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Effects of resource holding potential and resource value on tenure at nest sites in sand gobies

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Over a broad range of animal systems, male reproductive success depends on resource holding potential (RHP) and resource quality. In a field study, we randomly combined males of different sizes with nests of different sizes to investigate the relative role of resource holding potential and resource quality in determining a sand goby, *Pomatoschistus minutus*, male's nest tenure. Individually marked small and large males were given either small or large flowerpots for nests in isolation and were exposed to intruders after they had built nests. We found that nest tenure was longer for big males and owners of big nests. In most cases (34 of 51) the original nest owner was replaced by a bigger male. These replacements by larger males were probably due to takeovers by stronger intruders. Replacement males were larger at big nests. Our results support resource defense theory, as individuals with higher RHP and more valuable resources defended their nest for longer. On nine occasions males abandoned their nests. Owners of these nests were larger than the nest owners that were replaced. Hence, our results may provide an example of a situation in which sand goby males are able to judge the reproductive value of their current situation and act accordingly. *Key words*: male competition, resource holding potential, resource quality, sand goby, take over. [*Behav Ecol*]

Lack of availability and quality differences of breeding resources often lead individuals of the same species and sex to compete intensively to gain reproductive success (Darwin, 1871; Turner and Huntingford, 1986). In most cases it is the male sex that will actively compete to defend valuable resources, such as foraging areas or nest sites that will improve fitness, e.g., in terms of mate attraction (Andersson, 1994; Trivers, 1972). In these cases it is often the ability of a male to keep a territory that determines his reproductive success (Elwood et al., 1998). Contest theory proposes that asymmetries in individuals' abilities to defend resources determine the outcome of fights, i.e., individuals with the higher resource holding potential (RHP) win disputes (Parker, 1974). Although exceptions have been documented (Elwood et al., 1998; Hernandez and Benson, 1998), large body size is usually decisive in contest situations (Bridge et al., 2000; Lindström, 1992a; Renison et al., 2002), suggesting that RHP is frequently a function of large body size.

Other asymmetries are also important in determining the outcome of contests. Prior residency is one example (Davies, 1978; Kemp and Wiklund, 2001) and resource quality, e.g., mate, nest, or territory value (Bridge et al., 2000; Hack et al., 1997), has also been suggested to influence fighting and the outcome of fights. When resources are highly valuable, territorial males tend to fight longer and more intensely against intruders, while the latter also tend to challenge territorial males longer (Dearborn, 1998). In many systems the resource owner has better knowledge of resource quality, whereas intruders often would have to use some indirect measure of resource value (Enquist and Leimar, 1987;

Lindström, 1992a), and this can improve an individual's chances in the contest (Stamps, 1987). In addition, resource owners may already have made investments in the resource that will affect their overall resource budget (Sargent and Gross, 1985) and will affect their continued investment in resource defense (Beletsky and Orians, 1987; Tobias, 1997). This could include, for example, nest building and the presence of offspring. These investments will increase the value of the resource to the owner. Hence, the value of the resource is in most cases higher for the owner than for the intruder, and thus we may expect owners to invest more in the contest.

Resource quality can be a constraint on an individual's reproductive success. A male that defends a site with resources for fewer mates than he could attract is going to experience a cost in terms of lost potential mating opportunities. Therefore, such a male may be expected to move to a better site if one is available (Wolf et al., 1997). Individuals should thus opt for the most valuable resource. On the other hand, a high quality resource may attract both more competitors and competitors with higher fighting ability (Alcock, 2000; Switzer, 2002). The cost of defense would therefore be high relative to the individual's fighting ability, and eventually an intruder with a higher fighting ability would come by and conquer the resource. As a consequence, individuals are not always expected to opt for the maximum value resources but instead the optimum resource is a compromise of resource value and dependability. Analogous to this, models of mutual mate choice have suggested that low quality males may be better off preferring low quality females if competition for high quality females is intense (Fawcett and Johnstone, 2003). The outcome of this is assortative mating with respect to mate quality. The net value or fitness benefit of a breeding resource may similarly depend on how it translates into mating and especially reproductive success, which is a function of both resource quality and traits of the individual defending it. We thus would expect a correlation between male quality and the

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quality of the resource defended (Kvarnemo, 1995; Lindström, 1988).

For example, in sand gobies large nests are beneficial because they can simultaneously contain the eggs from more females than small nests (Lindström, 1992b). Hence, a large nest should be favored, as has previously been shown (Lindström, 1988). However, whether a male can defend a nest is a function of both nest site attractiveness and male fighting ability. If a male with small RHP occupies a large and attractive nest he is likely to lose his nest to a larger male without having produced any offspring (Lindström, 1992a). Small nests should not be defended if the male has a reasonably high RHP because such a male could successfully defend a nest that could provide him a much higher mating success. A male should therefore abandon a nest of low value relative to his RHP but also abandon a nest of too high value relative to his RHP. Hence, we may expect individuals to defend resources that are matched to their RHP.

The sand goby *Pomatoschistus minutus* (Gobiidae, Teleostei), a small bottom-dwelling fish that breeds in shallow water along the coast of Finland, is well suited to test these hypotheses. It exhibits exclusive paternal care, i.e., the male builds a nest under suitable substrates and attracts one or several females (Lindström, 1988, 1992b), which lay their eggs in the ceiling of the nest. The male fans and guards the eggs until hatching. Alternative reproductive tactics such as nest piracy and sneak spawning are common (Jones et al., 2001a,b; Lindström, 1992a).

In this field study we experimentally combined small and large males with either small or large nests to investigate the relative role of RHP and resource quality in determining a sand goby male's nest tenure. In most previous studies the focus has been on examining the duration of individual fights with respect to these factors. Studies that have examined resource tenure are usually observational (Alcock, 2000; Koenig, 1990; Switzer, 2002) and at most they have manipulated some aspect of territory quality (Wolf et al., 1997). However, without the simultaneous experimental control of both resource and owner qualities it is not possible to know to what extent these factors directly affect resource tenure. Here, we report the results of a field experiment in which we determined resource quality and owner quality independently and followed how individuals fared in non-staged encounters.

Previous work on the sand goby suggests that increased body size improves a male's ability to defend his nests (Lindström, 1988, 1992a) and, hence, one would expect nest tenure to increase. Large nests are more attractive and males fight more for large than for small nests (Lindström, 1992a); hence, one would expect nest tenure to be shorter in large than in small nests. The previous studies, however, have been primarily conducted under staged conditions or in situations that controlled only for nest size. Hence, they do not allow us to reliably assess the relative roles of RHP and resource value in determining resource holding success under natural conditions. Here we were especially interested in testing how male size and nest size interact in determining nest tenure. Based on the above we predicted that nest tenure should increase with increased male size. According to theory, nest tenure should increase in large nests due to high resource value (Enquist and Leimar, 1987). Empirical results, on the other hand, indicate that tenure may actually decrease due to higher intruder pressure (Koenig, 1990; Switzer, 2002). We also predicted that there should be an interaction between nest size and male size such that small males defending large nests should have the shortest nest tenure due to a highly attractive resource and a low RHP.

MATERIALS AND METHODS

This experiment was done in 2001 and 2002 during June and July, which is the main breeding season of sand gobies in the study population. Male sand gobies were collected from shallow water breeding areas (30 to 50 cm) near Tvärminne Zoological Station (southern Finland) using a hand trawl. They were maintained in large holding tanks (100 l) with continuous through flow of fresh seawater. During this time they were fed ad libitum live mysid shrimp and frozen Chironomidae larvae.

A total of 64 males were used in the experiment: 38 in 2001 and 26 in 2002. The total length (TL) of experimental males was 50.4 mm (SD = 5.8, $n = 38$) and 49.3 mm (SD = 5.3, $n = 26$) in 2001 and 2002, respectively (t test, $t_{62} = 0.71$, $p = .48$). They were divided into two non-overlapping size groups, small males (mean TL = 45.6 mm, SD = 2.4, $n = 34$) and large males (mean TL = 54.9, SD = 3.6, $n = 30$; t test, $t_{62} = 12.32$, $p < .001$), to represent male sizes below and above the population mean.

Each male was then marked by two pieces of colored electrical wire insulation on a monofilament string. Before the marking procedure males had been anaesthetized in benzocaine (ethyl p-amino benzoate). The monofilament was attached to the fish by piercing the dorsal muscle in front of the first dorsal fin using an injection needle and then pulling the monofilament through the needle. When the needle was removed the monofilament remained in the muscle. Both protruding ends had a colored piece of electrical wire insulation attached to them. These marks are easily visible in the field and provide a very efficient means for individual identification. Marked fish were then revived in a jet of fresh seawater and placed in an isolated tank to recover for 2 days. Methylene blue was added to the tank water in order to avoid fungus infections or disease that might result from the marking procedure. All fish survived the treatment without any signs of infection. In the field the marked fish behaved normally, and despite the markings being easy to read, they do not increase an individual's conspicuousness to predators. We never recovered any dead marked males, although dead sand gobies are frequently found during the breeding season. All manipulations reported in this study were authorized by the ethical committee for animal experiments of the University of Helsinki, permit no. 184/98.

The fish were then introduced into enclosures in the field at a natural breeding site. Each enclosure consisted of white plastic netting (mesh size 2 mm) that measured 80 × 80 cm and had a height of 75 cm. Each corner of an enclosure was supported by an iron pole that was 1 m long and pushed 50 cm into the soft sand bottom. To prevent fish from entering or exiting, all enclosures were placed in water shallower than 50 cm. The bottom 10–15 cm of the mesh was dug into the soft sand. This together with the inlaid poles guaranteed that the enclosure would remain tight despite water currents and wave action.

Depending on the treatment, each enclosure received either a small or a large nest site. Halved clay flowerpots were used, as sand gobies willingly accept these as nests. A small nest had a diam of 4 cm and a large nest of 10 cm. Because females lay their eggs in a single layer, nest size will eventually determine a male's maximum mating success (Lindström, 1992b). Small flowerpots have space for the eggs from 2–3 females, whereas a large flowerpot can easily host the eggs from up to 10 females. We then randomly assigned males of different size to these cages. Hence, we had males of all sizes in enclosures with small and large nests. It is important to realize that this also means that we experimentally controlled the combination of male size and nest size.

Table 1
Summary of complete parametric survival regression analysis using the extreme value distribution

	X_3^2	p	Coefficient	SE	Z	p
Full model	16.01	.001				
Variable						
Intercept			97.32	14.20	6.85	<.001
Nest size			-39.94	13.74	2.91	.004
Male size			-41.93	13.56	3.09	.002
Interaction			17.20	13.42	1.28	.200
Log (scale)			4.62	.09	53.44	<.001

The regression coefficients describe the effect of the treatments on the hazard. For example, the negative coefficient for male size means that the risk of nest loss (hazard) decreases with increasing male size. The positive scale parameter (which describes the position of the hazard function) shows that the hazard increases with time, i.e., the probability of losing the nest increases with time.

A male was considered to have built a nest when sand covered the flowerpot and there were clear building marks consisting of beams perpendicular to the flowerpot in the sand. Usually a male would also reside inside the nest with his head protruding. At this time the netting was carefully removed in order not to disturb the male. The identity of the nest holding males were checked every 6, 24, 30, 48, and 72 h after release, and thereafter every 24 h.

All owners of nests were expected to eventually abandon or be replaced from their nests. Hence, we tested the effect of male size and nest size on nest tenure with parametric survival analysis. Survival analysis is concerned with the distribution of lifetimes or, as in this case, with nest tenure times (Allison, 1995; Moya-Laraño and Wise, 2000). Survival analysis uses maximum likelihood estimates of the hazard function (the probability that a male will lose his nest during a given time period or event) of a lifetime variable (nest tenure). There are many different models for survival data, and what distinguishes one from another is the probability distribution for the lifetime variable. In this study we used the extreme value error distribution (Crawley, 2003). The analysis was performed on S-Plus v. 6.1 (Crawley, 2003; Insightful Corporation, 2001).

RESULTS

The longest time a male occupied a nest was 17 days (median 1 day, $n = 62$), while the shortest time in which a male was expelled was 20 min after the removal of the enclosure. Under the prevailing field conditions, with an average water temperature of 16°C, time to hatching is 8 days (Fonds, 1973). A total of seven (11%) males stayed that long and would have successfully hatched their broods. Out of the total of 64 males nine disappeared from their nests without being replaced within the ensuing observation interval, while 51 were eventually replaced by another male. Two males were taken by bird predators and two were still guarding their nests when we finished the field observations. The median time to replacement was 24 h (range 20 min–408 h, $n = 51$). To test if nest tenure time depends on male size and nest size we used a parametric survival analysis. Small males and males guarding small nests had shorter nest tenure than large males and males guarding large nests, but there was no interaction effect between male size and nest size (Table 1, Figure 1).

Males that disappeared from their nests without being replaced were on average bigger (mean TL = 53.6 mm, SD = 5.8, $n = 9$) than males that were replaced (mean TL = 49.1,

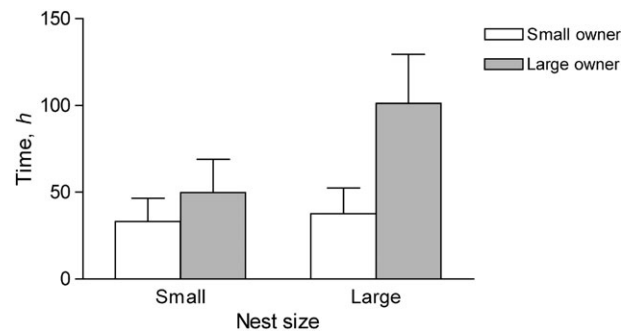


Figure 1
Nest tenure time as a function of male size and nest size. Error bars show 1 SD.

SD = 5.4, $n = 51$; t test, $t_{58} = 2.23$, $p = .030$). At nests where the original owner was replaced the replacing male was bigger than the owner in 34 cases out of 51 ($\chi^2 = 5.67$, $df = 1$, $p = .017$). In the remaining 17 cases the new male was smaller than the original owner. Whether a replacement was by a bigger or smaller male was independent of nest size ($\chi^2 = 0.16$, $df = 1$, $p = .69$). Based on contest theory we expected owners to defend big nests more than small nests. Therefore, takeovers at big nests should be predominantly by larger males. We found that at big nests replacement males were bigger than at small nests (ANOVA; effect of nest size, $F_{1,47} = 4.924$, $p = .031$; Figure 2), whereas replacement males were bigger when original owners were small than when original owners were large (original owner size effect, $F_{1,47} = 9.029$, $p = .004$; Figure 2). There was no interaction between nest size and owner size on replacement male size (interaction effect, $F_{1,47} = 0.161$, $p = .69$).

DISCUSSION

In this study we experimentally investigated how male size (resource holding potential) and nest size (resource quality) interact to affect male nest tenure in the field. We expected small males to lose nests early, especially if the nest was large. We also expected large males to have extended nest tenure. Indeed, we found that male size positively affected nest tenure and that nest tenure was longer at large nests. We also predicted an interaction between male size and nest size, with small males particularly vulnerable to takeovers at large nests and large males abandoning small nests in favor of larger ones. We found no indication of such an interaction in nest tenure times. However, we did find that the largest males

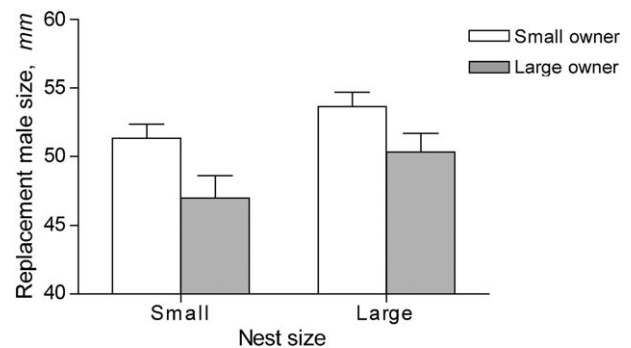


Figure 2
The size of males replacing the original owner as a function of nest size and original owner size. Error bars show 1 SE.

abandoned their nests, possibly to look for more favorable nest sites (see below).

Male body size also played an important role in determining which males were replaced and which males were replacement males. In the majority of cases in which a nest owner was replaced the new male was bigger than the original male, suggesting that the replacement occurred via an aggressive nest takeover (Jennions and Backwell, 1996; Lindström, 1992a). Large body size is beneficial in resource competition (Calsbeek and Sinervo, 2002; Davies and Halliday, 1979; Foster, 1996; Parker, 1974; Renison et al., 2002) and this is also the situation in the sand goby (Lindström, 1992a). In addition, in this study, replacement males in large nests were larger than in small nests, suggesting that a larger difference in RHP is required for a successful take over when resource value is high.

Resource defense theory predicts an increase in the level of defense for higher value resources (Bridge et al., 2000; Enquist and Leimar, 1987). Empirical studies have provided somewhat contradictory results concerning this prediction. For example, in many studies it has been found that defenders fight longer and more vigorously over females with a higher reproductive value (DiMarco and Hanlon, 1997; Hack et al., 1997). These studies are typically staged fights, where the size difference between the opponents and resource value is experimentally controlled. Contrary to these, field studies on resource tenure have found that territory tenure is often shorter on more valuable territories (Alcock, 2000; Koenig, 1990; Switzer, 2002). The discrepancy between these studies could be the difference in methodology. Unlike the field studies on territory tenure, studies on fight duration do not take into consideration differences in intruder pressure between resources of different quality. If intruder pressure is a main factor determining resource tenure, then fight durations may not be well correlated to resource tenure. In our study we controlled both owner resource holding potential and resource value while allowing intruder pressure to vary naturally, and we found that nest tenure was longer in large nests, which suggests that owners defended large nests more. Hence, even if intruder pressure would have been higher in large nests this did not affect nest tenure.

Another explanation could be a higher establishment cost for intruders in the sand goby (Parker and Rubenstein, 1981; Tobias, 1997). Owners typically defend their nests at the nest opening or even from inside the nest, making it increasingly difficult for an intruder to replace the owner. A replacement is facilitated by an increased size difference in favor of the intruder (Lindström, 1992a), as was found also in this study.

In addition to the above, a nest owner would normally have perfect information about resource quality, whereas intruders often must operate on imperfect information (Enquist and Leimar, 1987). This is also true for sand gobies. Sand goby males initially assess nest quality based on visual cues (Lindström, 1992a). While constructing the nest a male sand goby covers it with sand (Hesthagen, 1979), thus preventing visual evaluation of nest size, and this has been shown to misguide intruders in their nest size assessment (Lindström, 1992a). Therefore, the interactions between intruder and nest owner in this study involved a considerable asymmetry in nest size information, which should contribute to longer nest tenure in large nests.

There is also an asymmetry in resource value between owners and intruders because owners have already invested in their resource. This especially involves nest construction. Because of previous investment in the resource, owners may be more willing to invest in subsequent defense of the resource. Furthermore, many owners were already defending broods when the nest was taken over. The presence of a brood

would directly increase the value of the nest for the owner but not for the intruder. Large nests usually contain more eggs (Lindström, 1992b). Therefore, on average these nests would be more valuable to an owner, and this could explain why such nests were taken over only by the largest intruders.

Increased replacement male size at large nests could also be explained by only larger males being attracted to these nests. This, however, would not explain the increased nest tenure of original owners in these nests.

In some cases males disappeared from their nests without being replaced by new males. These males were on average larger than males that were eventually replaced by new males. An explanation for this result is that large males abandoned the nests offered because of the low reproductive value of these nests. A large male can usually expect to defend a high quality nest with space for eggs from a large number of simultaneous females (Lindström, 1992b), and it is possible that the small nests and even the large nests that we provided in this study did not fulfill those expectations. Because of their high resource holding potential, large males also have the ability to conquer valuable nest sites from a large range of defenders (Lindström, 1988, 1992a). Hence, we think that it is likely that our results represent an example of a situation in which the decision to defend or abandon a resource depends on an interaction between resource quality and individual traits. Future studies will need to rigorously examine if individuals can make such assessments.

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