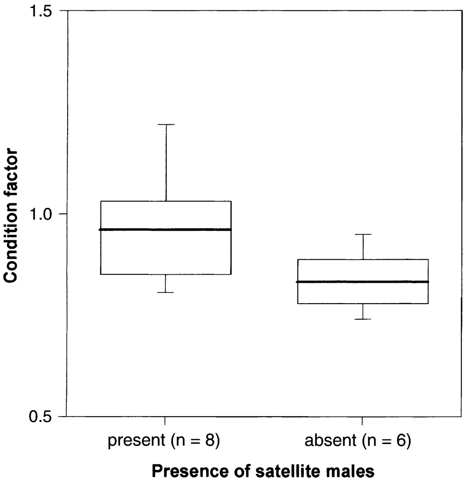

*Fig. 1:* Condition factors (weight/0.00699 × $L^{2.9}$) of nest-holders with and without an associated satellite male. Middle line = median; box = quartiles; whiskers = 90th and 10th percentiles

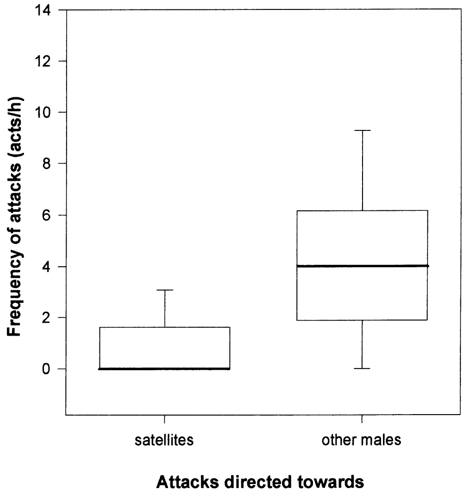

*Fig. 2:* Attacks directed towards satellites and conspecific males by nest-holders (n = 14). Descriptive statistics are as in Fig. 1

## Relationship Between the Presence of Satellites and the Mating Success of Nest-Holders

To assess the relationship between the presence of satellite males and the mating success of nest-holding males, we compared the number of spawnings that occurred in nests with and without an associated satellite male. We also compared the number of female visits and courtship acts and the behaviour of the nesting males in these two nest classes (i.e. with and without a satellite male). The numbers of female visits, female courtship acts directed towards the nesting male, and female spawnings were all significantly higher in nests with an associated satellite male than in nests without satellites (Table 2).

## Discussion

The functional significance of the occurrence of satellite males in *P. sanguinolentus* can be better understood if one considers the different perspectives of the different parties involved: nest-holders, parasitic males and spawning females.

### The Female Perspective

Nests with satellite males had approx. 5 times more spawnings than nests without satellites. There are two alternative explanations for this finding: either satellite males associate preferentially with more successful nests or females spawn preferentially with nests that have an associated satellite male. Increased attractiveness for females of nests with an associated satellite male has been suggested for other species (e.g. *Lepomis macrochirus*, Dominey 1981; *Symphodus ocellatus*, Taborsky et al. 1987), although the function of this preference has never been clearly demonstrated. Taborsky & Wirtz (unpubl. data in Taborsky 1994) suggested the hypothesis that females could be using the presence of satellite males to assess the chances that their eggs would be tended until hatching. In *P. s. parvicornis*, females could also benefit from the presence of a satellite male by reduced levels of spawning disruptions. Nests with satellites suffer less sneaking attempts, which may cause the nest-holding male to chase the intruder and interrupt spawning. In species with sneaker males it has been shown that both nest-holder males and females may reduce spawning when sneaker males are present (e.g. *Salvelinus malma miyabei*, Maekawa & Hino 1990; *Symphodus ocellatus*, Alonzo & Warner 1999).

An alternative explanation of female preference for nests with an associated satellite could be a mechanism of females copying the nest choice of satellites. Female mate choice copying has never been demonstrated for resource-based mating systems and this hypothesis would be plausible only if the mate choosing costs are high (Dugatkin & Fitzgerald 1997).

### The Nest-Holder Male Perspective

The occurrence of satellite males which steal fertilizations in the breeding territories of nest-holding males may confer both benefits and costs to the nesting male. Santos (1985b) found that satellite males are involved in more agonistic activities in the breeding territory than parentals. In the present study it was also found that, although nests with an associated satellite male suffered more territorial intrusions by other conspecific males, the nest-owners of these nests did not show a higher rate of attacks directed towards conspecific males, which suggests that satellite males are sharing the costs of territory defence. Moreover, during our focal observations on nest-holders we have often observed the respective satellite actively defending the nesting territory from other conspecific males.

Nest-holding males with an associated satellite male had higher body condition factors than nesting males without satellites, which may suggest an energetic benefit of the presence of the satellite male. A better condition may allow nest-owners to stay longer on their breeding territories and hence increase their reproductive success (i.e. increased endurance; Andersson 1994). This benefit in terms of shared territory defence has also been suggested for other teleost species in which satellite males occur (e.g. in a cichlid: Martin & Taborsky 1997; in Mediterranean wrasses: *S. ocellatus*, *S. roissali* and *S. tinca*, Lejeune 1985; Taborsky et al. 1987). An alternative cause of the observed correlation could be that satellite males prefer to associate with nest-holder males in better physical condition and thus of greater attractiveness to females. Experimental data are needed to distinguish between these two alternative explanations.

The presence of a satellite male may convey another benefit for the nest-holders in terms of the frequency of female spawnings. Since the satellites interfere in 62.5% of the observed spawnings and since the spawning rate in nests with associated satellites is significantly higher, the nest-holder would still have a net benefit from the presence of the satellite even if the latter fertilized the whole clutch in the spawnings in which he interfered (assuming that other sneaking males and satellites have the same fertilization success in their sneaking attempts). The overall parasitism rate was not significantly different between nest-holder males with and without satellites. Therefore, in the worst scenario the presence of a satellite would have no effect on the reproductive success of nest-holders and thus the tolerance of satellites could be viewed as a neutral situation. Nest-holding males better tolerated the presence of satellite males than that of other conspecific males. The degree of tolerance of satellites was positively correlated with the time a satellite spent in the territory of the nesting male, suggesting that nest-owners might require a high share of territorial defence in order to tolerate a satellite inside their breeding territories. Alternatively, satellites could simply spend more time in territories in which they are attacked less frequently. There was no significant correlation between the rate of attacks of nest-holders directed towards satellites and that of attacks directed towards other conspecific males, indicating that nest-holders tolerated satellites differently from other male intruders. Thus the positive relationship between satellite residence time and tolerance is not explained by the fact that satellites spend more time in the territories of less aggressive nest-holders.

Thus, there may be a threshold in terms of shared investment above which a nest-holder may benefit from tolerating the paternity costs imposed by the presence of a satellite. A similar hypothesis has also been suggested by Taborsky (1984) to explain the reciprocal relationship of nest helpers and parentals in the cichlid fish *Lamprologus brichardi*. In the wrasse *S. ocellatus* satellites are tolerated and fertilization stealings accepted, but satellites might save the bourgeois males from other purely parasitic competitors (Taborsky 1994). However, satellite removal had no effect on nest-holder defence effort or frequency of parasitized spawnings (Taborsky & Wirtz, unpubl. data in Taborsky 1994).

Other explanations for the tolerance of satellites by nest-holders have been proposed. These include the constraint that the expulsion of the satellite would prove impossible or that keeping satellites at a distance would be more costly than the loss of paternity imposed by them (e.g. Kodric-Brown 1977), female choice for multiple paternity (see Andersson 1994 for examples), and an increase in nest site attractiveness for females (e.g. Kodric Brown 1977; Ross & Reed 1978).

### The Satellite Male Perspective

This study focused on nest-holders, so our data on costs and benefits to satellite males are limited. Males acting as satellites were 1 yr old but not all males from this age class reproduced as satellites. Santos (1985b) suggested that only the males born early in the previous breeding season (year N) would become satellites in the following year (N + 1) because of a size advantage, which would be crucial for their ability to help defend a bourgeois male's breeding territory (i.e. the birth-date effect *sensu* Taborsky 1998). A preliminary analysis showed that, indeed, the larger males of the age class 0+/1 were the ones with higher gonadal investment (Oliveira et al. 2001). Thus, satellite behaviour is probably a condition-dependent transient strategy.

There seems to be a conflict between satellites and nest-holders, since the tolerance of nest-holders towards satellites may depend on satellite investment in shared territorial defence (see above) and satellites may associate with more than one nest (Santos 1985b). Satellites spent on average 46% of the observation time in the nest-holder's territory, which would leave 54% of their time to associate with another nest. Nest switches also occur and satellites may move from a nest they were associated with to a new nest (Santos 1985b). Since in crevice-nesting species available nesting space can be a limiting factor for mating success (DeMartini 1991; Hastings 1992), the potential spawning success of a given nest is expected to decrease as the breeding season progresses, but variation among nests is also expected (e.g. Oliveira et al. 1999). Satellites should choose nests according to their temporal variation in mating success. We found that satellites were preferentially associated with larger males, with larger nest sites and with nests with two openings. Larger males are more attractive to females (Oliveira et al. 2000) and usually have larger nests, which probably have a higher capacity to receive eggs, which in turn will increase the potential reproductive success of satellites. Nests with two openings offer satellites a better chance for stealing fertilizations from nest-holders. These results match the prediction of the satellite threshold model, according to which satellites should associate with the bourgeois males that are most attractive to females (Waltz 1982).

In conclusion, we would like to emphasize that nest-holders may gain from the presence of satellites and that satellites may adjust their helping behaviour to the mating success of nest-holders. These are not mutually exclusive hypotheses –

on the contrary, it is likely that both processes are at work in this system. Experimental research will be needed to determine the potential contributions of the two processes to the relationship found in this study between the presence of satellite males and nest-holder mating success.

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