

# Uncertainty in territory quality affects the benefits of usurpation in a Mediterranean wrasse

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Individuals should defend sites when the expected benefits of the territory exceed the cost of defense. However, if territory quality is unpredictable or difficult to assess, the expected pattern of territorial behavior is less clear. In a Mediterranean wrasse, *Symphodus ocellatus*, mating success is skewed with 2% of nesting males getting more than 20% of the spawning success. Yet, variation in mating success is not explained by any known physical characteristic of males or their territories. Instead, females prefer nests with a recent history of mating success because males are less likely to desert the offspring she leaves behind. Thus, territory quality is transient and determined by interactions between the sexes. I measured the frequency of territorial takeovers and the uncertainty in mating success among days at a nest. Observations indicated that *S. ocellatus* males usurped their neighbor's successful nests when males were unsuccessful and larger than their successful neighbor. Sites that achieved mating success had a significantly higher probability (0.84) of remaining successful between consecutive days than unsuccessful territories had of becoming successful (0.30). Unsuccessful males obtained higher and more certain fitness returns if they usurped a successful neighbor's territory. Interactions within and between the sexes drive uncertainty in success, which influences territorial behavior in this species. *Key words*: territoriality, stochasticity, labridae, sexual conflict, assessment. [*Behav Ecol* 15:278–285 (2004)]

Individuals should defend sites or take over territories when the expected benefits of the territory exceed the costs of defense or usurpation (see Brown, 1964; Calsbeek et al., 2002; Carpenter and MacMillen, 1976; Davies, 1978; Davies and Houston, 1984; Gill and Wolf, 1975; Noble, 1939; Piper et al., 2000; Ruxton et al., 1999; Schoener, 1983, 1987; Stamps and Krishnan, 2001; Switzer, 1993). Theoretical predictions have focused on cases in which resources are fixed or animals have good information about the costs and benefits of resource defense (see Carpenter and MacMillen, 1976; Davies, 1978; Davies and Houston, 1984; Gill and Wolf, 1975; Schoener, 1983, 1987; but see Ruxton et al., 1999; Stamps and Krishnan, 2001; Switzer, 1993). However, studies have shown that resources at a site can vary, information about resources may be incomplete, and the costs and benefits of resource defense are not always predictable (see Bollman et al., 1997; Nager et al., 2000; Orians and Wittenberger, 1991; Ruxton et al., 1999; Stamps, 1994; but see Rendon et al., 2001). This unpredictability can greatly influence territorial behavior.

When animals defend stable and predictable resources, a positive correlation is expected between the territory defender's quality (resource holding potential [RHP]) and the quality of the resource (Maynard Smith and Parker, 1976). Although examples exist in which this pattern has been found (see Alcock, 1987; Alcock et al., 1977; Andersson, 1994; Bart and Earnst, 1999; Brown, 1964; Campanella and Wolf, 1974; Jones, 1981; Petrie, 1984; Searcy and Kasukawa, 1989; Severinghaus et al., 1981; Shutler and Weatherhead, 1991; Wells, 1977), in other cases the relationship has not been supported (see Beletsky and Orians, 1993; Cordera et al., 1996; Pribil, 1998). These results could arise from unpredict-

able variation in the critical resource, making it difficult for high-quality individuals to defend the best territories. For example, in yellow-headed blackbirds, the food resources important to offspring growth and survival are not known until after territories are established (Orians and Wittenberger, 1991). As a result, females cannot predict the territory that will have the highest-quality food (Nager et al., 2000; Orians and Wittenberger, 1991). In this case, no correlation between individual and territory quality would be expected because territory quality is unpredictable. In other systems, the quality of the territory will vary owing to interactions between individuals. This will be especially common in cases in which territories are defended for reproduction. For example, the success of a male's reproductive territory may depend not only on resources intrinsic to the site but also on female choice among territories. If female choice among territories varies, a strong relationship may not exist between territory or resource quality and male RHP because the "quality" is dynamic rather than fixed.

In a Mediterranean wrasse, *Symphodus ocellatus*, males defend sites against conspecific males and predators (Lejeune, 1985; Taborsky et al., 1987; Yliff et al., 1997, 1998). Males go through a series of nest cycles in which they construct nests out of algae (1–4 days), spawn with females (2–4 days), and then usually fan and defend eggs (2–7 days) before leaving the nest site and starting another nest cycle (Lejeune, 1985; Taborsky et al., 1987). Females visit nests to spawn and appear to choose among nests (Alonzo and Warner, 2000a; Taborsky et al., 1987; Wernerus, 1985, 1988; Wernerus et al., 1989), but these territories do not offer any food resources to the female or her offspring. Instead, for females, the critical resource at these territories is male parental care. Males that have experienced high mating rates tend to remain with their nests through the parental care phase of the nest cycle, whereas males with low mating success often desert the nest before the eggs can develop (Taborsky et al., 1987). For males, territory quality is determined by their

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ability to attract females to their nest. Yet, females are only attracted to nests in which other females are spawning. Therefore, the critical resources affecting perceived quality of the territory are dynamic depending on interactions within and between the sexes.

In this species, alternative male strategies exist with large colorful males defending nests and small drab males sneaking spawns (Taborsky et al., 1987). Growth data from otoliths indicate that sneakers and nesting males represent separate life histories (Alonzo et al., 2000). Females appear to avoid spawning with small sneaker males. However, females usually spawn at nests with sneakers present because nests with high mating rates lead to nest fidelity by males and also attract sneakers (Alonzo and Warner, 2000a; van den Bergh et al., 1989).

In *S. ocellatus*, the distribution of mating success among nesting males is not explained by any measured behavioral or physical characteristics of the nest or nesting male, individual male identity, or nest site (Lejeune, 1985; Wernerus, 1985, 1988; Wernerus et al., 1987, 1989), and past research indicates that success is unpredictable before the nest cycle (Wernerus 1985, 1988; Wernerus et al., 1987, 1989). In contrast, because females are attracted to successful nests, less uncertainty may exist during a cycle. If territory quality is predictable after but not before the establishment of territories, an unsuccessful male could increase his mating success by taking over the nest of a nearby successful male, and nest takeovers should be common. By using a combination of field observations and experiments, I examined the predictability of nest success during the nest cycle, the conditions under which nest takeovers occur, and the benefits of usurpation by nesting males in *S. ocellatus*.

## METHODS

### The study site and species

Research was conducted May–June 1997 under natural conditions near the University of Liège (Belgium) Marine Laboratory, La Station de Recherches Sous-Marine et Océanographique (STARESO), located near Calvi, Corsica, France. I made all observations on rocky substrate along 200 m of shore in water less than 15 m deep by using scuba during approximately 100 h underwater. In 1997, before the beginning of the reproductive season, I caught and individually marked 128 nesting males by using a subcutaneous injection of Alcian blue, a vital stain, and measured their standard length to the nearest 0.1 mm. This marking method is less invasive than a tattoo, and marked individuals return within minutes to their nests. Nesting males have a distinct color pattern and are larger than all other individuals in the population, which easily distinguishes them from females and sneaker males (Lejeune, 1985; Taborsky et al., 1987). Females can be distinguished from sneaker males by the absence of a brightly colored spot on their opercules, by the shape of their abdomen and genital papillae, and by the absence of aggression toward them by the nesting male (Lejeune, 1985; Taborsky et al., 1987). Nests occur within meters of one another, and both females and sneakers move freely between nests. Experiments have shown that sneakers and females respond to changes at the nest and redistribute themselves among nests within 30 min (Alonzo and Warner, 1999; Alonzo and Warner, 2000a). In contrast, nesting males cannot move freely between nests because of the territorial behavior of other nesting males and the risk of losing their current nest.

### Measures of mating success

Finding a suitable measure of male mating success was critical to understanding territorial behavior in this species. Spawning success would seem to be the most direct measure of success, yet spawns were clumped in time. Given that observations had to be conducted by using scuba, this limited the amount of time I could spend observing each nest. I therefore considered using other measures of spawning success. My criteria for picking a suitable measure was that it showed high repeatability between observations of the same male within a short period of time and, therefore, low within-male variance compared with between-male variance. I used data I collected in earlier studies to test for a suitable measure. First, I analyzed data from 30-min observations of 28 nests taken in May–June 1996 (Alonzo and Warner, 1999). Each 30-min session was separated into 30 consecutive 1-min observations for each individual nest. In each minute, I tallied the total spawns and spawns that occurred without any sneakers (pair spawns). I also recorded the number of males with the sneaker phenotype present in the vicinity of the nest (within 3 m of the nest and oriented toward the nest) at the start of each 1-min interval. These data were analyzed by using ANOVA. I found that the among-male variance in total spawns (among-male sum of squares = 222.13) was much less than the within-male variance (within-male sum of squares = 1163.47). The same pattern existed for variation within- and between-males in pair-spawns (among-male sum of squares = 71.50, within-male sum of squares = 377.00). Thus, 1-min observations create very large sampling error on the direct measures of mating success. By contrast, variation among males in the number of sneakers at the nest was greater than the variation within males among observations (among-male sum of squares = 2907.96, within-male sum of squares = 1947.70). As a result, within-male variation in spawning was greater than within-male variation in the number of sneakers present at the nest. The repeatability of the number of sneakers at the nest (0.59) is four times greater than the repeatability of either the total number of spawn at the nest (0.14) or the number of pair spawns at the nest (0.14). This suggests that the number of sneakers might be a more reliable measure of mating success than is the number of spawns given the constraints on observation time.

This is, however, a counter-intuitive measure of mating success, as sneakers surely reduce fertilization success per spawn of the nest-holding male. Nevertheless, the number of sneakers is positively related to spawning success. This finding comes from several sources. First, past studies have shown that number of sneakers present at a nest, and the total number of spawns at the nest are significantly and positively correlated (Lejeune, 1985;  $r = .91$ ,  $p$  value not available; Wernerus et al., 1989  $r = .37$   $N = 39$   $p = .02$ ). To confirm this for my study, I examined 10-min observations of 88 randomly selected nests in May and June of 1994 (Alonzo SH, unpublished data). I counted the number of sneakers at each nest every minute over the 10-min period and averaged that value. I also recorded the total number of spawns and the number of spawns not joined by sneakers (pair spawns) in each observation. Although the total number of spawns at the nest may not indicate the mating success of nesting males because of the effect of shared paternity with sneakers, the number of pair-spawns is a measure of known fertilizations. In fish species with external fertilization, it is unlikely that sperm from previous spawning events will fertilize eggs in later spawning events, making each spawning event independent.

I found a significant and positive relationship between the number of sneakers present at the nest and total spawns ( $r^2 = .16$ ,  $\beta = 0.92$ ,  $F = 16.81$ ,  $p < .001$ ) as well as with pair spawns

(i.e., just the nesting male and a female mating,  $r^2 = .07$ ,  $\beta = 0.44$ ,  $F = 6.33$ ,  $p = .01$ ). A two-parameter Ricker equation (a logistic function with diminishing returns,  $y = \alpha x / [1 + \beta x]$ ) also produced a strong positive relationship between number of spawns and the presence of sneakers at the nest ( $r^2 = .25$ ,  $\alpha = 1.92$ ,  $\beta = 4.20$ ,  $F = 28.7$ ,  $p < .001$ ) as well as between pair spawns and sneakers at the nest ( $r^2 = .27$ ,  $\alpha = 1.84$ ,  $\beta = 4.12$ ,  $F = 32.3$ ,  $p < .001$ ). Although the relationship appears to be nonlinear, the number of sneakers present at the nest always corresponds with an increase in the mating success of nesting males. Furthermore, nests with sneakers and nests without sneakers have significant and large differences in total spawns (nests with sneakers: 10.58 [SE  $\pm$  1.66],  $n = 38$ ; nests without: 2.60,  $n = 50$  [SE  $\pm$  0.71],  $t = 4.41$ ,  $p < .001$ ) and pair spawns (nests with sneakers: 7.21 [SE  $\pm$  1.23],  $n = 38$ ; nests without: 2.40 [SE  $\pm$  0.71],  $N = 50$ ,  $t = 3.48$ ,  $p < .001$ ). Thus, the presence or absence of sneakers is a good indicator of being successful or unsuccessful in general. In *S. ocellatus*, although relative paternity (the percentage of eggs fertilized) will invariably decrease as the number of sneakers present at the nest increases, the total paternity (the number of eggs fertilized) nesting males obtain under natural conditions is associated with more sneakers present at the nest because sneakers are attracted to a higher frequency of spawning. Furthermore, the slope of the regression of spawns joined by sneakers on total spawns was 0.30 ( $r^2 = .6$ ,  $p < .001$ ), indicating that sneakers do not overwhelm nesting males as the spawning rate increases.

In summary, the number of sneakers associated with a nest is a proxy of mating success and is a more reliable measure of the success a male may obtain given the constraints I faced in observation time per nest. Thus, I used number of sneakers at a nest as a measure of nest success in all subsequent analyses.

### Nest surveys

In 1997, nests were surveyed daily to determine the occurrence of nest takeovers and the uncertainty in mating success at a nest between days. Nest cycles are not synchronous, and males always leave their nest at the end of the nest cycle and usually build a new nest on a nearby site (Wernerus et al., 1989). I surveyed the entire research area daily and placed numbered markers by all nests. I removed the markers only after the nest had been deserted for three consecutive days. I observed all nests within the study area daily for 1 min to determine the activity of the nesting male (building, spawning, or fanning), the individual mark of the nesting male, and the number of sneakers at the nest. This species is reproductively active during daylight, and past studies have not found any variation in mating rate with time of day (Lejeune, 1985). Nest surveys were conducted during the same period in the morning daily for consistency. I designated males as building when they carried and put algae into their nest. Males in the building phase of the nest cycle do not mate. In contrast, males in the spawning phase of the nest cycle actively court and spawn with females. Males in the fanning phase of the nest cycle use their pectoral fins to fan the surface of the nest, do not add algae to the nest, and do not spawn with visiting females. I determined the number of sneakers present at the nest by counting the number of sneakers oriented toward and within 3 m of the nest. Nests were surveyed daily unless weather conditions did not permit diving (only 3 of 53 days). The number of nests within a 10-m radius was measured after the nest cycle had been completed or the nest was deserted. From the survey data and these measurements, it was possible to determine the average number of active nests found within 10 m during the spawning period of each nest. This measure was used to

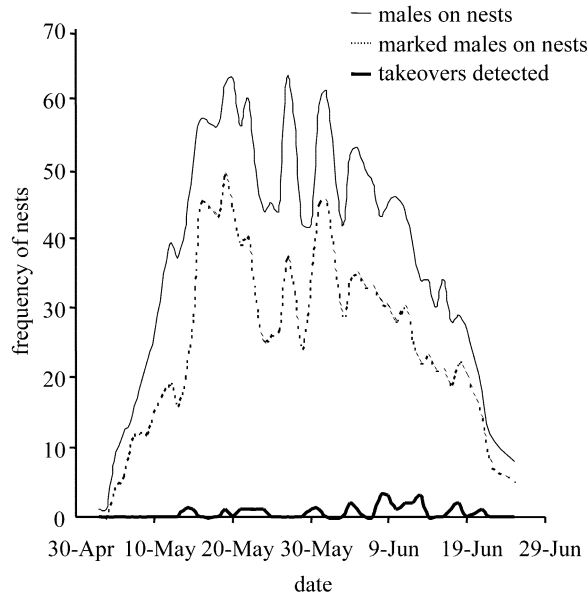
indicate local density and the number of successful neighbors within 10 m for each nest. Nests can be less than 1 meter to 10s of meters apart, and individual nests may have from zero to eight neighbors in a 10-m radius.

### Determining the occurrence of nest takeovers

Nests are abandoned at the end of the nest cycle or if they are unsuccessful (Taborsky et al., 1987). These nests are usually left unattended by other males after desertion. Therefore, I inferred that a nest had been taken over when the male changed between consecutive days. Aggressive interactions between nesting males are commonly observed (Taborsky et al., 1987), and abandonment of successful nests is rare (Taborsky et al., 1987). Takeovers could only be recognized if at least one of the males was marked. When a marked male took over another male's territory, I compared the number of sneakers present on consecutive days at the deserted nest with the nest taken over. I also compared the number of sneakers at the deserted nest with the nest taken over on the day before the takeover. I also compared the standard length of the original male and the usurping male. Standard length and the number of sneakers before and after takeovers were compared using paired *t* tests because differences did not deviate significantly from normality according to a Shapiro-Wilks test (Shapiro and Wilk, 1965; Zar, 1996). Because I expected larger males to take over the nests of smaller males and all males to take over nests with more sneakers, these tests were directional with  $\gamma = 0.1$  and  $\delta = 0.4$  and  $\alpha = 0.05$  (Rice and Gaines, 1994). Finally, the number of sneakers present at the nest on the day before and after the takeover were compared by using a sign rank test (because the data could not be normalized using any of the standard transformations) to determine any effect of a change in male identity on mating success (as measured by the number of sneakers present at the nest). By using logistic regression and forward model selection (Tabachnik and Fidell, 2001), I examined the effect of the maximum number of sneakers present during the cycle, local density of nests during the spawning phase of the nest cycle, number of unsuccessful neighbors during the spawning phase of the cycle, size of the original male, male identity, day in the season, and length of the nest cycle on the probability of a successful takeover occurring.

### Calculating uncertainty in success within the nest cycle

Because of the skewed distribution of mating success observed in this species (Alonzo and Warner, 2000a), males tend to fall into two main categories: Males at nests with no sneakers and low to no mating success (unsuccessful males) and males at nests with sneakers and higher mating success (successful males). I determined the number of between-day transitions from being successful or unsuccessful (as determined by the presence or absence of sneakers) within the spawning phase of a single nest cycle. By using the survey data, I determined the number of the four possible between-day transitions in success. Whenever multiple transitions were observed for a nest, one transition was chosen at random to create a set of independent observations. I then examined whether some transitions were significantly more probable than others by using a two-by-two  $\chi^2$  test for independence on this subsample (Siegel and Castellan 1988). I also examined the effect of day in the cycle on these transition probabilities by calculating the daily probability of each transition for the first 5 days of spawning and testing for an effect of day in the nest cycle. By using a randomization test (1000 iterations; Good, 2000), I calculated the 95% lower and upper confidence limits for the prediction that the frequency of each of the four transitions is



**Figure 1**

The frequency of nests within the study site varies during the reproductive season. The number of nests defended by marked males and the frequency of territorial takeovers are also shown. Territorial takeovers are more frequent later in the season.

independent of day in the nest cycle. I also examined the predictions that the conditional transition probabilities (e.g., unsuccessful tomorrow given successful today) and the frequency of successful and unsuccessful nests were independent of day in the nest cycle by using similar randomization tests.

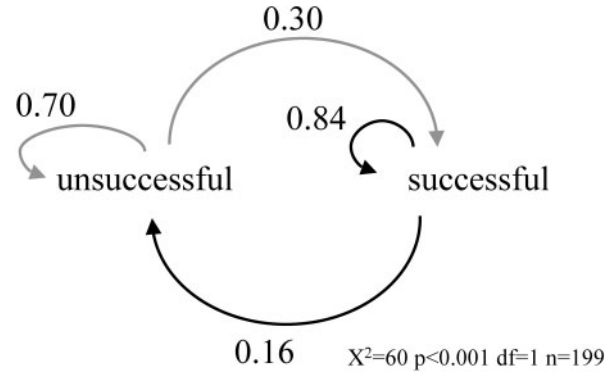
### Removal experiment

Although past research indicated that male identity does not explain any of the skew in mating success, I conducted one experiment to control for the effect of male identity on expected success following a takeover. In 1997, I experimentally removed eight males from successful nests and compared the success of the original and replacement male. Before removals, I observed these nests for 10 min and determined the average number of sneakers at the nest (as defined above), the number of females visiting (within 10 cm of the nest), and the total number of spawns. After the first observation, the nesting male was caught by using a small aquarium net and held in a live bait bucket. I observed the nest a second time 30 min after the original male's removal. I compared each of the observation variables by using a paired  $t$  test because the differences did not deviate significantly from Normal according to a Shapiro-Wilks test (Shapiro and Wilk, 1965; Zar, 1996). All tests were two-tailed. The minimum detectable difference of the  $t$  test was also calculated for each variable (with  $\alpha = 0.05$  and  $1 - \beta = 0.90$ ; Zar, 1996) to examine the ability of the small sample to detect any differences in number of spawns, number of female visits, and the number of sneakers present at the nest.

## RESULTS

### Takeovers of nest sites

A total of 128 males were marked before the reproductive season, and 59 of those males were seen defending a territory



**Figure 2**

Uncertainty in success: The conditional probability of a change in success state is represented as transition probabilities between “unsuccessful” and “successful” states. Being successful is an absorbing state where most individuals will stay successful once they achieve success.

within the research area. On average 62% (SE  $\pm$  0.023) of males defending nests on any day within the study area were marked. Two hundred forty-nine nests were observed throughout the 2-month period (Figure 1). In this time, I observed 31 successful takeovers at 30 nests: eight takeovers in which an unmarked male was taken over by a marked male, six when a marked male was replaced by an unmarked male, and 17 transitions between marked males. In 14 of the 25 cases in which a marked male took over a new nest, the same male had been observed at a different nest at the study site on the previous day. Of these 14 males taking over nests, 12 out of 14 of them were originally at nests with zero sneakers present, and the remaining two were at nests with one sneaker present. The number of sneakers at the nest taken over was significantly higher than at the deserted nest (deserted nest: 0.148 SE  $\pm$  0.10; nest taken over: 4.43 SE  $\pm$  0.89; Shapiro-Wilks:  $W_{13} = 0.93$ ,  $p = .27$ ; paired  $t$  test:  $t_{13} = 4.77$ ,  $N = 14$ ,  $p < .001$ ), which implies the usurping male gained by taking over the site. Similarly, the number of sneakers at the nest taken over on the day before the takeover (with the original male) was significantly higher than at the usurping male's original nest on the same day (deserted nest: 0.148 SE  $\pm$  0.10; nest taken over: 5.30  $\pm$  SE 1.33; Shapiro-Wilks:  $W_{13} = 0.92$ ,  $p = .20$ ; paired  $t$  test:  $t_{13} = 3.78$ ,  $N = 14$ ,  $p = .001$ ). Males that successfully usurped another male were significantly larger than was the original male (original male: 75 mm  $\pm$  SE 0.92; male taking over: 77.7 mm  $\pm$  SE 0.71; Shapiro-Wilks:  $W_{17} = 0.97$ ,  $p = .67$ ; paired  $t$  test:  $t_{17} = 2.00$ ,  $N = 17$ ,  $p = .03$ ). The probability of a takeover occurring was increased by day in the season, length of the nest cycle, and the maximum number of sneakers found at the nest (best-fit model predicting the probability of a takeover:  $N = 204$  nests; maximum number of sneakers:  $\beta = 0.086$ ,  $\chi^2 = 2.10$ ,  $p = .148$ ; day in the season (that nest building began):  $\beta = 0.087$ ,  $\chi^2 = 9.32$ ,  $p = .002$ ; length of the nest cycle:  $\beta = 0.157$ ,  $\chi^2 = 7.73$ ,  $p = .005$ ; intercept =  $-3241$ ,  $\chi^2 = 9.34$ ,  $p = .002$ ). Local density, number of successful neighbors during the spawning period, and original male size or identity did not explain any variation in the probability of a nest takeover. Nests that experienced takeovers had longer spawning phases overall (without takeovers, 4.44  $\pm$  0.21 days; with takeovers, 5.72  $\pm$  0.53; two sample  $t$  test:  $t = -3.19$ ,  $N = 246$ ,  $p > .0016$ ) but did not have longer spawning phases than other successful nests (i.e., nests that attracted sneakers) that did not experience a takeover (without takeovers, 5.70  $\pm$  0.22; with takeover, 5.71  $\pm$  0.53; two sample  $t$  test:  $t = -1.27$ ,  $N = 178$ ,  $p = .20$ ).

**Table 1**  
**Estimates of transition probabilities by the number of days spawning or courting during the nest cycle**

Day	Successful to successful	Successful to unsuccessful	Unsuccessful to successful	Unsuccessful to unsuccessful
1	<u>0.33</u> 66 (88, 107)	0.09 17 (16, 27)	<b>0.20</b> 39 (23, 38)	<b>0.39</b> 78 (44, 61)
2	0.45 77 (74, 90)	0.09 16 (13, 24)	<b>0.18</b> 31 (18, 24)	0.27 46 (36, 52)
3	0.53 68 (54, 71)	0.10 13 (9, 18)	0.15 19 (12, 24)	0.22 29 (28, 41)
4	<b>0.60</b> 58 (39, 54)	0.10 10 (6, 15)	<u>0.07</u> 7 (9, 19)	0.23 22 (20, 33)
5	<b>0.60</b> 34 (21, 32)	0.18 10 (3, 10)	0.11 6 (4, 12)	<u>0.12</u> 7 (10, 21)

Only the first 5 days of spawning are considered because less than 20% of nests spawned for more than 5 days, making the sample sizes too low for statistical inference. The observed proportion of nests and frequency of transitions are given with the lower and upper confidence limits given in parentheses.

Transitions that are significantly less frequent than expected by chance are underlined, and those that are more frequent than expected by chance are in bold.

### Transition probabilities

I counted the total number of daily transitions between success states (determined by the absence or presence of sneakers) during the spawning phase of the nest cycle for all nests. In the randomly selected subsample, 199 independent nest transitions were observed. To determine the uncertainty involved, I calculated the following conditional probabilities: given that a nest was unsuccessful on day 1, the probability it was also unsuccessful on day 2 was 65/93. The probability of going from unsuccessful to successful across days was 28/93. When successful, the probability of remaining successful was 89/106. The probability of a transition from being successful to unsuccessful was 17/106. These transition probabilities give the uncertainty for a male associated with each state (Figure 2). Future success was not independent of present success state (Figure 2). Transition probabilities between present success states varied across the nest cycle (Table 1). There was a statistically significant increase over the nest cycle in the frequency of successful to successful transitions compared with the other three possible transitions (Table 1 and Figure 3). However, this increase in frequency was driven mainly by an increase in the frequency of successful nests later in the nest cycle (because males desert unsuccessful nests) rather than an increase in the conditional probability of remaining successful once already successful (Table 1 and Figure 3).

### Removal experiment

In every case, a new male took over the nest within 10 min of a nest owner's removal. This new male actively courted and spawned with females. I found no significant differences in the number of spawns, the number of female visits, or the number of sneakers present at the nest between the first and second observation even though the identity of the nesting male changed between these two observations (Table 2). Despite a small sample size, it would have been possible to detect small differences in the number of female visits and the number of sneakers present at the nest (Table 2). By contrast, the minimum detectable difference in mating success was 10 spawns per 10 min. However, successful nests experience similar levels of variation in mating success even without a change in male identity (Alonzo and Warner 1999). Consistent with the nest survey results, marked males who took over nests were usually (four out of six cases) males that had nests near the experimental nest. These males also tended to be unsuccessful (i.e., no sneakers observed in five out of six cases).

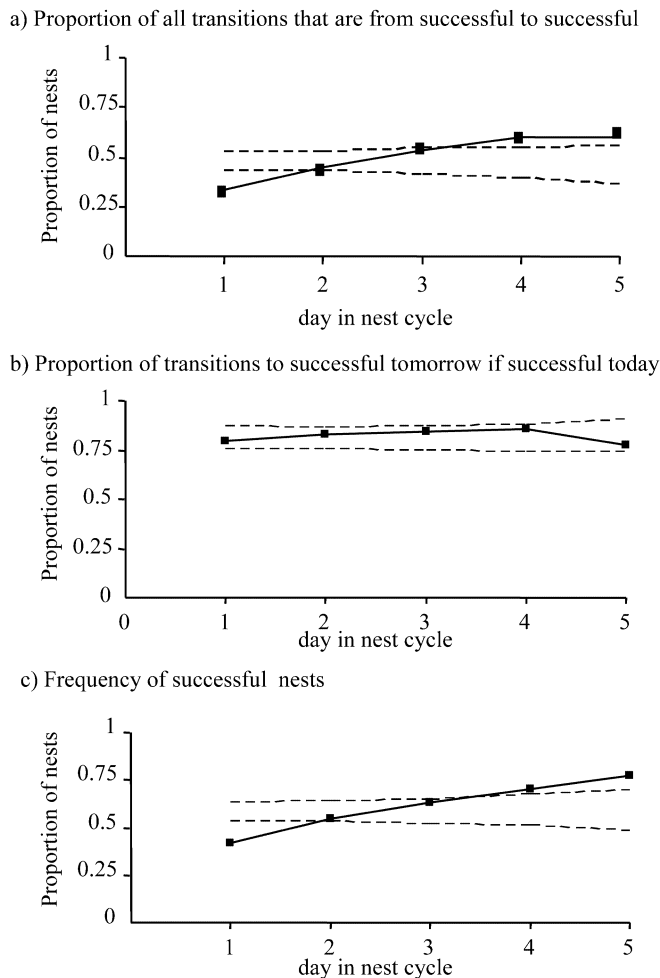
### DISCUSSION

Nest takeovers are a regular occurrence in *S. ocellatus* (at least 12% of all nests and a 40% chance per nesting male because males defend about four nests per season). Usurping males moved from nests without sneakers to those with sneakers and therefore probably improved their success. Unsuccessful males usually took over their successful neighbor's nests, and the males that managed to take over nests were larger than the original male. This pattern indicates that, although size is not a very good predictor of overall male mating success in this species (Wernerus et al., 1989), relative RHP may play a role in takeover ability. Males may be opportunists, taking over nearby nests that are successful if their successful neighbor is smaller.

Furthermore, the unpredictability of mating success at a site before the establishment of territories followed by a relatively high certainty of success within a nest cycle (Figure 2) can explain the occurrence of takeovers in this species. This pattern, however, depends on the fact that female behavior is not affected by the identity of the male on the nest. Thus, the relative certainty of success within the nest cycle and uncertainty between nest cycles is a direct result of females choosing nests for parental care certainty rather than individual male or nest characteristics.

The probability of a successful takeover also increased with time in the season and the length of the nest cycle. A few possible explanations exist for a temporal increase in the frequency of takeovers. First, the direct costs or benefits of a takeover may change over the season. For example, the probability of a successful takeover or the skew in mating success could increase during the season. Second, age data from otoliths indicated that all nesting males were 2 years old, and that 3-year-old males were not found in this population (Alonzo et al. 2000). Males may attempt takeovers with a greater probability late in the season as their opportunities for future success decrease. The increased probability of a takeover with longer nest cycles could occur even if all nests are exposed to the same daily risk of takeover. Because males desert unsuccessful nests it is more probable, however, that longer nest cycles are associated with takeovers simply because successful nests are not deserted.

Past research indicates that female behavior drives the skew in mating success, and females are in conflict with nesting males over parental care (Alonzo and Warner, 2000a). Females and sneakers, and sneakers and nesting males are also in conflict because both females and nesting males attempt to avoid spawning with or at the same time as sneaker males (Alonzo and

**Figure 3**

Patterns of success across the spawning phase of the nest cycle. Black squares represent the proportion of all possible transitions that are from being successful to successful per day in the nest cycle (as indicated by the presence of sneakers at the nest) (a), the proportion of successful nests that remain successful per day in the nest cycle (b), and the frequency of successful nests across the nest cycle (c). Dashed lines represent the lower and upper 95% confidence limits based on the randomization tests described in the text. Black squares that are higher or lower than the confidence limits indicate an effect of day in the nest cycle on the observed pattern. The difference in transition frequencies in panel a are driven by the change in the frequency of successful nests in panel c over the nest cycle rather than a change in the conditional probabilities in panel b.

Warner, 1999, 2000b; van den Berghe et al., 1989). The results presented here indicate that nesting males will also be in conflict with other nesting males, owing to competition for successful nest sites after the establishment of territories.

**Table 2****Nest takeovers do not change nest success**

Variable	Before	After	$t_7$ statistic	$p$	Minimum detectable difference
Sneakers at the nest	9.00 ± 2.82	8.95 ± 3.04	0.50	.78	0.66
Female visits	22.00 ± 3.85	22.63 ± 3.96	-0.42	.69	5.67
Total spawns	6.13 ± 5.22	8.13 ± 8.51	-0.73	.49	10.38

Mean ± SD is given before and after the takeover. Results of the paired  $t$  tests and minimum detectable differences for  $\alpha = 0.05$  and  $1 - \beta = 0.90$  are also given.  $N = 8$  in all cases.

In the current study, I used the presence of sneakers at a nest as a proxy for the expected mating success of nesting males. A positive relationship between the number of sneakers at the nest and pair spawning exists and the number of sneakers at the nest is more repeatable than any direct measure of spawning for short observations. It is also possible that conspecifics may use sneakers as an indicator of nest success. Sneakers can be easily observed from meters away, whereas spawning females can only be seen when very close to a nest. Nesting males could use the presence of sneakers as a cue of a neighbor's success without risking aggression or leaving one's current nest. If sneakers are the cue used to indicate success to neighboring males, the presence of sneakers at the nest may carry the additional cost of allowing successful males to be easily targeted for territorial takeovers.

In this species, it is the pattern of female choice that allows nesting males to take over successful nests and have those nests remain successful. If females preferred physical characteristics of the male instead of transitory mating situations, takeovers would not be beneficial. Therefore, the territorial behavior of males is indirectly influenced by female choice. In this species, female choice generates uncertainty in mating success early in the nest cycle and certainty in success later in the nest cycle. Furthermore, female choice is a direct result of conflict between females and nesting males over nest desertion. Subsequently, understanding patterns of male territorial behavior requires an understanding of interactions within and between the sexes and how they influence the predictability of territory quality.

Variability and uncertainty in territory quality will exist in many species, and patterns of uncertainty should influence territorial behavior. For example, in another Mediterranean wrasse (*S. tinca*) the benefits of parental care (and thus territory defense) vary over the reproductive season (Luttbeg and Warner, 1999; Warner et al., 1995). Therefore, the perceived quality of a territory will vary through time for males and females. In this species, large "pirate" males occasionally take over successful territories (van den Berghe, 1988), and the frequency of males defending territories varies over the season with territory quality (Luttbeg and Warner, 1999; Warner et al., 1995). In the pied flycatcher, females have incomplete information about the presence of other females on the territory, and whether females join and defend territories should depend on their certainty of success at that territory (Alatola and Lundberg, 1984). In yellow-headed blackbirds, reproduction must occur while the abundance of food resources important to offspring growth and survival are still uncertain (Orians and Wittenberger, 1991). Thus, we would not expect takeovers to occur in this species. Food resources are similarly unpredictable in some great tit populations (Nager et al., 2000), and male competition among sites may be independent of the quality of a territory for raising offspring because of this uncertainty. Territory quality is the outcome of a variety of social interactions and variable environmental conditions. As a result, the benefits of

territory defense will often vary, and this variation may or may not be predictable. Understanding patterns of territorial defense will require that we consider both how territory quality varies as well as whether the quality of a site is predictable.

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