The unexpected but understandable dynamics of mating, paternity and paternal care in the ocellated wrasse

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Although theory generally predicts that males should reduce paternal care in response to cues that predict increased sperm competition and decreased paternity, empirical patterns are equivocal. Some studies have found the predicted decrease in male care with increased sperm competition, while even more studies report no effect of paternity or sperm competition on male care. Here, we report the first example, to our knowledge, of paternal care increasing with the risk and intensity of sperm competition, in the ocellated wrasse (*Symphodus ocellatus*). Theory also predicts that if paternal care varies and is important to female fitness, female choice among males and male indicators traits of expected paternal care should evolve. Despite a non-random distribution of mating success among nests, we found no evidence for female choice among parental males. Finally, we document the highest published levels of extra-pair paternity for a species with exclusive and obligate male care: genetic paternity analyses revealed cuckoldry at 100 per cent of nests and 28 per cent of all offspring were not sired by the male caring for them. While not predicted by any existing theory, these unexpected reproductive patterns become understandable if we consider how male and female mating and parental care interact simultaneously in this and probably many other species.

Keywords: parental care; sexual selection; mate choice; sperm competition; paternity

1. INTRODUCTION

The advent of molecular techniques brought a revolution to our understanding of animal mating systems by demonstrating the widespread existence of multiple male paternity (proportion of offspring sired per male) and female promiscuity even in supposedly monogamous species with biparental care (Gowaty *et al.* 1989; Westneat & Sherman 1997). Males are generally predicted to respond to decreased paternity by decreasing their parental effort, as long as cues of decreased paternity exist and males can expect higher paternity in future reproductive bouts (Westneat & Sherman 1993; Hunt & Simmons 2002; Sheldon 2002; Wolff & Macdonald 2004; Houston *et al.* 2005; Seki *et al.* 2007; Kokko & Jennions 2008; but see Woodroffe & Vincent 1994). Theory also predicts that if females exhibit adaptive mate choice, they will choose among males based on characteristics of the male or reproductive site that predict the direct or indirect benefits of mating, which in the case of paternal care are traits that predict male parental effort or quality (Shuster & Wade 2003; Andersson & Simmons 2006; Kokko & Jennions 2008). It is also generally expected that extra-pair paternity should be low in species with male-only care, since female fitness depends largely on male care (Moller 2000; Moller & Cuervo 2000; Tallamy 2000; Barreto & Avise 2008; but see Härdling & Kaitala 2001). While empirical support exists for these predictions, an equivalent number of studies fail to find the expected patterns (reviewed in Alonzo *in press*).

Here we argue that this disconnect between our expectations and observed patterns exists because these predictions are based on an inherent but underappreciated contradiction: when predicting how female choice for male care will evolve, we have assumed that females can respond to *a priori* indicator traits that predict male parental effort or quality. Yet we also predict that male parental effort will change in response to female mating behaviour and individual patterns of paternity. In reality, female mating behaviour both influences and is influenced by male parental investment and patterns of paternity. Therefore, understanding male and female patterns of mating and parental care requires considering the dynamic interplay between these traits and their simultaneous effects on observed patterns.

Here, we report unexpected patterns of paternal care, paternity and female mate choice in a species with obligate and exclusive male care. A key role of theory is to explain and predict observed patterns. While our results would not have been predicted *a priori* by the existing theory, the patterns reported here are understandable if we consider how female mating behaviour and male parental investment interact. Hence, they illustrate both the limitations of our general understanding and the need to consider the complex interactions that arise when males and females interact with respect to mating and parental investment if we wish to understand the diversity of reproductive patterns observed in nature.

In the ocellated wrasse (*Symphodus ocellatus*, a Mediterranean fish in the family Labridae), large colourful nesting males actively court females, defend territories and provide obligate care by defending and aerating the

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fertilized eggs as they develop (Lejeune 1985). Breeding is seasonal and parental males go through multiple nest cycles where they build a nest, spawn for a few days and care for offspring for 3–5 days before the eggs hatch and disperse as pelagic larvae. Males then typically move to a nearby site, build a new nest and start another nest cycle (Taborsky *et al.* 1987). While most nesting males provide parental care, about one-third of males desert their young before hatching and these eggs are eaten almost immediately by conspecific and other egg predators (Taborsky *et al.* 1987). Females produce a new batch of eggs every few days and visit multiple nests before typically selecting one nest site for spawning (Taborsky *et al.* 1987). Females do not defend nests or care for the offspring (Taborsky *et al.* 1987). Smaller ‘sneaker’ males join a nesting male and female during a spawning and release large quantities of viable sperm but do not provide any parental care (Alonzo & Warner 2000a). These males are morphologically and behaviourally distinguishable from both nesting males and females (Taborsky *et al.* 1987). The risk and intensity of sperm competition are high in this species, and both are positively correlated with the presence of sneakers at the nest (Parker 1998; Alonzo & Warner 2000a). Sneaker males thus provide an obvious cue to parental males of increased sperm competition (Alonzo & Warner 2000a). The distribution of sneakers is skewed among nests and varies for individual nesting males both within and between nest cycles (Alonzo & Warner 2000b). Hence, parental males at a nest with many sneakers in the current nest cycle have a high probability of having fewer sneakers (and thus possibly higher paternity) in future nest cycles.

Mating success also varies among parental males, and females appear to select among males or nest sites. In this species, male care is essential to female fitness as eggs do not survive without paternal care, and past research has found that females prefer to spawn with nesting males and attempt to avoid sneakers (Alonzo & Warner 2000b). There is no evidence that nests or nest sites differ in quality or explain observed variation in mating success (Wernerus *et al.* 1989). While reducing the number of sneakers at the nest increases the spawning rate at a nest, sneakers are attracted to nests with high mating rates (Alonzo & Warner 2000b). This leads to a positive correlation between female presence and sneaker presence, despite a female preference for fewer sneakers at the nest (Alonzo & Warner 2000b). Studies of female mate choice have also found that females are more likely to mate at nests that have had high recent mating success and are more likely to spawn in the presence of other spawning females (Alonzo 2008). However, past research failed to identify any other behavioural or physical characteristics of the male or nest site that explains the distribution of mating success among nests (Lejeune 1985; Wernerus *et al.* 1989; Alonzo 2004, 2008).

Based on the biology of the species and the general theory described above, one would predict the following patterns: (i) female choice among males is expected to be based on traits of the male or aspects of the nest site that indicate future paternal care and offspring survival; (ii) high nesting male paternity is predicted because this species exhibits exclusive and obligate male care (which is generally disfavoured by low paternity). High paternity is also predicted because paternal care is essential to

female fitness in this species such that evolution is predicted to favour female mating patterns that increase male paternity and thus paternal care; and (iii) male parental care is predicted to decrease in the presence of high sperm competition from sneaker males as a result of low expected paternity by parental males. Below we report the results of our study with respect to these predicted patterns and discuss their general implications for our understanding of the interaction between sexual selection and paternal care.

2. MATERIAL AND METHODS

(a) *Study site and species*

The field research reported here was conducted from the University of Liège (Belgium) Marine Laboratory (La Station de Recherches Sous-Marine et Océanographique, STARESO), in the Baie de Revellata near Calvi, Corsica during the breeding season (May–June) in four different years in which we were able to conduct fieldwork at this site (1996, 1997, 2000 and 2005). All observations were made using SCUBA along 200 m of shore in water of less than 15 m depth.

As earlier studies failed to find any physical or behavioural traits that could explain nesting male mating success, we used detailed behavioural observations to estimate daily parental male mating success over their lifetime to determine whether male identity (and thus something about the male) could explain among-male variation in nesting male mating success. We then used genetic paternity analyses and behavioural observations to examine nesting male paternity and the effect of sperm competition from sneakers on nesting male paternity and paternal care.

(b) *Field observations*

For 3 years (1996, 1997, 2000), all of the nests within the study area were observed on a daily basis throughout the entire two-month reproductive season. In 2005, all nests within the study area were observed daily for three weeks at the beginning of the breeding season. A total of 310 parental males were caught, individually marked using a vital stain (alcian blue) and (in 2005 only) fin clipped at the beginning of the mating season (85 in 1996, 128 in 1997, 59 in 2000 and 38 in 2005). In all years, we recorded the spawning and parental care behaviour of the nesting male, the number of sneakers at the nest and the presence of females at all nests daily at over 700 different nests (187 nests in 1996, 247 in 1997, 261 in 2000 and 32 in 2005). Methods for these behavioural observations and details of the study area are given elsewhere (Alonzo & Warner 2000b; Alonzo 2004). These daily observations allow us to estimate the complete history of mating success of individual nesting males because these males defend nests within only a single reproductive season (Alonzo *et al.* 2000). In 1996, we also took detailed behavioural data during 10 min observations at 67 randomly selected nests to determine whether there was any evidence of a skewed distribution of mating success among nesting males.

To estimate nesting male paternity, in 2005, we made daily 10 min observations at nests with individually marked (and genotyped) males and collected 11 nests at the end of the spawning phase of the nest cycle for which the same nesting male had been observed to be present at the nest throughout the entire nest cycle, and for which we also had

Table 1. Variation in the six microsatellite DNA loci used for the paternity analyses. (Shown for each locus are the total number of individuals genotyped (including larvae), number of unique alleles, expected heterozygosity (H_E), observed heterozygosity (H_O), polymorphic information content (PIC) and the mean non-exclusion probability for the first parent. The microsatellite loci were originally described in Arigoni & Largiader (2000). Combined non-exclusion probability (first parent): 0.0025.)

locus	number of individuals	number of alleles	H_E	H_O	PIC	non-exclusion probability
Soc 1017 PBBE	953	30	0.897	0.933	0.928	0.241
Soc 1109 PBBE	950	24	0.821	0.844	0.830	0.459
Soc 1198 PBBE	952	17	0.783	0.760	0.732	0.617
Soc 1063 PBBE	954	17	0.822	0.817	0.793	0.532
Soc 3121 PBBE	951	36	0.921	0.921	0.915	0.277
Soc 3200 PBBE	954	38	0.914	0.928	0.923	0.250

daily observations in which we recorded the number of sneakers present at the nest (to determine the expected risk and intensity of sperm competition). Nests were then maintained in aerated sea water in the laboratory until all larvae emerged. For this species, it is not possible to collect or count the eggs in a nest without either destroying the nest or waiting for the larvae to emerge. We quantified the number of larvae emerging from nests on a daily basis (5 days per nest for a total of 55 measures) by catching the larvae as they hatch synchronously at night (Lejeune & Michel 1986) and counting them under a dissecting microscope. For nests with more than 60 larvae emerging on any single day, we genotyped a subset of the larvae emerging on that day. Otherwise all emerging larvae were genotyped. Overall, we genotyped between 64 and 201 larvae per nest. We therefore have paternity and larval data that allow us to estimate daily paternity (for up to 5 days per nest), the number of larvae sired per day, and larvae sired over the nest cycle for each nesting male. An additional 54 fish were caught and fin-clipped for genotyping to determine the microsatellite allele frequencies in the population for use in the paternity analyses (16 females, 15 sneaker males and 23 nesting males).

(c) Paternity analyses

Parental assignment and reconstruction analyses were performed for each offspring using six polymorphic microsatellite loci (Soc1017PBBE, Soc1198PBBE, Soc3200PBBE, Soc1063PBBE, Soc1109PBBE and Soc3121PBBE; Arigoni & Largiader 2000). First, DNA was isolated from paternal candidate adult males, reared larvae and representative adults in the population using DNAeasy Blood and Tissue and QIAamp DNA Micro Kit protocols (Qiagen, Valencia, CA, USA). Microsatellite loci were amplified individually with the following thermocycler programme: 2 min at 94°C; 30 cycles of 25 s at 94°C, 25 s at 56°C, and 25 s 72°C, using fluorescently labelled forward primers. PCR products were run following standard protocol for the ABI 3720 capillary genetic analyser. Genotypes were obtained from 10 nesting males, 954 larvae and the 54 additional randomly sampled reproductively mature adults from the population. The six loci combined provided an exclusion probability of 0.9975 (see table 1 for details). Nesting males were excluded as parents if there was a mismatch at one or more loci (i.e. the nesting male was assigned paternity to a larva if at least one of the two alleles at each loci matched with the nesting male's). This provided an estimate of the number and proportion of larvae that were sired by the territorial male. For comparison, we also examined two alternative methods

of paternity assignment. First, we also analysed the data by allowing one mismatched allele between the male and larvae collected from the defended nest. Second, exclusion was confirmed with paternity allocation software PASOS (Duchesne *et al.* 2005), a likelihood-based method for assigning parentage in open systems with incomplete sampling. All genotyped larvae from all nests, and all female and all male parental candidates were included in a single analysis. A correctness rate was calculated with simulation within the program. The results reported are for strict exclusion (zero mismatches) because the paternity assignment method had no effect on the qualitative patterns and had only a small effect on the quantitative patterns.

(d) Statistical analyses

Statistical analyses were calculated manually or performed in SAS (v. 9.1). Using a chi-squared goodness-of-fit test, the distribution of mating success among nesting males was compared with the expected Poisson distribution under random mating with the same average mating rate as observed in the data. Because the presence of sneakers was a strong predictor of nesting male siring success (reported here) as well as total mating success at the nest (Alonzo 2004), we used daily sneaker presence at the nest to examine whether male identity (determined by the presence of the male's individual mark given at the beginning of the breeding season) was a significant predictor of mating success in a general linear model. Male standard length, nest location and date were also examined as potential predictor variables, but were found to have no effect on mating success.

To examine daily patterns, we used general linear mixed models with nest as a random effect to determine the relationship between daily parental male siring success or paternity (criterion variables) and the presence of sneakers at the nest (from the daily surveys of the nest), and the number of larvae emerging from the nest on a given day (predictor variables, Sokal & Rohlf 1995). Because we estimate nesting male siring success from the number of larvae and paternity, these three variables were not used within any single analysis. General linear models are commonly used to estimate the functional relationship between variables and identify statistically significant predictor variables (Sokal & Rohlf 1995). Here, we use these general linear mixed models to determine which variables are reliable predictors (and potential cues of) of among-day variation in male paternity and siring success.

Paternity and number of larvae emerging were associated with the behaviour variables from 5 days prior because past

research (Lejeune & Michel 1986) and time to emergence in this study found that larvae only start to emerge 5 days following spawning at the colder water temperatures observed during our research. Developing eggs were kept in tanks supplied with constantly flowing sea water pumped in from the research site (and thus at the same water temperature as nests in natural conditions), and the water temperature was checked on a daily basis both in the tanks and underwater while on SCUBA to verify that consistent water temperatures were maintained. One could also determine from our data how many days it was before the last larvae emerged from the time the nest was removed from the study site (making further spawning impossible) and this was typically 5 days for actively spawning nests.

To examine variation among nests within the nest cycle, we used partial correlation coefficient analyses to disentangle the relationships between nesting male paternity, maximum sneaker presence and total number of larvae emerging from the nest. We also used among-nest measures in a path analysis to determine how the maximum sneaker presence and total number of larvae emerging from the nest interact to determine nesting male paternity in that nest cycle.

A logistic regression was used to detect an effect of the presence of sneakers at the nest during the spawning phase of the nest cycles on the probability that the parental male would desert the nest without providing care. The analyses were done using both the maximum and average number of sneakers observed at a nest over the entire spawning phase of the nest cycle. Males were categorized as providing care (if they were observed fanning and not spawning) or deserting (if they were never observed fanning) following the spawning phase of the nest cycle. It is not possible to include the number of eggs in the nest in this analysis because eggs do not survive nesting male desertion and egg number cannot be sampled without destroying the nest.

3. RESULTS

(a) *Female mate choice*

Ten minute observations of the mating rate at 67 randomly selected nests found a significantly skewed and non-random distribution of mating success among nests (χ^2 -test: $\chi^2_{1,66} = 597$, $p < 0.0001$), with most males achieving very low mating success and a few males experiencing high mating success. From our daily field observations over 3 years, we observed a total of 70 individually marked males during multiple nest cycles (at a total of 189 different nests, range 2–5 per male). Nesting male identity did not explain any significant portion of the striking variation among nesting males in mating success (general linear model: $F_{69,119} = 1.10$, $n = 189$, $p = 0.32$; *a posteriori* test in SAS: effect size $\delta^2 = 2.8$, with 95% CI: -5.9 to 11.5 , s.e.m. = 4.43). Hence, a mating skew exists among males at short time scales, but disappears between nest cycles.

(b) *Paternity and paternal care*

Extra-pair paternity (i.e. paternity of males other than the parental male) was found in 100 per cent of nests and 94 per cent of all days in the nest cycle. While variation in paternity existed (figure 1a), on average 28 per cent of all larvae genotyped were not sired by the parental male (265 out of 954). Surprisingly, among-day variation in extra-pair paternity was not significantly predicted by

Figure 1. Male siring success is positively correlated with the presence of sneaker males. (a) The paternity (proportion of offspring sired) of the parental male was uncorrelated with the presence of sneakers at the nest (general linear mixed model among days: $F_{1,36} = 2.46$, $p = 0.13$, $n = 39$). (b) The estimated number of offspring sired per day by the parental male was positively associated with the presence of sneakers at the nest (general linear mixed model among days: $F_{1,36} = 13.70$, $p = 0.0007$, $n = 39$). Filled circles represent daily measures of paternity, siring success and sneaker presence (across all nests). Paternity could only be calculated for days on which larvae emerged from the nest, giving 36 daily paternity measures across 10 nests. Solid lines represent the predicted relationship from the general linear mixed model based on among-day comparisons (a) intercept: 0.67 , $t_{21} = 7.05$, $p < 0.0001$, slope = 0.02 , $t_{21} = 1.57$, $p = 0.13$; (b) intercept: 88.6 , $t_{21} = 0.85$, $p < 0.40$, slope = 78.0 , $t_{21} = 3.70$, $p = 0.0007$). Among nest analyses give similar patterns.

the presence of sneakers around the nest (controlling for the effect of nest, figure 1a). Instead, an increase in the number of sneakers present at the nest was associated with a significant increase in the number of offspring sired on that day by the parental male (figure 1b). This arises despite the fact that the number of sneakers present at a nest is strongly correlated with the short-term risk and intensity of sperm competition within an observation (Alonzo & Warner 2000a). In a few cases, we observed extra-pair paternity at a nest despite having observed no sneakers present at the nest (in the daily observation of the nest, figure 1). Sneaker males, not resident at the nest, are still nearly always found in the general area, and thus this extra-pair paternity is probably the result of opportunistic spawning by sneaker males resident at nearby nests. Here, variation in parental male siring success is best predicted by variation in the number of offspring emerging from the nest on the same day (general linear mixed model, $F_{1,53} = 2126$, $p < 0.0001$, $n = 55$).

Figure 2. Disentangling the interactions between mating success, sperm competition and nesting male reproductive success. The results of the two path analyses are presented here. We examined the effect of sneaker presence and the number of offspring in the nest on (a) nesting male paternity and (b) nesting male siring success, given the non-independence of sneaker presence and number of larvae in the nest. Path coefficients are given by the directional arrows and the correlation between predictor variables is given by the double headed arrows.

Table 2. The relationships between sneaker presence (S), offspring number (O) and paternity (P) and the results of significance tests to determine whether the partial correlations were significantly different from zero.

interaction	correlation	partial correlation	t-test, p-value
sneakers and offspring	$r_{SO} = 0.80$	$r_{SO\ P} = 0.80^{**}$	$t_9 = 3.5$, $p < 0.007$
sneakers and paternity	$r_{SP} = 0.31$	$r_{SP\ O} = 0.29$	$t_9 = 0.80$, $p = 0.44$
offspring and paternity	$r_{OP} = 0.18$	$r_{OP\ S} = -0.13$	$t_9 = -0.33$, $p = 0.75$

$^{**}, p < 0.01$.

Owing to interactions among these variables, it is also useful to examine partial correlations between paternity, total number of larvae emerging from the nest, and the presence of sneakers at the nest over the nest cycle. In contrast to the analyses presented above, the analyses reported next are based on a single measure for each nest in order to examine among-nest variation in these variables. We found that, when we control for variation in paternity, the number of sneakers present at the nest and the number of larvae emerging from the nest were significantly and positively correlated (table 2). However, sneaker presence and paternity were not significantly related to one another and, if anything, exhibited a positive correlation when we control for variation in the number of larvae (table 2). Path analysis allows us to ask how variation in the number of offspring emerging from the nest and the presence of sneaker males affect either nesting male paternity or siring success, while acknowledging the correlation between sneaker and offspring number. These analyses found that the presence of sneakers is positively associated with nesting male paternity while having a small but negative effect on nesting male siring success overall (figure 2).

Finally, we asked whether male parental effort increased with certainty of paternity as predicted. We

Figure 3. The probability of male care increases with the presence of sneakers at the nest. Contrary to theoretical predictions and previous empirical studies, male care increases as a function of the presence of sneakers at the nest. The maximum sneaker presence is presented here. The average number of sneakers at the nest yields similar results. The solid line gives the predicted relationship between sneakers and the probability of male care (logistic regression; $\beta = 0.38$, $\chi^2 = 170.3$, $p < 0.001$, intercept = -1.36 , $\chi^2 = 82$, $p < 0.001$), bars give the observed proportion of males caring for the nest and the numbers above the bars are the sample sizes (number of nests observed per sneaker number).

observed 639 nests on a daily basis throughout the entire cycle for which we were able to determine the presence of sneakers at the nest during spawning and whether or not the nesting male provided parental care after the spawning phase of the nest cycle. In contrast to general expectations, males were more likely to provide care at nests where sneakers have been present and sperm competition has been high (figure 3).

4. DISCUSSION

While extensive research has focused on the predicted and observed relationship between paternity and paternal care, few studies have considered how interactions within and between the sexes simultaneously affect male and female mating behaviour, male parental care and extra-pair paternity. Here we show that males were more likely to provide parental care when the risk and intensity of sperm competition had been high (figure 3). To our knowledge, this is the first example of male care increasing with increased sperm competition. While not predicted by existing theory, this pattern can be explained by the fact that individuals which provide care have higher total reproductive success because variation in total mating success, rather than paternity, drives the striking variation in parental male success (figure 1).

(a) Understanding patterns of female mate choice

Although mating success is non-randomly distributed among nests at any point in time (as reported above), the observed mating skew among nesting males did not persist over time. In the ocellated wrasse, nesting male mating success is driven by female mate choice for nest sites with high recent mating rates (Alonzo 2008), rather than male identity (as reported here) or associated

traits such as colour pattern, defence of the nest or courtship rate (Wernerus *et al.* 1989; Alonzo 2004). In addition, there is no evidence that characteristics of the nest or nest site explain any of the variation in mating success (Wernerus *et al.* 1989), and a previously unsuccessful nesting male can be made successful experimentally without any change to the nest or nest site (Alonzo 2008). While females exhibit a preference for successful males (as has been found in some other species; Westneat *et al.* 2000), here (unlike in these other species) this preference occurs in the absence of any evidence of females choosing first based on indicator traits of the male or his nest site. While females could be choosing among nests based on some other aspect of the male or nest site, it would have to be something completely undetectable that changes rapidly (within a few hours) to explain the observed distribution of mating success. Males were also just as likely to go from unsuccessful to successful between nest cycles as the reverse, which implies decreasing male condition over the season cannot explain the observed pattern. Thus, the most parsimonious explanation is that females prefer to mate with males at successful nests because nesting males with high siring success are more likely to provide care (Alonzo 2008) and do not choose among nests based on any other traits or aspects of the nest site. In this species, the best indicator of male care is the recent mating success of the parental male, indicated possibly by the presence of other females, new eggs and sneakers. Past research has shown the first female to spawn in a nest will initiate spawning (in a previously unsuccessful nest) when joined by another spawning female (Alonzo 2008). For females choosing among nests, the past and present mating behaviour of other females might be the most reliable indicator of paternal care in this species.

(b) Explaining patterns of paternity and paternal care

In the ocellated wrasse, 100 per cent of nesting males experienced extra-pair paternity and cared for many offspring not their own, without any help from females or other males. This is in sharp contrast to the general prediction that species with male-only care should exhibit high paternity and that low paternity is only expected in species where male care is not very important for offspring survival (Moller 2000; Moller & Cuervo 2000; Tallamy 2000; Sheldon 2002; Houston *et al.* 2005; Seki *et al.* 2007, but see Härdling & Kaitala 2001; García-González *et al.* 2003; Thomas & Manica 2005). While many species in the genus exhibit male care, facultative care is ancestral, and parental care has been lost entirely in a closely related species (Hanel *et al.* 2002). It is therefore unlikely that evolutionary constraints alone explain the persistence of male-only care in this species. High levels of extra-pair paternity have also been reported for others in species with exclusive male care (approx. 10–20% of offspring, e.g. Jones *et al.* 2001; Mackiewicz *et al.* 2005; Gomendio *et al.* 2008; Neff & Clare 2008; Rios-Cardenas & Webster 2008; but see Barreto & Avise 2008). The levels of extra-pair paternity we report here are comparable to estimates of extra-pair paternity in many birds with biparental care (Westneat & Sherman 1997), but fall below the highest estimates of extra-pair paternity, which have

been found in species of birds with female parental care and care from helpers at the nest (Mulder *et al.* 1994; Hughes *et al.* 2003). Clearly, however, the general argument that low paternity inherently disfavours paternal care does not apply broadly across species.

We also found that nesting males that had experienced higher sperm competition had higher total siring success (table 1) because these nests had more total larvae emerging from them than nests with few sneakers. This surprising pattern explains the otherwise counterintuitive observation that male parental effort actually increases with sneaker presence and risk of sperm competition. Previous research has shown that females prefer nests with high mating success because nesting males at these sites are more likely to provide parental care (Alonzo 2008). However, sneaker males are also attracted to nests with high mating success because of their greater mating opportunities, even though females attempt to avoid spawning with sneakers (Alonzo & Warner 2000b). As a result, females, sneakers and non-parental males all have higher expected reproductive success at nests with high mating success despite sperm competition.

In the ocellated wrasse, nesting male paternity is probably higher than sneaker male paternity (given that sneakers are much more common than nesting males but do not sire most of the offspring). In a recent paper, Kvarnemo (2006) presented a heuristic model that illustrates the important idea that paternal care may be favoured if males have higher paternity when they provide care. However, this model cannot explain patterns of paternal care in our study species because, although egg survival is functionally zero without care, nesting males desert their nests relatively frequently (figure 3). Instead, one needs to consider the effect of current care on both current and future expected mating success to understand the patterns reported here. Further theory examining the connection between male and female mating behaviour and parental investment is needed.

(c) The dynamics of mating and paternal care

While we can explain these unexpected patterns based on our current knowledge of this species, it is important to note that these patterns would not have been predicted *a priori* based on our current general understanding of female choice for direct benefits and male paternal investment in response to paternity. Instead, understanding these patterns requires the consideration of multiple interactions that arise simultaneously during mating and parental care not captured by the existing theory (figure 2).

The typical pattern considered by theory is that males or territories vary in intrinsic quality, such that males compete for high quality territories and females choose among males based on male or territory quality because their offspring have higher expected fitness when sired and/or raised by these males on good territories. However, in this species, all the evidence suggests that variation in nesting male or nest quality does not explain female choice, mating success or paternal care. Therefore, it is unpredictable *a priori* which nest site and which nesting male will be successful. This alters the dynamics of mate choice and male competition in many ways. For

example, nesting males cannot compete for the best sites ahead of time (Alonzo 2004), and both females and sneakers must base their choice among nests on the behaviour of other individuals in order to ensure their offspring survive. These dynamics also lead to positive feedback loops with respect to both mating success and sperm competition. For comparison, consider the situation where nests vary in some static quality but the presence of sneakers decreases the attractiveness of nests to females. Then, females and sneakers would be predicted to exhibit something like an ideal free distribution among nests, where the static benefits of the nest quality trade-off with the presence of sneakers (which decrease both female fitness and the mating success of other sneakers). By contrast, if the quality of a nest depends on paternal care, which is an increasing function of mating success, then as more females are attracted to the nest the nest becomes more attractive and more successful. High mating success then attracts sneakers to the nest and together these dynamics lead to the strikingly skewed distribution of both mating success and sperm competition among nests. Hence, in this species, and we argue probably in others, the social (or behavioural) interactions within and between the sexes determine patterns of mating and care, as well as selection on traits related to mate choice and male competition, in ways that cannot be predicted or understood by a more traditional and static view of the interactions between mating and parental care. While the mating system of this species may not be typical, these kinds of interactions within and between the sexes exist in many, if not most, species (Alonzo *in press*). We argue that a more dynamic view of the interactions within and between the sexes with respect to mating and care is needed if we wish to more fully explain and predict observed patterns.

This research adhered to the Association for the Study of Animal Behaviour/Animal Behaviour Society Guidelines, the legal requirements of France and the US, all institutional requirements, and was approved by the Animal Care and Use Committee of the University of California Santa Cruz and Yale University.

We thank Joanne Klein, Pierre Lejeune, Tom Near and Lisa Wooninck for assistance and logistical support. We also thank Associate Editor Leigh Simmons and two anonymous reviewers for their comments and suggestions. This research was supported by a grant from the National Science Foundation (IOB-0450807 to S.H.A.) and Yale University.

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