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Male mating success in the Azorean rock-pool blenny: the effects of body size, male behaviour and nest characteristics

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Larger male Azorean rock-pool blennies *Parablennius sanguinolentus parvicornis* received more female visits, were courted more often by females and received more spawnings. Larger males also received a higher number of male intrusions, attacked more conspecifics and defended larger territories. Larger males showed more nest cleaning behaviour and a marginally non-significant trend for higher egg fanning rate. Male courtship, male attack rate against conspecifics and parental behaviour were all correlated with the frequency of female spawnings received by each male even when controlling for male size, suggesting that these behaviour patterns influence male mating success. On the other hand, a positive partial correlation was found between female courtship and the frequency of female spawnings, controlling for the number of female visits, which suggests a role for female mate choice on male mating success. Finally, males nesting in chambers in the bottom of pools received more spawnings than males nesting either in crevices or under boulders. However, nest opening area was associated significantly negatively with male mating success, when controlling for male size. Thus, the present data suggest strongly that male characteristics overrule nest characteristics in determining male mating success in the Azorean rock-pool blenny.

Key words: sexual selection; blennies; female preferences; male competition.

INTRODUCTION

In resource-defence polygynous mating systems male fitness is assumed to be correlated positively with the quality of the resources held by the male and the ability of males to compete for and defend resources from competitors (Emlen & Oring, 1977). In such mating systems female preferences should be based primarily on resource quality, particularly when those resources include parental care (Trivers, 1972). Hence, if the opportunity for female mate choice exists, it reinforces the effects of intrasexual selection. Thus, the variation found in mating success among nest-holder males in polygynous species can be explained by the variation in both male and nest-site quality. However, the best-quality nesting sites are occupied usually by high-quality males. That leads to a difficult distinction between the relative importance of the male and of the resource quality, when evaluating the partial contribution of the two for male breeding

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success. For example, in a careful experiment Sikkel (1995) manipuated algal cover in the nests of the garibaldi *Hypsipops rubicundus* (Girard, 1854) and demonstrated that male courtship behaviour was influenced by nest-site quality, measured as the thickness of the algal mat. Nevertheless, there has been a considerable effort to assess the relative importance of male and nest-site quality for male reproductive success in polygynous teleost species. Male characteristics influencing the access to females include male body size (Downhower *et al*., 1983; Keenleyside *et al*., 1985; Thompson, 1986; Bisazza & Marconato, 1988; Magnhagen & Kvarnemo, 1989; Oliveira *et al*., 1999), courtship intensity (Schmale, 1981; Keenleyside *et al*., 1985; Torricelli *et al*., 1988) and parental abilities (Downhower & Brown, 1980; Brown, 1981; Bisazza & Marconato, 1988; Côté & Hunte, 1989, 1993; Knapp & Kovach, 1991; Forsgren, 1997) among others. Evidence exists also for the effect of territory quality (Jones, 1981; Sargent, 1982; Kodric-Brown, 1983; Thompson, 1986; Hastings, 1988*a*) or nest quality (i.e. presence of eggs in the nest: Marconato & Bisazza, 1986; Unger & Sargent, 1988; Kraak & Videler, 1991; Kraak & Groothuis, 1994; Santos, 1995) on male fitness. The relative importance of site and male quality varies undoubtedly among species according to mating system and type of parental care (Dugatkin & Fitzgerald, 1997).

The rock-pool blenny *Parablennius sanguinolentus* (Pallas, 1811) is a benthic fish inhabiting the rocky shores of the Mediterranean and Atlantic (Zander, 1986), and is very abundant in the rocky intertidal of the Azores Islands (Santos *et al*., 1994). The taxonomic status of the Azorean population of this species is controverisial, with some authors considering it a separate species *Parablennius parvicornis* (Vallenciennes, 1836) (Zander, 1979). However, in a revision of the literature, Santos (1992) concluded that the available evidence could not support the existence of two separate species and proposed the existence of two sub-species, *Parablennius sanguinolentus sanguinolentus* and *Parablennius sanguinolentus parvicornis* in the Azores. In this species, during the breeding season, which lasts from May to August (Santos, 1989), the males defend a reproductive territory on which they prepare a nest in a natural crevice. The males court the females by signalling the location of the nest and circling and leading the females; spawning occurs inside the nest. The eggs are adhesive and are deposited on the inner surface of the nest. The males guard, clean and aerate the eggs until they hatch. Thus, this species exhibits a polygynic and polyandric mating system with exclusive male parental care (Santos, 1992; Santos & Barreiros, 1993).

In the present paper the contributions of male and nest site characteristics are investigated relative to male mating success in the Azorean rock-pool blenny, using an observational approach.

MATERIALS AND METHODS

STUDY SITE

The study site was located in a flat basaltic intertidal platform at Feteira on the south coast of Faial Island, Azores (38°31′ N; 28°27′ W) Rock intertidal pools are present in these type of platforms, resulting from the collapse of the top of lava tubes (furnas) due to erosion. Male *P.s. parvicornis* nest in these shallow rock pools (maximum depth 0·75 m) under boulders or inside crevices (Santos, 1985).

DATA COLLECTION

Behavioural observations were conducted during low tide in June and July 1999. At high tide, strong wave action precluded observations. A total of 49 h of nest focal observations (*sensu* Martin & Bateson, 1993) were conducted on 33 nests. Each observation lasted 20 min and on average three observations were made per nest on different days (mean observation time per nest was 86·5 min, with a minimum of 20 min and a maximum of 180 min). The distribution of the observations during the day ranged from 0933 to 1936 hours. 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, sneaker male, satellite male or female); details of all social interactions involving the nest-holding male, including agonistic and courtship behaviour given (male courtship is characterized by loop-swimming and leading the female to the nest) and received (female courtship is characterized by pectoral fin-flickering and opening and closing the mouth while presenting the flank in front of a nest, when a male is inside); and the identity of the intervenients. The following activities performed by the nest holder were recorded also: feeding, patrolling (i.e. an excursion out of the nest without feeding and without any intruder present); nest cleaning and egg fanning. The available ethogram for this species by Santos & Barreiros (1993) was followed, in which a detailed description of the behaviour patterns can be found.

Nests were mapped and followed on a daily basis during the 2 months of the field work. Nest-holder males were recognized individually using a combination of individual marks (e.g. scars) and relative size differences.

To study the relationship between nest-holder male size, nest characteristics and mating success, the following variables were used.

(1) Body size. Male body size was not measured directly because nest-holder males were not captured before the observations, to avoid any disturbances. Their capture from inside the nests would require using an anaesthetic (e.g. quinaldine), which could affect the survival of the brood. Thus nest-holder males were classified by consensus among the observers into three size classes: extra-large (XL), large (L) and medium (M). 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 length. There were significant differences among the three classes considered [Kruskal–Wallis ANOVA: $H_{3,22}=15{\cdot}7$, $P=0{\cdot}001$; mean ± S.D. (n): XL=12·7 ± 0·6 (6); L=11·6 ± 1·0 (9); M=9·3 ± 0·8 (6); Dunn's multiple comparisons test ($P<0{\cdot}05$): XL>L>M].

(2) Nest site characteristics. Each nest was classified according to the following nest type-classes: type A=sand bottom cave; type B=chamber in the bottom; type C=under boulder, type D=crevice in vertical wall. Nest opening maximum width and height were taken to the nearest mm with a ruler. The approximate nest opening area was calculated by multiplying nest width by its height. Nest inner depth, which can be used as an indicator of nest size, was assessed by probing the nest with a flexible string and measuring the maximum length of string inserted inside the nest. Nest depth was defined as the distance from the topside of the nest to the hydrographic zero. This distance was measured, while recording the exact time, with a tape measure, from the top of the nest to the water surface. Later a tide table was used to compute the distance to the hydrographic zero (Instituto Hidrográfico, 1999). Distance to the nearest neighbour was taken also with a measuring tape to the nearest cm as the shortest line between the focal nest and its closest nest openings. 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) was used as an indicator of territory size.

(3) Mating success. Because of the topographical complexity of the nesting cavities, the percentage of nest surface covered with eggs could not be evaluated with confidence. Thus, the number of observed female spawnings in each nest was used as a measure of male mating success. Operationally, a spawning episode was defined as any female entrance into the nest in which the female stayed for more than 30 s. In several of these

instances females lay with their bellies against the nest wall and quivered. Thus, the chances that the female nest entrances that were counted were not spawnings is low, because when females enter a nest for other purposes (e.g. egg cannibalism) they are attacked promptly by the nest-holder male.

DATA ANALYSIS

Some variables violated the assumptions of parametric statistics so non-parametric tests were used. All tests were two-tailed.

To assess the importance of body size on mating success of nest holding males, the number of spawnings that occurred in nests of males of different size classes (i.e. XL, L and M) were compared. Also, the number of female visits and female courtship acts directed towards nesting males were compared as well as sneaking attempts and the behaviour of the nest-holder males.

To determine the importance of nest type on the mating success of nest holding males, the number of spawnings that occurred in each of the classes of nest type were compared. The behaviour of males nesting in different nest types and the number of female visits, sneaking attempts and female courtship acts received by males of different nest type classes, were analysed also.

To investigate the potential relationship between nest type and male body size simulation statistics were applied to the analysis of contingency tables to avoid the problem of increasing type I errors (ACTUS, Estabrook & Estabrook, 1989). Spearman rank correlations were employed when appropriate.

To assess the relative importance of nest characteristics on male mating success, Kendall rank-order partial correlations were computed between the frequency of female spawnings and each nest characteristic while controlling for nest-holder body size.

To investigate potential effects of male behaviour on male mating success Kendall rank-order partial correlations were computed between a set of male behaviours and the frequency of female spawnings received by each male.

The significance of the Kendall rank-order partial correlation coefficients was determined using the critical values given in Siegel & Castellan (1988).

All the statistical procedures were run on the software package Statistica v.5.0A (Statsoft Inc., U.S.A.).

RESULTS

Larger males received a significantly higher number of both female visits and female courtship acts which resulted in a higher number of spawnings (Table I). Male courtship was significantly higher in XL males than in L males while M males showed intermediate levels of courtship (Table I). Larger males also received a significantly higher number of conspecific visits, were involved in a higher number of attacks towards conspecifics and defended larger territories. Concerning parental behaviour, larger males presented a non-significant trend for more fanning behaviour and had significantly higher levels of nest cleaning behaviours (Table I). There were no significant differences in the number of sneaking attempts suffered by nest holding males of the different size classes (Table I).

Although the number of female visits to different nest types did not differ significantly, type B nests received more female courtship acts and spawnings (Table II). There were no significant behavioural differences among males nesting on different nest types except for the frequency of nest cleaning behaviour, which was significantly higher in males nesting in type B nests. Both territory size and the number of sneaking attempts suffered were not significantly different among nest type classes also (Table II). Several nest physical

TABLE I. Differences in nest characteristics and behavioural variables among nest-holding males of different body-size classes. Statistical values refer to Kruskal–Wallis ANOVA. The same letter after the values in each row indicates $P>0{\cdot}05$ (Dunn's multiple comparisons test)

Variable	$H_{2,32}$	P		Mean ± S.E. (n)	
			XL	L	M
Nest opening area (mm^2)	0·44	0·80	162·2 ± 90·7 (7)	110·5 ± 32·3 (18)	69·0 ± 10·6 (7)
Nest size (mm)	7·18	0·03	162·8 ± 13·4*a* (7)	111·9 ± 42·9*b* (18)	111·4 ± 23·4*b* (7)
Nest depth (cm)	1·11	0·57	32·7 ± 19·6 (7)	24·1 ± 15·2 (18)	22·4 ± 14·7 (7)
Distance to the nearest neighbour (cm)	3·64	0·17	57·6 ± 8·6 (7)	36·2 ± 4·9 (18)	36·0 ± 7·2 (7)
Territory size (radius, cm)	8·21	0·02	34·4 ± 3·4*a* (6)	11·7 ± 3·9*b* (18)	15·9 ± 5·3*b* (8)
Female visits (acts h^{-1})	7·27	0·03	4·3 ± 0·9*a* (6)	2·5 ± 0·8*a,b* (18)	0·8 ± 0·5*b* (8)
Female courtship (acts h^{-1})	25·5	<0·0001	1·7 ± 0·4*a* (6)	0·08 ± 0·08*b* (18)	0*b* (8)
Female spawnings (acts h^{-1})	10·4	0·006	0·75 ± 0·17*a* (6)	0·13 ± 0·07*b* (18)	0·18 ± 0·09*b* (8)
Male courtship (acts h^{-1})	6·43	0·04	0·83 ± 0·33*a* (6)	0·20 ± 0·17*b* (18)	0·38 ± 0·31*a,b* (8)
Other conspecific visits (acts h^{-1})	5·69	0·06	23·7 ± 3·5*a* (6)	16·6 ± 2·6*a,b* (18)	12·2 ± 2·4*b* (8)
Sneaking attempts (acts h^{-1})	2·38	0·31	0·89 ± 0·37 (6)	0·75 ± 0·42 (18)	0·81 ± 0·61 (8)
Attacks towards conspecifics (acts h^{-1})	5·96	0·05	9·9 ± 1·9*a* (6)	6·4 ± 0·9*a,b* (18)	3·5 ± 0·9*b* (8)
Egg fanning (acts h^{-1})	4·81	0·09	12·4 ± 5·4 (6)	3·3 ± 1·4 (18)	7·5 ± 3·9 (8)
Nest cleaning (acts h^{-1})	12·7	0·002	4·5 ± 3·2*a* (6)	0·44 ± 0·34*b* (18)	0·06 ± 0·06*b* (8)
Proportion of attacks towards heterospecific intrusions	5·04	0·08	0·11 ± 0·02 (6)	0·04 ± 0·009 (18)	0·06 ± 0·02 (8)

TABLE II. Differences in nest characteristics and behavioural variables among nest-holding males using different nest types. Statistical values refer to Kruskal–Wallis ANOVA. The same letter after the values in each row indicates $P>0{\cdot}05$ (Dunn's multiple comparisons test)

Variable	$H_{3,32}$	P	Mean ± S.E. Type A (n=15)	 Type B (n=4)	 Type C (n=4)	 Type D (n=9)
Nest opening area (mm^2)	11·7	0·008	100·7 ± 13·3*a*	30·5 ± 5·8*b,c*	341·9 ± 162·6*a,c*	76·0 ± 34·4*c*
Nest size (mm)	8·3	0·04	10·1 ± 1·0*a*	12·3 ± 1·2*a,b*	18·4 ± 1·6*b*	12·3 ± 1·7*a*
Nest depth (cm)	11·4	0·01	24 ± 11·9*a*	17·8 ± 8·5*a*	53·5 ± 5·1*b*	18·7 ± 14·6*a*
Distance to the nearest neighbour (cm)	2·7	0·44	36·1 ± 6·2	49·5 ± 10·6	54·8 ± 8·9	40·3 ± 7·4
Territory size (radius, cm)	5·4	0·14	14·5 ± 4·0	35·8 ± 5·7	15·0 ± 15·0	12·3 ± 5·1
Female visits (acts h^{-1})	6·4	0·09	2·5 ± 0·9	3·3 ± 1·1	4·5 ± 2·3	0·76 ± 0·36
Female courtship (acts h^{-1})	9·7	0·02	0·13 ± 0·10*a*	1·6 ± 0·6*b*	0*a,b*	0·28 ± 0·19*a*
Female spawnings (acts h^{-1})	11·9	0·007	0·13 ± 0·08*a*	0·88 ± 0·13*b*	0*a*	0·26 ± 0·13*a*
Male courtship (acts h^{-1})	1·1	0·77	0·53 ± 0·27	0·25 ± 0·25	0	0·12 ± 0·08
Other conspecific visits (acts h^{-1})	5·9	0·12	13·4 ± 1·7	22·5 ± 4·5	32·7 ± 10·5	15·1 ± 2·9
Sneaking attempts (acts h^{-1})	6·2	0·10	0·48 ± 0·33	1·2 ± 0·4	0·17 ± 0·17	1·42 ± 0·81
Attacks towards conspecifics (acts h^{-1})	4·4	0·21	5·5 ± 1·0	11·1 ± 2·7	7·7 ± 2·5	5·34 ± 1·33
Egg fanning (acts h^{-1})	6·7	0·08	6·5 ± 2·4	16·6 ± 7·3	3·5 ± 3·5	1·87 ± 1·48
Nest cleaning (acts h^{-1})	15·5	0·001	0·73 ± 0·44*a*	6·0 ± 4·7*b*	0*a*	0*a*
Proportion of attacks towards heterospecific intrusions	5·75	0·12	0·06 ± 0·01	0·10 ± 0·03	0·02 ± 0·01	0·03 ± 0·01

Table III. Relationship between male body size and nest type used in breeding males of *P.s. parvicornis* (ACTUS: $\chi^2_6=13\cdot5$, $P=0\cdot04$)

Male body size	Nest type Type A	Type B	Type C	Type D
XL	1	3	1	1
L	8	0	3	7
M	5	1	0	1

Table IV. Kendall rank-order partial correlations ($\tau_{xy,z}$) between a set of nest characteristics (x) and the frequency of female spawnings in each nest (y) controlling for nest-holder body size (z) ($n=32$)

Nest characteristic	$\tau_{xy,z}$	P-value
Nest opening area	− 0·28	<0·05
Nest size	− 0·05	N.S.
Nest depth	− 0·15	N.S.
Distance to the nearest neighbour	− 0·02	N.S.
Territory size	0·12	N.S.

All non-significant results (N.S.) have $P>0\cdot20$.

characteristics were correlated with the behavioural activities displayed at nest. Nest-opening area was correlated negatively with the number of spawnings ($n=32$ nests, $r_s=-0\cdot35$, $P<0\cdot05$) while nest inner depth was correlated positively with female courtship ($n=32$ nests, $r_s=0\cdot47$, $P<0\cdot01$) and the number of conspecific male visits ($n=32$ nests, $r_s=0\cdot53$, $P<0\cdot01$).

The distribution of males of different size classes by different nest types was not random (Table III). Nest types A, C and D were occupied to a large extent by L males and nest type B by XL males. Although there were no significant differences among different male size classes concerning nest opening area (Kruskal–Wallis ANOVA for nest opening area by male body size class: $H_{2,32}=0\cdot44$, $P=0\cdot80$) larger males defended larger nests (Kruskal–Wallis ANOVA for nest size by male body size class: $H_{2,32}=7\cdot18$, $P=0\cdot02$; Dunn multi-comparison test ($P<0\cdot05$): XL males>L males=M males). Thus, the differences in mating success among nest types could be due to the variation in body size of the males adopting them. Moreover, no significant effects of nest characteristics on male mating success were found when controlling for the effect of nest-holder body size (Table IV).

Male courtship and parental care behaviour (i.e. egg fanning and nest cleaning) were associated significantly with a higher frequency of female spawnings received by nest-holder males, even when controlling for variation in body size among males (Table V). Male courtship was associated significantly with the

TABLE V. Kendall rank-order partial correlations ($\tau_{xy,z}$) between a set of male behavioural traits (x) and the frequency of female spawnings (y) in each nest controlling for nest-holder body size (z) (n=33)

Male behaviour	$\tau_{xy,z}$	P-value
Male courtship	0·51	<0·001
Egg fanning	0·38	<0·005
Nest cleaning	0·41	<0·001
Attacks towards conspecifics	0·38	<0·005
Attacks towards heterospecifics	−0·08	N.S.

All non-significant results (N.S.) have P>0·20.

frequency of female spawnings even when controlling for the frequency of female visits received by each male (Kendall rank-order partial correlation: $\tau_{xy.z}=0{\cdot}46$, $n=33$, $P<0{\cdot}001$).

Also, female behaviour seems to be an important factor determining male mating success, as is suggested by the significant positive association between the frequencies of female courtship and female spawnings at each nest, when controlling for the number of female visits (Kendall rank-order partial correlation: $\tau_{xy.z}=0{\cdot}44$, $n=33$, $P<0{\cdot}001$).

DISCUSSION

The data suggest that male characteristics are more important factors determining male mating success than are nest-site characteristics in the Azorean rock-pool blenny. Apart from the nest-opening area, none of the other nest characteristics were associated with male mating success when controlling for male size. Because male size is correlated also with male competitive ability, these results suggest that the males compete for the better nesting sites and that females use male clues, not nest-site characteristics, when looking for prospective mates.

The nest-opening area was associated negatively with frequency of female spawnings. In blenniids usually males use nests that fit their body size tightly. That enables better defence of the nest against potential intruders, both conspecific competitor males and heterospecific nest predators (e.g. *Lypophrys spp*., Kotrschal, 1988). Thus, females may benefit directly, in terms of reduced egg predation, by choosing males nesting in nests with a narrow entrance.

On the other hand, a number of male characteristics appeared to be associated with the frequency of spawnings received by each male. These are body size, male courtship, male parental behaviour (i.e. egg fanning and nest cleaning) and the frequency of attacks towards conspecifics.

Both male courtship and the frequency of attacks against conspecifics can be viewed as indicators of male sexual motivation, which would confer on them an advantage both in terms of male–male competition and on inter-sexual selection. The significant effect of attack frequency towards conspecifics also reinforces the hypothesis that male *P. s. parvicornis* compete actively for nest sites in this population. Thus, male-male competition should be viewed as playing an important role in sexual selection. However, the effects of female mate choice should not be ruled out because female courtship behaviour also had a major influence on male mating success, even when controlling for the frequency of female visits. Therefore these results suggest strongly active female mate choice.

Bigger males received more female visits and more female courtship acts which resulted in more spawnings. XL males had a mating success *c.* 5 times higher (0·75 *v.* 0·15) than that of the other males (i.e. L and M combined). A large body of literature suggests the occurrence of female mate preferences for larger males in species with male parental care including blennioids (Thompson, 1986; Hastings, 1988*a*, *b*; Petersen, 1988; Côte & Hunte, 1989; Oliveira *et al.*, 1999). However, the multiple regression analysis suggests that male size *per se* might not be the key variable for female mate choice because it is excluded from the stepwise model and, by itself it explains only a small proportion of the variation observed in male mating success (univariate $r^2=0{\cdot}13$). Nonetheless, male size may be under indirect female mate choice because it is associated with other variables that explain better the variation observed in female spawnings that each nest received, namely male parental behaviour (i.e. egg fanning and nest cleaning) and male courtship. Thus, in this species females may have a preference for male parental abilities or for more vigorous males as assessed by male courtship intensity, which is more intense in larger males.

Female preference for parental abilities has been demonstrated in other teleost species with extensive parental care (Dugatkin & Fitzgerald, 1997) and larger males are probably better parents (e.g. mottled sculpins *Cottus bairdi* Girard, 1850; Downhower *et al.*, 1983). In *P. s. parvicornis*, larger males tend to be more effective against heterospecific intruders which could be potential egg raiders.

Female choice for visual-display behaviour occurs in a larger number of species from invertebrates (e.g. fiddler crabs, Latruffe *et al.*, 1999) to birds (e.g. widowbirds, Andersson, 1991). However, in fishes there is a lack of evidence for visual display based female mate choice, partially due to the interdependence between male and female behaviour (Houde, 1997). The present study controlled for this causal uncertainty by calculating the association between the frequency of male courtship behaviour and the number of female spawnings received by males while controlling for the frequency of female visits each male received. Thus, potential flaws in the causal relationship between male display and female behaviour do not contaminate the association found between male courtship and mating success. In a number of other teleost species, females use male courtship intensity as a mate choice criterion (Karino, 1995; Grant & Green, 1996; Rosenthal *et al.*, 1996; see Andersson, 1994 and Houde, 1997 for a further discussion of this issue). Female preference for courtship vigour can bring them either direct or indirect benefits. Knapp & Kovach (1991) demonstrated that courtship intensity is a reliable indicator of male parental investment in the bicolour damselfish *Stegastes partitus* (Poey, 1868). Male vigour could be associated also with male genetic quality, and thus females that mate preferentially with males that court them more intensely may benefit indirectly in terms of offspring viability (Reynolds & Gross, 1992).

Although there were significant differences in the number of female visits to different nests, according to nest-holder male size, those differences were of a smaller magnitude than the ones found for female courtship. This indicates that there is a differential proportion of visiting females that court males of different sizes. No females were observed courting M males, whereas the majority courted XL males. However, spawnings with M males did occur, without female courtship. These results suggest female competition for access to larger males and that female courtship may also serve to inhibit male aggression during the initial phases of the spawning sequence, which would not be necessary when spawning with less choosy smaller mates. Thus, the potential occurrence of mate choice by larger nesting males exists in *P. s. parvicornis* also.

Moreover, if the frequency of male courtship is divided by the number of female visits received by the males of different size classes, a clear picture emerges. On average, M males courted half of the females that visited them, while larger males courted 1/8 of the visiting females, which again suggests that M males were either more motivated to mate or were less choosy. Intermediate-size males suffered more body injuries than smaller and larger males, pointing to higher competition among the males of this size class (Santos & Nash, 1996).

Sneaking rate (i.e. frequency of sneaking attempts per female spawning) indicates that smaller males are under a higher pressure than XL males. There was one sneaking attempt per successful spawning in XL males while in smaller males there were *c.* five sneaking attempts per successful spawning. This might be the result of smaller males being less aggressive than XL males. Thus, an additional benefit for females to spawn in XL male nests is to avoid mating interferences by other males, which may disrupt spawning (Sheppey & Ribbink, 1985).

In conclusion, both intrasexual selection, in the form of male-male competition for nesting sites, and female mate choice may determine the variation found in male mating success in *P. s. parvicornis*. Female mate choice may be based on direct benefits by choosing better fathers or on indirect benefits by choosing more vigorous males that may father offspring of higher viability. Further experimental studies are needed to disentangle the potential roles of these hypotheses for explaining sexual selection in the rock-pool blenny.

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