

# The effect of resource holding potential, nest size and information about resource quality on the outcome of intruder-owner conflicts in the sand goby

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**Summary.** Sand goby, *Pomatoschistus minutus* Pallas, males need a nest site for successful breeding. The value of the nest increases with size, as larger nests can hold more eggs. In the field using artificial nest sites, takeovers occurred in 29.0% of the cases. The winning intruders were on average 16.3% larger than the owners. These, in turn, were significantly smaller than the non-replaced males. Replacement probability increased with nest size. Prior ownership was of no importance in experimental situations, but might have affected takeover probabilities in the field. Males assessed the size of a potential nest site on the basis of its external appearance. When intruders and owners were given opposite information about nest size the experiments resulted in takeover rates of around 50% in situations where takeover rates were expected to be extreme. This suggested that intruders might update their information about a site's true value during the fight. The continuous assessment, in turn, might affect their motivation to continue fighting. On average, larger males were more active in initiating displays. However, smaller opponents challenged their larger opponents more actively when they were defending a large nest than when they were defending a small nest. The greater willingness to defend might provide the intruder with more information about the real value of the nest.

## Introduction

Male-male competition may take many forms, but commonly it includes the occupation and defence of limited resources to which females are attracted (Emlen and Oring 1977; Kodric-Brown 1983, 1990). Accordingly males that occupy the best resources will be expected to have the highest reproductive output. Therefore one would expect that the best resources are frequently contested and that they should therefore be occupied by the males with the highest competitive ability.

The outcome of conflicts over resources can be determined by correlated or uncorrelated asymmetries (Parker 1984). An example of a correlated asymmetry is a difference in resource holding potential (RHP) between the contestants (Parker 1974) and the outcome will be in favour of the individual with the higher RHP. Studies on animal contests have frequently shown that size difference is an important RHP asymmetry that predicts contest outcome (for review see Archer 1988).

Prior ownership represents an uncorrelated asymmetry and ownership is often expected to settle the contest (Maynard Smith 1982). When fighting costs are high relative to the payoff from winning, prior ownership should determine the outcome (Hammerstein 1981). Additionally, the owner should win when the resource has only short-term value (Grafen 1987). It has been proposed that one reason for owner advantage is that high-quality individuals accumulate at the resource sites through repeated contests (Leimar and Enquist 1984).

In contest situations one of the adversaries may have more information about the resource than the other. This occurs especially in an owner-intruder situation where the owner has normally spent much more time at the resource. Intruders, on the contrary, must estimate resource value in some other way, e.g. the distribution of resource values or the appearance of the resource. One of the expected outcomes of fights where only the owner has the opportunity of directly estimating resource value is that the owner's probability of winning should increase with resource value (Enquist and Leimar 1987). However, if the intruder also can gain information about the resource value directly from the resource, this should also affect winning probabilities.

In the sand goby (*Pomatoschistus minutus*, Pallas), a small littoral fish, males excavate nests under suitable objects (e.g. stones and mussel shells) on sandy bottoms. Females attach their eggs to the roof of the nest and the male cares for them until they hatch. This system is characterized by a clearly defined resource critical for successful breeding. As the size of the nest site determines the number of eggs a male can guard simulta-

neously (Lindström 1988) his fitness value is to a large extent determined by the nest size. The availability of nest sites is limited in nature, which results in male-male competition (Lindström 1988). Therefore many males are faced with a situation in which their only way of obtaining a nest is to fight for one already occupied. This is especially so because the sand goby normally only lives for 1 year (Fonds 1973; Healey 1971) and males tend to raise many batches of eggs sequentially in the same nest (personal observation). Thus nests are unlikely to be vacated unless the owner dies. Furthermore occupying a nest site early in the season should be advantageous, as early breeding will allow the young a longer growth period. The sand goby system thus closely approximates the conditions described by Grafen (1987) under which ownership should not be respected, i.e., a situation in which an individual that does not possess a resource can expect zero fitness.

Studies on fish species with breeding systems similar to the sand goby suggest that body size (weight or length) is often an important determinant of the potential to acquire a nest site and the quality of that site (e.g., Breitburg 1987; Downhower and Brown 1980; Goto 1987; Lindström 1988; Marconato et al. 1989). In this study I examine the idea that smaller nest owners are replaced more often than larger owners because of their poor ability to defend their nests, and whether the replacement probability depends on nest size. Finally, I consider how information about nest size affects the contest.

## Material and methods

The data for this study was collected during 1988–1990 at two study sites near the Tvärminne Zoological Station, southern Finland. Water depth at the study sites was ca. 40 cm and the water temperature was 12–18°C. Males were caught from nests using aquarium nets and measured using calipers to the nearest 0.1 mm.

*Male size and nest size.* During June in 1989 I provided 20 tiles of each of three different sizes (5 × 5 cm, 7.5 × 7.5 cm and 10 × 10 cm) as nest sites in the field. The tiles are readily used by breeding males. The distance between individual tiles was 2–4 m.

When a nest site had been occupied the owner was caught, measured, and marked. The males were marked by injecting a spot of white acrylic dye under the skin at different locations. Together with the size measurement this enabled individual recognition. After 5 days the current nest holder was caught, measured and his identity was checked.

*Nest size.* The question of how nest size affects conflict outcomes was tested in field cages made of galvanized metal net (mesh 3 mm, area 1 × 1 m and height 1 m). They were situated in a sandy-bottomed bay at a depth of 40 cm. Water with associated zooplankton could pass freely through the cage walls, to ensure that individuals in the cages had adequate food.

The experiment was designed to test whether nest size affects contest outcome. A male was put into the cage together with a nest site, either measuring 5 × 5 cm or 10 × 10 cm. The fish was allowed 24 h to build a nest. If he had not done so during this time he was replaced. After the owner had built a nest, I introduced an intruding male, who always was more than 5% larger in standard body length than the owner. Simultaneously with the introduction of the intruder the nest roof was cleaned of sand, as males often covered their nests. The size of the fish residing in the nest was recorded at 12, 24, 36 and 48 h after the introduction of the intruder. The experiment was terminated when a takeover had occurred, or after 48 h.

*Information about nest size.* To manipulate the information about nest size, the resource quality, I made nest sites that were small but appeared large and that were large but appeared small. The apparently large site consisted of a 10 × 10 cm tile divided into four squares with 5-cm-high walls. The walls ensured that only one 25-cm<sup>2</sup> area could be used at a time as spawning substrate. The tiles were placed so that the whole 100-cm<sup>2</sup> area was visible. This nest type therefore appeared larger than it really was. I will hereafter call this nest type “fake large”.

The apparently small site was made of a 10 × 10 cm tile with a 5 × 5-cm tile glued upon it. It was laid on the sandy bottom so that only the small tile was visible; the large tile was carefully covered with sand. Thus, although the site appeared to be only 25 cm<sup>2</sup> it could in fact hold a much larger egg mass than that. Because this site type appears smaller than it is, I will hereafter call it “fake small”.

To test if males could distinguish between the apparent and the real size of a nest site, I performed the following choice test. I put out fake large sites in pairs with true 10 × 10 cm<sup>2</sup> tiles and fake small sites in pairs with true 5 × 5 cm<sup>2</sup> tiles. The area usable as egg substrate was different for the nests in a pair. However, they appeared similar to a potential coloniser. The distance between the sites in a pair was 10 cm, allowing a simultaneous comparison of both sites (Lindström 1988). The pairs were checked every 4 h until one of the nests had been colonised.

The effect of information about nest size on intruder-owner conflicts was tested using a procedure similar to the previous experiment. However, as nests I used fake large or fake small nests. Owners and intruders thus had differing information about the quality of the resource they were contesting. It must be remembered, though, that owners always had a correct assessment of the nest area whereas intruders were provided with false information.

*Fighting behaviour.* To investigate whether the fighting behaviour of an individual could provide information about nest quality the following experiment was arranged. The fights were staged in the field. Each replicate consisted of three opaque plexi-glass walls, each 40 cm long and 15 cm high, placed parallel on a sandy bottom. The walls were pushed 8–10 cm into the sand at 20 cm distance from each other. In the two interspaces thus formed one fake large nest site and one 10 × 10-cm tile was placed. The surroundings of each replicate were cleaned of objects to eliminate all landmarks except the nest site and the two walls on each side of it.

A trial began when both nests in a replicate had been occupied for at least 5 h and neither of the males yet had any eggs. Both fish were caught and their lengths measured. Differences in their size and coloration pattern allowed individual identification. The middle wall and the nests were removed and the two other walls were moved 10 cm towards the center. The two nests were replaced by a new one, the type of which (fake large or true large) was randomly determined. Thus, when the fish were returned, the situation looked just the same to the males, except that now there was only one nest site present. Preliminary tests had shown that due to the lack of conspicuous landmarks apart from the nest and the wall, each male would perceive the site as his own. These preliminary observations also showed that ownership of the nest is settled within less than half an hour.

I recorded the behaviour of the males on a portable tape recorder for 30 min. I then checked the ownership three times at 60-min intervals after the beginning of the experiment. I used the number of displays initiated by an owner per 15 min as a measure of his willingness to defend his nest.

## Results

### *Replacement of males in the field*

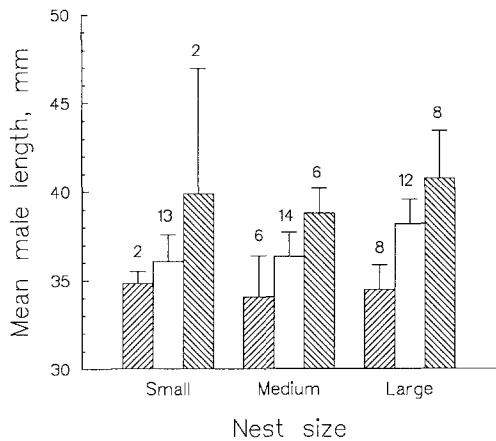
On five occasions males from the small nests could not be found or recaptured. Replacements occurred in 29.0% of the cases (Fig. 1) and the new owner was on average 16.3% longer (SD = 8.5,  $n = 16$ ; Fig. 1) than the

**Table 1.** Logistic regression on replacement probability of nest guarding males

Predictor variables	Coefficient	SE	<i>t</i>	<i>P</i>
Constant	13.796	5.165	2.67	0.0101
Male size	-0.459	0.152	3.01	0.0041
Nest size	0.026	0.012	2.14	0.0375

Model deviance,  $\chi^2 = 51.35$ ,  $df = 52$ ,  $P = 0.500$

The dependent variable is whether a takeover had occurred (1) or not (0) and the model including the length of the initial owner and the nest size fits the data very well. The total number of cases is 55



**Fig. 1.** The standard lengths (mean with +95% confidence limits) of males breeding in nests of the three size classes (small = 25 cm<sup>2</sup>, medium = 56 cm<sup>2</sup> and large = 100 cm<sup>2</sup>). Replaced males (*first diagonally hatched bar*) are males found in their nests only at the initial capture. Non-replaced males (*white bar*) were also found in their own nests at recapture 5 days later. Replacement males (*second hatched bar*) are the new males found in the nests at the time of recapture. *F* and *P* values of ANOVAS comparing body length of the males across nest sizes were: replaced,  $F_{(2,13)} = 0.10$ ,  $P = 0.902$ , non-replaced,  $F_{(2,36)} = 2.45$ ,  $P = 0.101$ , and replacement,  $F_{(2,13)} = 0.59$ ,  $P = 0.568$ . The numbers above the bars indicate the number of observations in each class. For example in large nests 12 males maintained their status as owners, whereas 8 were replaced (and 8 males occupied their nests)

previous owner. In only one case the new male was smaller than the original owner (small nest, difference 2 mm).

To analyse the effect of owner size and nest size on the probability of replacement I used a logistic regression analysis. According to the model, owner size was the most important factor determining whether he would still be found in the nest (Table 1). The smaller the initial owner was, the more likely it was that he had been evicted. Replacement was also more frequent for males in large nests (Table 1, Fig. 1). However, nest size was not as important as owner size. A small male therefore experiences a considerable risk of being replaced, especially if he occupies a large nest.

Replaced males in nests of different sizes did not differ in body size (Fig. 1; note however small sample sizes), whereas there was a (non-significant) tendency for non-replaced owners in large nests to be larger than

males of similar status in small nests (Fig. 1). Neither did replacement owners in nests of different size differ in body length. However, replacement owners were much larger than non-replaced ones (*t*-test,  $t = 3.62$ ,  $df = 53$ ,  $P < 0.0001$ ).

#### Nest size

In this experiment an intruder was introduced into an enclosure in which there was a nest occupied by an owner. When takeovers had taken place they almost always occurred between 12 and 24 h (10 out of 12) after the introduction of the intruder. The intruder, who in these experiments was always 5% larger than the owner, always evicted the original owner from a large nest (10 times out of 10 trials), whereas owners were victorious in most trials with small nests (8 times out of 10 trials). Takeovers were thus significantly more frequent when the contested nest was large than when it was small (Fisher's exact test,  $P = 0.0004$ ), a result similar to the findings of the previous section.

#### Information about nest size

Males could not distinguish between manipulated nests and similar looking non-manipulated nests. In 10 cases out of 26 fake large non-nests were chosen and in 12 cases true large nests (binomial probability = 0.416). On 4 occasions both nests were occupied. When the choice was between fake small and similar-looking true small nests, small nests were occupied 12 times and fake small nests 5 times ( $P = 0.072$ ). Thus there seems to be a slight bias towards non-manipulated nests. The reason for this is probably the fact that a nest can be dug only on two sides of a fake small site, as the large tile below the small one will hinder digging attempts.

When the choice was between fake large and fake small nests males always selected the fake large site (16 times in total,  $P < 0.001$ ). Correcting for the fact that fake small nests might be harder to colonise does not change the result ( $P = 0.0015$ ). Males base their decision to occupy an empty nest mainly on its external size. Therefore it is probable that an intruder's first estimate of the value of a contestable site is also based on the appearance of the nest.

In the enclosure experiments with fake large nest takeovers occurred in 6 out of 10 trials. With fake small nests the result was 5 takeovers out of 10 trials. Thus, when the intruder was provided with false information about nest size, takeovers were randomly distributed in relation to nest type. Compared to the situation with true large nests, takeovers occurred significantly less often when the nest was of the fake large type (Fisher's exact,  $P = 0.043$ ). These nests had the same external appearance, but because the owner was defending a small nest (therefore a nest of low value) it should have given it up more easily. The intruder again saw a large nest with a high fitness value and should therefore have been eager to conquer it. Thus the result that takeovers occurred less frequently does not support the expectation.

With fake small nests versus true small nests the expectation was that takeovers would be less common.

This is because the owner was now defending a large and valuable site and therefore should be more willing to defend it, whereas the intruder had only a small nest to win. The difference between takeovers in true small and fake small nests was not significant (Fisher's exact,  $P=0.175$ ) but the direction of the difference was again wrong.

Using a logistic regression with the outcome as the dependent variable, I also tested whether the sizes of the opponents explained any of the variance in the results. As explanatory variables I used the relative size difference between the opponents ((length of intruder – length of owner)/length of owner), the size of the intruder and the size of the owner. It turned out that none of these variables was powerful enough to be included in the model. The model with the best fit was achieved by using only the standard length of the intruder (deviance of model  $\chi^2=23.59$ ,  $df=18$ ,  $P=0.169$ ) as the independent variable. However, the regression coefficient of this variable is not significant ( $b=0.387$ ,  $SE=0.231$ ,  $P=0.111$ ). The sizes of the opponents thus do not seem to be important in explaining the pattern of takeovers. However, it must be remembered that the difference in length was always  $>5\%$  (range 5.06–35.69%) in favour of the intruder.

#### Fighting behaviour

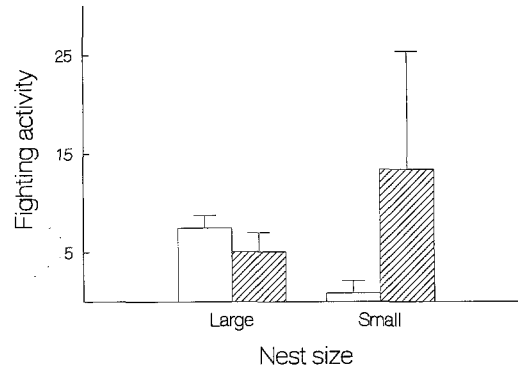
I recorded the time budgets of 20 fights so that 10 contests started with the larger male in the larger nest and 10 with the larger male in the smaller nest.

Within about 1 min after the start of the trial both males had re-located the nest site. The first display took place when about 154 s had elapsed ( $SD=33.1$ ,  $n=20$ ). This time interval was correlated with the absolute size difference between the fishes ( $r=0.61$ ,  $n=20$ ,  $P<0.01$ ). The smaller the difference the earlier a display occurred. Before the first display both fishes had good visual contact with each other. Neither the display activity (displays initiated by both males summed) nor the proportion of time spent in display was correlated with the size difference.

The first display was invariably initiated by the larger male when he had had the larger nest. Small males were the first to display on four occasions. This happened when they had occupied a large nest. Thus there was a weak tendency for males with large nests to display first (Fisher's exact,  $P=0.043$ ).

Small fish initiated more displays when they had a large nest than when the nest had been small (Mann-Whitney test,  $U=7.6$ ,  $P=0.032$ ,  $n=20$ ; Fig. 2). Large males, however, did not change their behaviour in relation to nest size (Mann-Whitney,  $U=25.0$ ,  $P=0.076$ ,  $n=20$ ; Fig. 2). On average the large male was more aggressive than the small male, initiating more displays (Wilcoxon signed rank test =  $-35.50$ ,  $n=18$ ,  $P=0.014$ ; Fig. 2).

The outcomes of the fights resulted in 85% of the nests being occupied by the larger male. All of the contests (10/10) where the larger fish had had a big nest were won by the large male. When the large male's nest



**Fig. 2.** The results of staged contests between males defending either large or small nests. The bars show number of displays initiated per 15 min (average + 95% confidence limits). When, for example, a small male (white bar) was defending a small nest the larger (hatched bar) male was defending a large nest and vice versa. The nests were so manipulated that externally they appeared similar. Ten of the contests started with the larger male in the large nest and 10 with the larger male in the small nest

had been small the larger male was the winner in 7 out of 10 trials. Male size was therefore the absolutely most important factor in determining conflict outcome. In all the cases when the small male was the winner (3) it had previously owned a large nest. This indicates that the likelihood of winning a contest depends on the subjective resource value, i.e., the estimate a male has of his nest's fitness value.

#### Discussion

This study shows that the size of a male sand goby is one of the most important factors determining his ability to take over and maintain a nest site. As the size of an owner increases, the proportion of males in the population that can successfully challenge his position decreases. However, nest size also affects the risk of takeover. A takeover by a larger intruder is more likely if the resource is very valuable, i.e., a large nest site. A small owner seems to experience an increased risk of losing his nest if the nest is large and hence attractive to other males.

Size difference has often been shown to determine contest outcomes in various situations (e.g. Dixon and Cade 1986; Hastings 1988; Tokarz 1985; Turner and Huntingford 1986; Verrell 1986). With sand gobies it was clear that small males were most likely to be forced to leave their nests. The males that took over these nest sites were not only larger than the previous owners but they were also larger than the males that were able to maintain their status as owners. This strongly indicates that the intruder has to have some initial size advantage before he can replace the owner. This result also implies that in the long run the best fighters in the population will accumulate in the nests, producing a situation in which further takeovers are unlikely to be observed.

In the sand goby it is clear that a large enough size difference overrules any owner advantage. This was also suggested by Hammerstein (1981) on theoretical grounds and has been shown to occur for example in crabs (Hyatt

and Salmon 1978) and spiders (Wells 1988). Magnhagen and Kvarnemo (1990), also studying the sand goby, were able to show a rather clear owner advantage in the aquarium. Prior ownership is expected to be used as a conflict settlement rule when costs are high relative to payoffs (Maynard Smith and Parker 1976). The ownership should also be important in situations where the resource has only short term value (Grafen 1987). In the sand goby the payoff of taking over a nest is extremely high and of long-term value, as it is necessary for successful breeding. This is especially important since the lifespan of the species only includes one breeding season. Thus a male's lifetime reproductive success may depend on winning a nest site. The cost can also be high, as fights frequently result in wounds on the head and badly torn fins. However, they probably never result in fatal damages (personal observation).

The important point is that as the likelihood of finding an empty nest decreases the value of owning one increases. This also decreases the likelihood of an "owner respecting" strategy (the "Bourgeois" strategy sensu Maynard Smith and Parker 1976) being an evolutionary stable strategy (ESS). This applies if there is no correlation between male size and expected future reproductive horizon. In fish growth is often indeterminate so that large individuals are older than small ones, thus potentially leading to a situation where large individuals actually have a shorter expected lifetime. If this was the case then large individuals might be found to take over and occupy sites simply because they have more to win and less to lose, which of course would alter some of the above conclusions. Whether expected lifetime and size is correlated for breeding sand gobies is unknown. However, breeding males found dead constitute a random sample of live breeding males (Lindström unpublished) and this suggests that large males may not expect a shorter future lifetime. Instead, nest guarding is generally energetically stressful in fish, causing weight loss (Lindström and Hellström 1992; Unger 1983) and suppressed growth (Magnhagen 1986), thus decreasing body condition and expected lifetime for nest guards. The effect of this should be to decrease the fighting abilities of owners, making it easier for takeovers to occur.

The pronounced effect of nest size on takeover rates, especially in the cage experiment, indicates the importance of resource quality on the behaviour of these fishes. The increase in takeover rates with increasing nest value could come about in two ways. First, males that attack owners with the largest nests are also the strongest fighters in the population. If this was the case then one would expect replacement males to be larger in large nests than replacement males in small nests. This was however not the case, although sample sizes were rather small. The second alternative is that intruders selectively contest only the best resources, i.e., large nests experience a higher intruder pressure. The decision to make a takeover attempt may then only depend on the RHP difference. If it is favourable enough for the intruder he will challenge the owner and probably also win the contest.

If a male has to fight for possession of a nest then there are two factors that should be important. Firstly,

the challenged owner should not be too large for him to have a reasonable chance of winning. Secondly, as he has to pay the cost of fighting in any case, he should try to maximize the payoff from a successful takeover. This means that he should not select a nest at random but should try to get a nest of a reasonable size. In a population this would result in a situation where real fighting ability, i.e. size, is the only determinant of conflict outcomes. The results of the present study support these predictions.

The field takeover rate averaged 29%. This value is much lower than the average rate found in the cage experiments (57%). In the field most of the males probably had eggs in their nests when their ownership was challenged whereas this was not the case in the cage experiments. The presence of eggs in the nest would increase the subjective value of the resource for the owner whereas the intruder would still perceive the value of the nest as unchanged. The increase in the subjective value should increase the motivation of the owner to defend the nest (Enquist and Leimar 1987). Potentially this would lead to a situation in which takeover rates were lower and/or the size difference between the opponents would have to be more pronounced in favour of the intruder for a takeover to occur.

In an aquarium experiment Magnhagen and Kvarnemo (1990) found that intruding large males were able to occupy the nest of smaller owners in 23% of the trials. In their experiment, small owners were first allowed to acquire eggs and thus the situation was very similar to the field situation in my study. Their value, (23%) is very close to that found here (29%) indicating that the presence of eggs might indeed affect takeover rates.

Male sand gobies often cover their nests with sand. This is most likely a way to make the nest cryptic and thus avoid detection by predators (Lindström and Ranta 1992). For example white mussel shells are extremely visible to visual hunters like birds. However, covering by sand could also serve to deceive a potential intruder about the size of the nest. Covering might either make the nest look smaller than it is or totally prevent other males from estimating the size of the nest and therefore its potential fitness value. In this case intruders would have to rely on estimates based on the distribution of nest sizes in the area (Enquist and Leimar 1987) which may yield a lower payoff estimate for the site.

Most game theory models on contest behaviour in animals assume constancy of the two crucial variables: the payoff,  $V$ , and the cost,  $C$ . However, these are likely to vary e.g. with the fighting rules adopted by the population (Grafen 1987). They may also vary with the characters (e.g. competitive ability) of the individual in question. The value of a nest to a sand goby male not only depends on the number of eggs it can contain but must also be a function of the probability that the individual will be able to keep it for the time it takes for the eggs to hatch. The smaller a male is the less likely this becomes and if intruder pressure increases with nest value then a large nest will be of less value to a small male than to a large male.

Costs of fighting are also likely to vary with male

size. In the sand goby males often bite each other and the larger the size difference between the opponents the more severe are the wounds that the larger male can cause. Consider the extreme situation where one of the opponents is big enough to eat the other. The costs for the small male in this case are certainly not the same as if he was fighting an opponent that he could eat himself. Thus the subjective value of a large nest site to a small male might be smaller than for a large male. For a female's reproductive success a nest takeover would be a disaster since males who lose their nests have their eggs eaten by the new owner (Lindström and Hellström 1992). In fact small males in large nests receive eggs less frequently than similar-sized males in small nests (Lindström MS) indicating that females might choose mates on the basis of their expected ability to defend the nest.

The results of the experiment in which I provided intruders and owners with different information about the resource value were not in line with the expectations. When intruders were given the impression of a large nest which in reality was small (fake large) one would have expected to see at least as many takeovers as when the nest size was genuinely large. Similarly few takeovers would have been expected when the size of the nest appeared small. Instead takeover rates were close to 50% in both situations. This indicates that the intruder updates his information during the encounter and possibly following the fight. This information could be achieved either by the intruder actually entering the nest or through the fighting behaviour of the owner (Enquist and Leimar 1987).

In the staged fights the larger male was in general more active and also won the majority of the fights. This accords with findings of other studies lacking an initial role asymmetry (Turner and Huntingford 1986). The resource value affected fighting behaviour in small males. When they defended a large nest they were more active than when defending a small nest. Similar changes in fighting behaviour with resource quality has been reported for hermit crabs (Dowds and Elwood 1983) in which smaller individuals initiated more fights when defending good quality shells. Intruding sand gobies might thus update their information on nest quality using the fighting behaviour of the owner and consequently decide if they should continue fighting.

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