Behavioral Ecology

The official journal of the
ISBE
International Society for Behavioral Ecology

Behavioral Ecology (2020), 31(2), 432–439. doi:10.1093/beheco/arz206

Original Article

Defense against outside competition is linked to cooperation in male–male partnerships

Jennifer K. Hellmann,[a] Kelly A. Stiver,[b] Susan Marsh-Rollo,[c,d] and Suzanne H. Alonzo[d]
[a]Department of Evolution, Ecology, and Behavior, School of Integrative Biology, University of Illinois at Urbana-Champaign, 505 S Goodwin Ave, Urbana, IL 61801, USA, [b]Psychology Department, Southern Connecticut State University, 501 Crescent St, New Haven, CT 06515, USA, [c]Department of Psychology, Neuroscience and Behaviour, McMaster University, 1280 Main St W, Hamilton, ON L8S 4K1, Canada, and [d]Department of Ecology and Evolutionary Biology, University of California Santa Cruz, 130 McAllister Way, Santa Cruz, CA 95060, USA

Received 22 March 2019; revised 11 October 2019; editorial decision 11 November 2019; accepted 26 November 2019; Advance Access publication 14 December 2019.

Male–male competition is a well-known driver of reproductive success and sexually selected traits in many species. However, in some species, males work together to court females or defend territories against male competitors. Dominant (nesting) males sire most offspring, but subordinate (satellite) males are better able to obtain fertilizations relative to unpartnered males. Because satellites only gain reproductive success by sneaking, there has been much interest in identifying the mechanisms enforcing satellite cooperation (defense) and reducing satellite sneaking. One such potential mechanism is outside competition: unpartnered satellites can destabilize established male partnerships and may force partnered satellites to restrain from cheating to prevent the dominant male from replacing them with an unpartnered satellite. Here, we manipulated perceived competition in the Mediterranean fish *Symphodus ocellatus* by presenting an "intruding" satellite male to established nesting and satellite male pairs. Focal satellite aggression to the intruder was higher when focal satellites were less cooperative, suggesting that satellites increase aggression to outside competitors when their social position is less stable. In contrast, nesting male aggression to the intruder satellite increased as spawning activity increased, suggesting that nesting males increase their defense toward outside competitors when their current relationship is productive. We found no evidence of altered spawning activity or nesting/satellite male interactions before and after the presentation. These results collectively suggest that response to outside competition is directly linked to behavioral dynamics between unrelated male partners and may be linked to conflict and cooperation in ways that are similar to group-living species.

Lay Summary: Response to outside competitors is directly linked to spawning success and cooperation in established male reproductive coalitions. In a Mediterranean wrasse *Symphodus ocellatus*, we presented male partnerships with an unfamiliar competitor to induce perceived opportunities for partner choice. Dominants at successfully spawning nests and subordinates in less cooperative partnerships were more aggressive to intruders. These results demonstrate that the existing quality of current partnerships influences response to outside competition, but that this response is status-dependent.

Key words: **alternative reproductive tactics, biological market theory, cooperation, outside options, satellite male, sneak**

INTRODUCTION

In many sexually reproducing species, traits such as male weaponry, elaborate courtship displays, and large body size have evolved in response to male–male competition (Andersson 1994). Despite this driving role of male intrasexual competition in sexual selection, an increasing number of studies are finding that male–male cooperation is also important in determining male reproductive success (reviewed by Taborsky 1994; Díaz-Muñoz et al. 2014).

In a range of taxonomic groups, males work together to initially attract or retain access to mates, as is the case with coordinated courtship displays in birds (McDonald and Potts 1994; Krakauer 2005) and cooperative coalitions in both mammals (Packer et al. 1991; Connor et al. 1992; Noë 1992) and fishes (Taborsky 1994; Oliveira et al. 2002; Stiver and Alonzo 2013). Typically, these coalitions consist of a dominant male who obtains most or all of the fertilizations with females and a satellite or subordinate male that helps the dominant male defend reproductive territories or females from other males (Díaz-Muñoz et al. 2014). In some cases, such as male coalitions in dolphins (Krützen et al. 2003) and coordinated displays in turkeys (Krakauer

---

Address correspondence to J.K. Hellmann. E-mail: hellmann@illinois.edu.

2005), these cooperating males are related and indirect fitness benefits may explain the subordinate's apparent loss of direct fitness gains. However, in other birds (McDonald and Potts 1994; DuVal 2007), mammals (Packer and Pusey 1982; Langergraber et al. 2007), and fishes (Stiver and Alonzo 2013; Stiver et al. 2013), cooperating males are often unrelated. In these cases, subordinate males can benefit from increased access to extra-pair fertilizations (Stiver and Alonzo 2013) or delayed benefits of dominance ascension and territory inheritance (McDonald and Potts 1994; Ortega and Arita Héctor 2002; DuVal 2007). The existence of immediate and long-term direct fitness benefits of these associations suggest that male–male cooperation among non-kin is an underappreciated mechanism driving intrasexual selection in many species (Díaz-Muñoz et al. 2014).

Although the benefits gained from male–male cooperation are increasingly understood, much less is known about the factors that enforce cooperation and reduce cheating in systems where competition among non-kin is the norm. Systems in which there are short-term interactions between unrelated partners, with no delayed benefits of dominance ascension and territory inheritance, can offer important insights into the factors promoting cooperation because the fitness gains of the partnership (current reproductive success) can be measured directly. Theory predicts that in these partnerships competition for social positions should be an important mechanism regulating cooperation because partners are not bound by kinship and are relatively easy to replace (Cant and Johnstone 2009). Specifically, when there are more satellite/subordinate males than possible partnerships with nesting/dominant males, nesting males may be able to credibly threaten to end the partnership if satellites do not sufficiently cooperate (because nesting males can easily replace a noncooperative satellite with a more cooperative satellite). Therefore, this outside competition may favor satellites being more cooperative and cheating less than they would in the absence of this outside competition from other satellite males (Noë and Hammerstein 1994, 1995). This outside competition has been shown to govern how individuals shift between cooperative and competitive behaviors in group-living organisms (Bruintjes and Taborsky 2008; Hellmann et al. 2015; Grinsted and Field 2017; Hellmann and Hamilton 2019) and heterospecific interactions (Noë and Hammerstein 1994; Bshary and Noë 2003; Hammerstein and Noë 2016).

Given the role of outside competition in enforcing cooperation in conspecific groups and heterospecific interactions, we seek to understand the extent to which outside competition favors cooperation in male coalitions. To do this, we manipulated perceived competition in the ocellated wrasse (*Symphodus ocellatus*), a Mediterranean fish with three male alternative reproductive types/phenotypes. During the breeding season, large and colorful territorial males go through multiple 10-day nest cycles during which they build nests, spawn with females for 3–5 days, and care for the resulting eggs (Taborsky et al. 1987). During the spawning phase, the risk of sperm competition and extra-pair paternity is high (Alonzo and Warner 2000; Alonzo and Heckman 2010), as sneaker and satellite males are present at the nest in addition to females (Figure 1). Sneaker males do not court females, but parasitically spawn in nests of nesting males; satellite males aid in defense against sneakers and other satellite males, but will also sneak spawns at the nest (Taborsky et al. 1987). The reproductive strategies that males adopt throughout their lifetime depend on prereproductive growth rate: males transition between their first and second reproductive seasons from a sneaker to a satellite male, from a satellite to a nesting male, or from a nonreproductive male to a nesting male (Alonzo et al. 2000).

This cooperative relationship appears to have a fitness benefit for both nesting and satellite males: the satellite male reduces sneaker male spawning for the nesting male (Stiver and Alonzo 2013) and satellite males are permitted to be in closer proximity to the nest than sneaker males (Taborsky et al. 1987), which likely improves their reproductive success. However, this relationship is also risky because nesting males may lose paternity to the satellite male and the satellite male expends energy and risks injury while defending another male's nest against reproductive competitors (Stiver and Alonzo 2013). Natural satellite takeovers have been observed relatively frequently in the wild (personal observation, all authors), suggesting that there is competition for satellite positions. Given that nesting and satellite male partnerships have clearly defined fitness benefits (reproductive success over one spawning cycle), this system

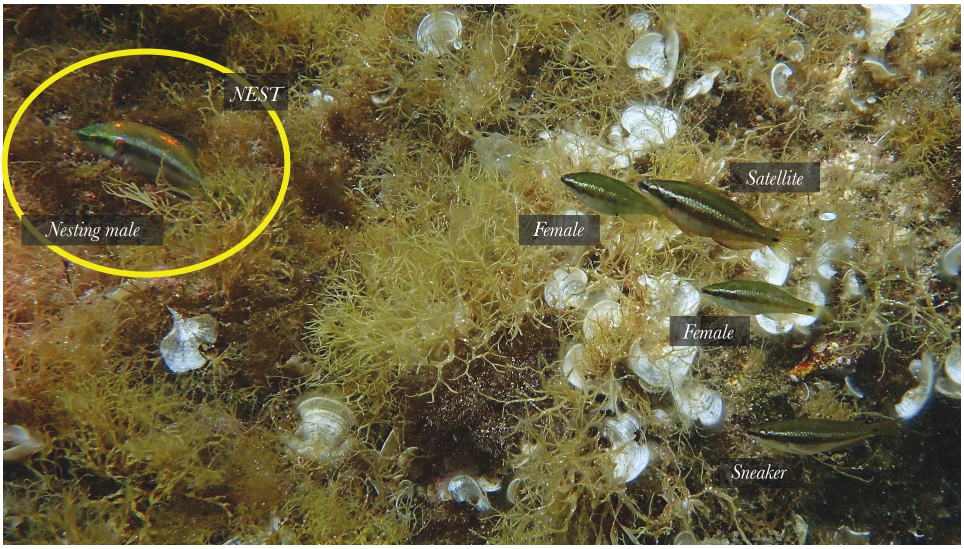

Figure 1
Three male morphs and females of *Symphodus ocellatus*. The nesting male provides parental care (nest building and defense, egg fanning), courts females, chases sneakers, and tolerates satellite presence but not spawning. Satellites are allowed in closer proximity to the nest compared to sneakers, and will court females, defend the nest against sneakers, and attempt to sneak-spawn. Note that this nesting-male has an orange elastomer mark visible below his dorsal fin.

offers an excellent opportunity to gain insights into what factors influence the balance between cooperative and competitive behaviors.

In order to understand how outside competition influences cooperative dynamics between the nesting and satellite male, we presented nests with an intruder satellite male (an unfamiliar satellite caught from a different nest) or a sham control. We observed nesting male and focal satellite aggression to the intruder satellite, as well as observed nest dynamics before, during, and after the presentation to assess changes in nesting and satellite male behavior or reproduction. We predicted that nesting males and satellite males at productive nests (i.e., nests with high spawning activity) would be more aggressive to the intruder satellite, because both partners gain relatively high fitness benefits from maintaining their current relationship (Ortega and Arita Héctor 2002). For nesting males, we also predicted that aggression to the intruder would be highest when the focal satellite is cooperative, because highly cooperative satellites seem to reduce extra-pair fertilizations and increase nesting male reproductive success and may therefore be more valued by the nesting male (Stiver and Alonzo 2013). Finally, we predicted that focal satellite males would be more cooperative (more aggressive to sneaker males, less sneaking) after the presentation of an intruder satellite relative to before the presentation, because the introduction of outside competition should enforce cooperation and reduce cheating (Noë and Hammerstein 1994, 1995; Bshary and Noë 2003).

Collectively, this experiment should elucidate the extent to which response to outside competition is dependent upon reproductive success and conflict with current partners and the ways in which outside competition may disrupt behavioral dynamics between partners. If outside competition alters the relative balance of cooperative (e.g., defense) and competitive (e.g., sneaking) behaviors in male coalitions, it likely alters the strength of sexual selection in these systems by influencing the degree of reproductive skew and variance in male reproductive success.

METHODS

Experimental methods

Between May and June 2017, we sampled 37 *S. ocellatus* nests found near the University of Liege Marine Station (STARESO) in the Baie de Revellata near Calvi, Corsica, France (42.5806° N, 8.7243° E) using SCUBA (depths ranging from 3 to 11 m). We selected nests for inclusion in the study based on the following criteria that we assessed during a brief survey: nests must be in the spawning phase of the nest cycle (defined by witnessing the nesting male actively court and spawn with females: Taborsky et al. 1987), have a clear satellite male present, have at least two sneakers present at the nest, and have at least one female present at the nest. Satellite males are distinguished from sneaker males based on physical appearance (intermediate in coloration and size between nesting and sneaker males: Warner and Lejeune 1985, Taborsky et al. 1987; Figure 1) as well as behavior: satellites are aggressive toward sneakers, attempt to court females, and are permitted in closer proximity to the nest than sneaker males. For comparison, mean nesting male standard length (length from tip of nose to caudal peduncle) in this study was 73.8 mm ± 0.4 SE standard length, mean focal satellite length was 59.4mm ± 1.1 SE standard length, and mean sneaker length from all sneakers caught during the same field season was 45.8 mm ± 0.5 SE standard length. Once the nest was located, we conducted a 10-min observation in which we recorded reproductive behavior at the nest, including the number of females that visited the nest, spawning activity, the number of sneaker males at the nest (recorded every 60 s), and sneaking behavior by satellite and sneaker males. We also recorded the social interactions among males at the nest, including aggression between nesting, satellite, and sneaker males and submission from the satellite male to the nesting male. For a more detailed description of *S. ocellatus* reproductive and social dynamics, see Stiver and Alonzo (2013).

Within 2 min of the end of the initial 10-min observation period, experimental nests were either presented with an intruder satellite male (*n* = 20 nests) or sham manipulation (*n* = 17 nests). For the intruder satellite presentation, we used two large hand-nets to gently catch a large satellite male (mean 58.5 mm ± 0.6 SE standard length) from a different nest at the same field site immediately prior to the initial observation period. We released him into a clear Plexiglas presentation tube (20.33 cm diameter, 45.72 cm high) with a clear bottom and mesh netting at the top of the tube. The tube was placed away from the presentation nest in an open area and left uncovered to minimize stress of the intruder satellite male during the initial observation period. After the initial observation period, the presentation tube containing the intruder satellite was placed level with the nest in the water column, approximately 30–40 cm away from the nest. Manipulation for the sham control was identical to the experimental presentation, except without a satellite male in the presentation tube. We did not conduct a third control, in which we introduced a different stimuli fish into the tube (e.g., female, sneaker, heterospecific); while nesting and satellite males freely swim in the tubes and engage with outside fish, other fish (who spend more time hidden near rocks or seagrass during the breeding season) become stressed and are unresponsive. Experimental nests were haphazardly assigned to treatment groups based on availability of intruder satellite males, which was assessed prior to selecting nests for observation. All intruder satellites were caught at least 10 m from the focal nest, to prevent disturbance to the focal nest due to the removal of a satellite from a nearby nest or any disturbance caused by catching fish.

We recorded dynamics at the nest during the intruder satellite presentation or sham presentation for 10 min, including nesting and satellite male aggression toward the intruder male. Intruder satellite males were free swimming in the tube and engaged aggressively with the focal nesting and satellite males. We then moved the presentation tube at least 3 m away from the nest (no focal fish interacted with the tube in the postobservation period) and immediately conducted a third 10-min observation to observe if any changes in nest dynamics due to the satellite presentation persisted when the intruder satellite was no longer present. After the third observation, we caught the nesting male and satellite male from the focal nest and we brought them to the surface, at a slow pace to minimize potential discomfort from distention of the swim bladder. The fish were then weighed, measured, and individually marked with visible implant elastomer (Northwest Marine Technology, Inc., Shaw Island, Washington). These marks allowed us to ensure that we only included focal nests for which neither the nesting male nor the satellite male had been previously used in the study. Intruder satellite males were selected from other nests at the field site: they were satellite males who were either previously observed as a focal satellite or they were unmarked satellite males from nests that had not yet been observed. If we used an unmarked male for the intruder satellite, we also brought him to the surface to weigh and measure him, as well as mark him to ensure that he was only used as an intruder satellite once. We were unable to catch two focal satellites at control nests as well as two nesting males at an experimental and control nest; consequently, those observations were not included in any analysis below that included fixed effects of length.

Statistical analysis

To test our initial predictions, we used principal components analysis (R package factoextra) to obtain separate measures of spawning success (nest productivity) and cooperative/competitive dynamics between the nesting male and satellite. To get a measure of nest productivity, we combined three measures of spawning success (total number of female spawns, proportion of females visiting the nest that spawned, and number of spawns between just the nesting male and female (i.e., spawns without sneaks by the satellite or sneaker males)). We extracted one principal component (eigenvalue 2.43, behaviors scaled and centered) that explained 81.1% of the variation in these three parameters (Figure 2). Positive values indicate nests with high spawning activity (total spawns: 38.3% contribution, total pair spawns: 38.4%) and a high proportion of females visiting that spawned (23.3%). To get a measure of cooperative/competitive dynamics, we ran a separate PCA using four behaviors: aggression from the nesting male to the focal satellite, submission from the focal satellite to the nesting male, aggression from the focal satellite to sneakers, and total focal satellite sneaks. We then extracted two principal components (Figure 2). The first axis (nesting/satellite male conflict) explained 44.0% of the variation (eigenvalue 1.76) and was characterized by heavy negative loadings of aggression from the nesting male to the focal satellite (45.8% contribution) and submission from the focal satellite to the nesting male (49.7%). Consequently, positive values indicate nests with low conflict (low aggression/submission). The second axis (satellite cooperation) explained 26.9% of the variation (eigenvalue 1.08) and was characterized by heavy negative loadings of aggression from the focal satellite to sneakers (42.7% contribution) and positive loadings of satellite sneaking (52.9%). High values indicate nest with uncooperative satellites (high sneaking behavior, low defense).

We first sought to understand how spawning success (i.e., nest productivity) and cooperative/competitive dynamics between the nesting male and satellite during the initial observation period were associated with nesting male and focal satellite male aggression to the intruder satellite (two separate models, n = 19 nests). We used generalized linear models with negative binomial distribution (to account for overdispersed count data; R package MASS), with fixed effects of spawning success, nesting/satellite male conflict, and satellite cooperation (the three PCs described above). We also included fixed effects of focal satellite length and nesting male length in both models. To reduce overfitting of these models due to the low sample size, we removed nonsignificant fixed effects if they worsened model fit (assessed by the Anova function in R). The full model is reported in Supplementary Table 1. To control for multiple testing, we used a Bonferroni correction and assessed the significance at $\alpha = 0.025$.

Next, we sought to understand if the presentation of the intruder satellite altered nest productivity and cooperative/competitive dynamics between the nesting male and satellite, either during the presentation of the intruder or in the observation period following the removal. We used linear mixed effects models (R package lme4, lmerTest) with the three PC axes as dependent variables. For all three models, we included fixed effects of treatment, observation period, and their interaction to understand if differences in nest dynamics before, during, and after the presentation varied between treatment groups. We also included fixed effects of satellite and nesting male standard length. All three regression models included a random effect of nest identity to control for repeated observations (before, during, and after the presentation) on the same nest. To control for multiple testing, we use a Bonferroni correction and assessed the significance at $\alpha = 0.0167$.

As model fit did not improve when we included a random effect of observer for any of the models above (including the models testing predictors of aggression to the intruder satellite), we removed this random effect to prevent overfitting of the models. For all models, we report R-squared values (delta) as a measure of goodness-of-fit (R package MuMln).

Animal welfare note

All methods, including the use of a elastomer markings, were approved by Institutional Animal Care and Use Committee of University of California Santa Cruz (protocol ID Alons1711) and Southern Connecticut State University (protocol ID S16-02 19) and adhere to the guidelines set forth by the Animal Behaviour Society/Association for the Study of Animal Behaviour. No fish were physically harmed during the course of the experiment and all fish were returned to the field site at the completion of each day's trial.

RESULTS

Are nesting and satellite males from more productive or cooperative nests more aggressive to intruders?

In line with our predictions, we found that nesting male aggression to the intruder satellite was significantly higher at nests with high spawning activity in the period prior to the intruder presentation

Table 1

Nesting male and satellite male aggression toward the intruder satellite

	Nesting male aggression *R^2=0.72*		***Satellite male aggression*** *R^2=0.75*	
	Z_{16}	*P*	Z_{15}	*P*
Spawning behavior	3.98	**<0.001**	---	---
Nesting male/satellite conflict	---	---	---	---
Satellite behaviors	---	---	2.40	**0.02**
Nesting male length	---	---	4.10	**<0.001**
Satellite male length	-3.67	**<0.001**	3.05	**0.002**

Results of generalized linear mixed models testing how nesting male and focal satellite male aggression toward the intruder satellite was predicted by behavioral dynamics at the nest prior the presentation of the intruder satellite (n = 19 nests). Fixed effects tested include spawning behavior (high values denote high spawning), nesting and satellite male conflict (high values denote low satellite submission and low nesting male aggression to satellites), and satellite cooperation (high values indicate high satellite sneaking and low satellite defense) and the standard length of the nesting male and focal satellite male. Significance was assessed at $\alpha = 0.025$. Dashed lines indicate fixed effects that were removed during model selection.

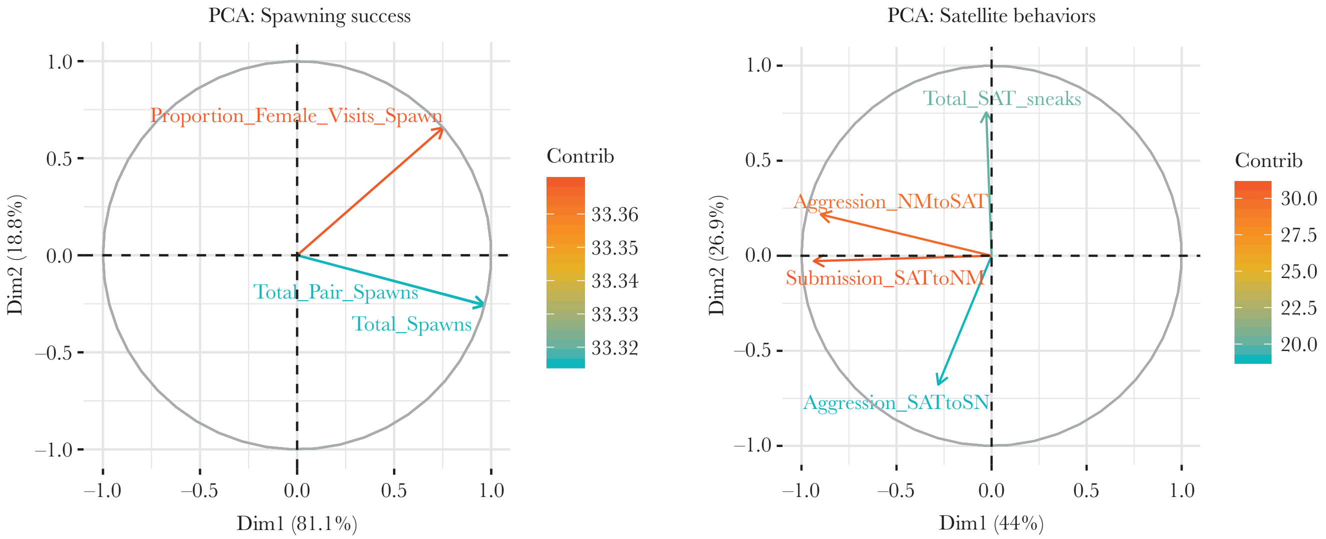

Figure 2

Results of principal components analysis. (A) We combined three measures of spawning success at the nest (total spawns, total pair spawns with no sneaking, and proportion of females visiting the nest that actually spawn) to get one composite measure of nest productivity (high values indicate productive nests). (B) We combined four important satellite behaviors into two axes. PC1 describes nesting/satellite male conflict, with high values indicating low conflict (low aggression from the nesting male to the satellite and low submission from the satellite to the nesting male). PC2 describes satellite cooperation, with high values indicating uncooperative satellites (those that snuck fertilizations frequently and showed little defense against sneaker males). For both graphs, the colors indicate the contribution to the first axis (Dim1) and the percentage on the axes indicates the amount of variation accounted for by each principal component.

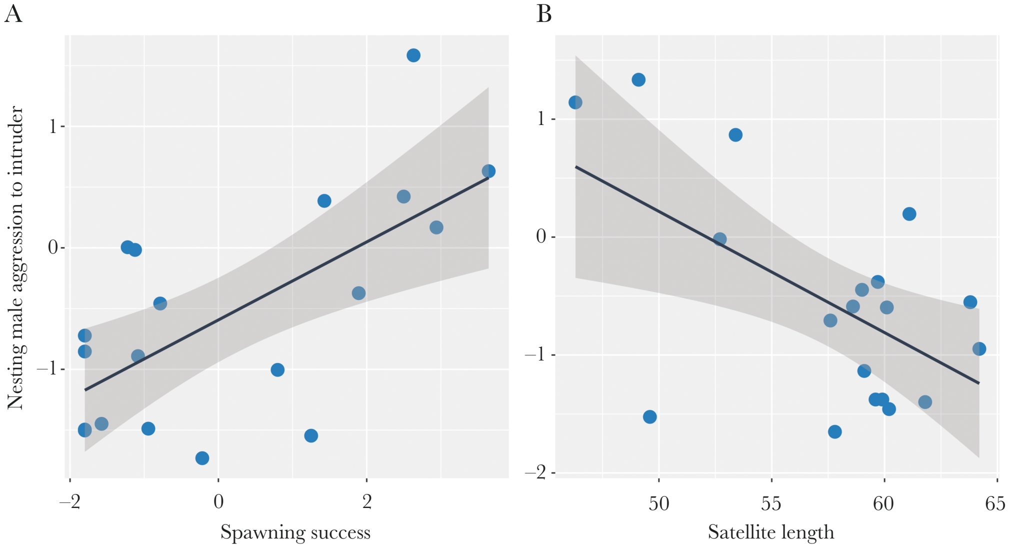

Figure 3

Nesting male aggression to the intruder satellite increased at nests with higher spawning success (A) and at nests with smaller focal satellites (B). Data presented are the residuals of the regression model without the variable of interest, plotted against spawning success and satellite size (respectively). The gray bands around the regression line indicate the standard error of the regression line.

(*n* = 19 nests; Figure 3A; Table 1). However, nesting male aggression to the intruder satellite did not vary with nesting/satellite male conflict or satellite cooperation at the nest in the prepresentation period (Table 1). Focal satellite male aggression to the intruder satellite was not significantly altered by nest productivity or previous levels of nesting/satellite male conflict (Table 1). However, focal satellites were more aggressive to the intruder satellite when they were less cooperative (snuck more, defended less against sneakers: Figure 2B) in the initial observation period (Table 1; Figure 4A).

Nesting males did not adjust their aggression to the intruder satellite based on their own size, but were more aggressive to the intruder satellite when they were paired with a smaller satellite (Table 1; Figure 3B). In contrast, focal satellite males were more aggressive to the intruder satellite when they were larger and when they were paired with a larger nesting male (Table 1; Figure 4B).

We found no significant difference between nesting males and focal satellites in their overall frequency of aggression toward the intruder satellite (Wilcoxon signed rank test: V = 67.5, P = 0.45).

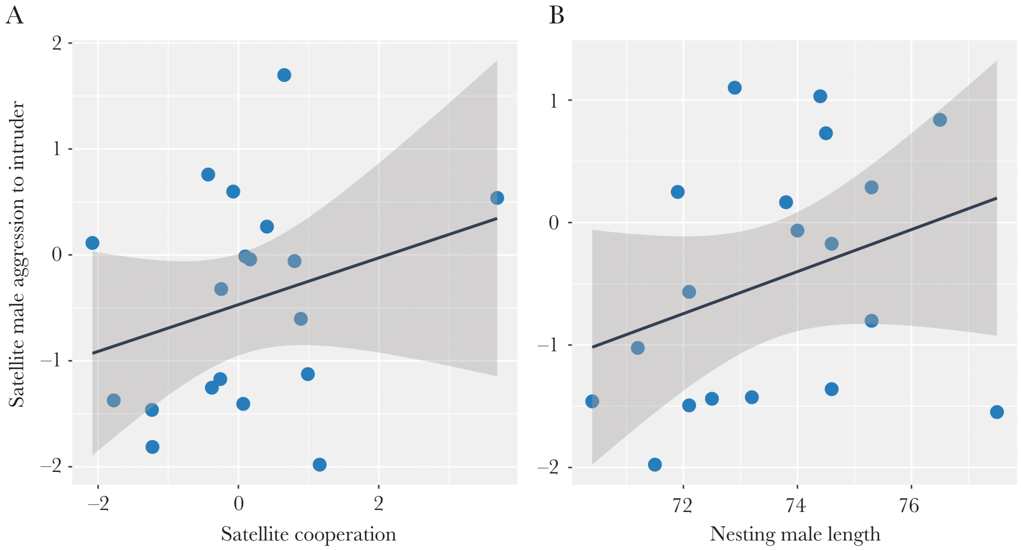

Figure 4

Focal satellite male aggression to the intruder satellite was higher (A) at nests where the satellite was less cooperative (less defense and more sneaking behavior), and (B) for focal satellites paired with larger nesting males. Data presented are the residuals of the regression model without the variable of interest, plotted against satellite cooperation and nesting male size (respectively). The gray bands around the regression line indicate the standard error of the regression line.

Further, aggression to the intruder satellite by the nesting male and focal satellite at a given nest were not significantly correlated (Spearman rank correlation: S = 1285, $P = 0.89$).

Do dynamics at the nest change due to the presence of the intruder satellite?

Next, we sought to understand how interactions between the nesting and focal satellite males in the period before, during, and after the presentation changed due to the presence of the intruder satellite ($n = 33$ nests, $n = 99$ observations). We found no significant main or interactive effects of treatment or observation period on spawning behavior, nesting and focal satellite male conflict, or satellite cooperation, suggesting that our experimental manipulation did not significantly perturb existing dynamics at the nest (Table 2). Nesting male or focal satellite size also did not significantly predict behavioral or reproductive dynamics at nests (nonsignificant effects in all models: Table 2).

DISCUSSION

Competition for social positions and reproductive opportunities has been shown to drive cooperation in a variety of group living species, with individuals who face outside competition for their social position often exhibiting higher levels of within-group cooperation than they would otherwise (Bruintjes and Taborsky 2008; Cant and Johnstone 2009; Hellmann and Hamilton 2014). Consequently, variation in cooperative behavior can only be fully understood by considering how opportunities for switching partners may be linked to cheating and cooperation in established partnerships. Here, we sought to understand how response to an unknown satellite intruder was linked to the social and reproductive behaviors of an already established nesting and satellite male partnership. We found that nesting males were more aggressive to the intruder satellites when there was high spawning activity at the nest, but focal satellites did not significantly alter aggression to the intruder satellites based on spawning activity at the nest. However, focal satellites were more aggressive to the intruder satellite when focal satellites were less cooperative. Further, we found no evidence that the presentation of the intruder satellite altered spawning success or satellite behaviors at the nest, suggesting that, although behavioral dynamics seemed to predict the extent to which the intruder satellite was perceived as a threat, there may be relatively minimal effects in how fluctuations in outside competition alter already established relationships.

As predicted, we found that nesting males in more productive partnerships were more aggressive to the intruder satellite. This is consistent with the idea that the threat of disruptions to the nesting-satellite male relationship might be particularly deleterious at nests with high spawning activity. This may be due to the fact that nesting males suffer more sneaking when the satellite is not present (Stiver and Alonzo 2013), which would have outsized effects on nesting male fitness at nests with high spawning activity. We did not find that satellite males significantly altered aggression to the intruder satellite based on spawning success at the nest. It is perhaps unsurprising that satellite male behavior is less contingent on nest productivity: given that nesting males sire the majority of offspring at any given nest (Alonzo and Heckman 2010), satellite male reproductive success from a given partnership might be less dependent on overall spawning success at the nest and more contingent on other factors, such as sneaking behavior.

We found no evidence that nesting males altered their aggression to the intruder satellite based on the amount of conflict between the nesting/satellite male or focal satellite cooperation, suggesting that nesting males do not adjust their response to outside competition based on the amount of cooperation shown by the focal satellite male. In contrast, focal satellite males did increase their aggression to the intruder satellite when the focal satellite was less cooperative. This suggests that, consistent with our predictions, satellites adjust their defense against outside competitors relative to the stability of their own social position. This is consistent with previous

Table 2

No changes in nesting dynamics due to presentation treatment across observation periods

	Spawning success *Marginal R^2 = 0.07* *Conditional R^2 = 0.39*			***Nesting/satellite conflict*** *Marginal R^2 = 0.03* *Conditional R^2 = 0.44*			***Satellite cooperation*** *Marginal R^2 = 0.07* *Conditional R^2 = 0.42*		
	F	df	*P*	*F*	df	*P*	*F*	df	*P*
Presentation treatment	0.001	1, 29	0.97	0.24	1, 29	0.63	0.00	1, 29	1.00
Observation period	2.48	2, 62	0.09	1.69	2, 62	0.19	0.65	2, 62	0.53
Nesting male length	0.82	1, 29	0.37	0.36	1, 29	0.55	1.03	1, 29	0.32
Focal satellite length	0.30	1, 29	0.59	0.05	1, 29	0.83	1.22	1, 29	0.28
Treatment × observation period	1.11	2, 62	0.34	0.20	2, 62	0.82	1.12	2, 62	0.33

Results of linear mixed effects model examining changes in nesting dynamics (n = 33 nests, n = 99 observations) due to presentation treatment (intruder satellite or sham control) and observation period (before or after the presentation), and their interaction. We also controlled for variation in nesting dynamics due to nesting male and focal satellite standard length. Significance was assessed at $\alpha = 0.0167$.

studies finding that reductions in helping behavior can induce evictions in a number of species (Mulder and Langmore 1993; Fischer et al. 2014; Hellmann et al. 2015). Consequently, satellites in partnerships where they are less cooperative with the nesting male may face a threat of being evicted from their current position and therefore, may increase defense against outside competitors.

Interestingly, nesting male defense against the intruder satellite was higher when they were paired with smaller focal satellites. Given that fighting ability is strongly linked to body size (Arnott and Elwood 2009), it is likely that smaller satellites are less capable of defending against outside satellites and nesting males may have to compensate for this reduced fighting ability in smaller satellites. Indeed, we did find that smaller satellites were less aggressive to the intruder satellite, which is consistent with how many individuals behave when they are in physical contests with larger opponents (Arnott and Elwood 2009).

Although satellites and sneakers are physically and behaviorally distinct from each other, it is possible that focal nesting and satellite males perceived the intruder satellite as another reproductive competitor (similar to how they perceive sneakers) rather than as a threat to the focal satellite's position. However, our data suggest that at least the focal satellites discriminated between sneakers and other satellite males; focal satellite aggression to sneakers in the prepresentation period was not correlated with aggression to the intruder satellite, suggesting that satellites differentially allocate aggression to intruding satellites and sneakers.

Previous work on group-living species has found that outside competition can enforce cooperation of subordinate individuals and regulate conflict between dominant and subordinate individuals (Cant and Johnstone 2009; Hellmann and Hamilton 2014; Hellmann and Hamilton 2018; Hellmann and Hamilton 2019). Here, we demonstrate that outside competition can also interact with behavioral dynamics between unrelated male partners, with focal satellites increasing their aggression to outside competitors when their social position is less stable and nesting males adjusting their aggression to outside competitors based on the productivity of the current relationship. These results demonstrate that variation in cooperation and conflict between unrelated males directly informs how individuals respond to outside competition. While our brief manipulation did not alter spawning success or cooperative dynamics at the nest, it is possible that longer term fluctuations in the broader social context, such as variation in the number of neighboring nests or in the number of available partners, could alter the stability of already established partnerships (Hellmann et al. 2015; Hellmann and Hamilton 2019). Future studies exploring this could provide important insights into whether outside competition can drive plasticity between partners and induce cooperation in the absence of delayed or indirect fitness benefits. Further, assuming these partnerships increase nesting male and satellite male reproductive success, exploring cooperation and reproductive success in the context of partner choice should provide important insight into how traits related to partner choice and partnership maintenance may be sexually selected in this species and other species with reproductive cooperation among unrelated males.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online

FUNDING

This research was funded by a National Science Foundation Grant IOS-1655297 to S.H.A. and K.A.S., the University of California Santa Cruz and a Connecticut State University American Association of University Professors Faculty Development Grant to K.A.S.

CONFLICT OF INTEREST

The authors report no conflicts of interest.

Thank you to Dr. Pierre Lejeune and the entire staff at the Station de Recherches Sous-Marines et Oceanographique (STARESO) for assistance during the field work.

Data accessibility: Analyses reported in this article can be reproduced using the data provided by Hellmann et al. (2019).

Handling editor: Michael Taborsky

REFERENCES

Alonzo SH, Heckman KL. 2010. The unexpected but understandable dynamics of mating, paternity and paternal care in the ocellated wrasse. Proc Biol Sci. 277:115–122.

Alonzo SH, Taborsky M, Wirtz P. 2000. Male alternative reproductive behaviours in a Mediterranean wrasse, *Symphodus ocellatus*: evidence from otoliths for multiple life-history pathways. Evol Ecol Res. 2:997–1007.

Alonzo SH, Warner RR. 2000. Allocation to mate guarding or increased sperm production in a mediterranean wrasse. Am Nat. 156:266–275.

Andersson M. 1994. Sexual selection. New York (NY): Princeton University Press.

Arnott G, Elwood RW. 2009. Assessment of fighting ability in animal contests. Anim Behav. 77:991–1004.

Bruintjes R, Taborsky M. 2008. Helpers in a cooperative breeder pay a high price to stay: effects of demand, helper size and sex. Anim Behav. 75:1843–1850.

Bshary R, Noë R. 2003. Biological markets: the ubiquitous influence of partner choice on the dynamics of cleaner fish – client reef fish interactions. In: Hammerstein P, editor. Genetic and cultural evolution of cooperation. Cambridge: MIT Press.

Cant MA, Johnstone RA. 2009. How threats influence the evolutionary resolution of within-group conflict. Am Nat. 173:759–771.

Connor RC, Smolker RA, Richards AF. 1992. Two levels of alliance formation among male bottlenose dolphins (*Tursiops sp.*). Proc Natl Acad Sci USA 89:987–990.

Díaz-Muñoz SL, DuVal EH, Krakauer AH, Lacey EA. 2014. Cooperating to compete: altruism, sexual selection and causes of male reproductive cooperation. Anim Behav. 88:67–78.

DuVal Emily H. 2007. Adaptive advantages of cooperative courtship for subordinate male lance-tailed manakins. Am Nat. 169:423–432.

Fischer S, Zöttl M, Groenewoud F, Taborsky B. 2014. Group-size-dependent punishment of idle subordinates in a cooperative breeder where helpers pay to stay. Proc Biol Sci. 281:20140184.

Grinsted L, Field J. 2017. Market forces influence helping behaviour in cooperatively breeding paper wasps. Nat Commun. 8:13750.

Hammerstein P, Noë R. 2016. Biological trade and markets. Philos Trans R Soc Lond B Biol Sci. 371:20150101.

Hellmann JK, Hamilton IM. 2014. The presence of neighbors influences defense against predators in a cooperatively breeding cichlid. Behav Ecol. 25:386–391.

Hellmann JK, Hamilton IM. 2018. Dominant and subordinate outside options alter help and eviction in a pay-to-stay negotiation model. Behav Ecol. 29:553–562.

Hellmann JK, Hamilton IM. 2019. Intragroup social dynamics vary with the presence of neighbors in a cooperatively breeding fish. Curr Zool. 65:21–31.

Hellmann JK, Reddon AR, Ligocki IY, O'Connor CM, Garvy KA, Marsh-Rollo SE, Hamilton IM, Balshine S. 2015. Group response to social perturbation: impacts of isotocin and the social landscape. Anim Behav. 105:55–62.

Hellmann JK, Stiver KA, Marsh-Rollo SE, Alonzo SH. 2019. Data from: defense against outside competition is linked to cooperation in male-male partnerships. Dryad Digital Repository. http://dx.doi.org/10.5061/dryad.n8pk0p2r8

Krakauer AH. 2005. Kin selection and cooperative courtship in wild turkeys. Nature. 434:69–72.

Krützen M, Sherwin WB, Connor RC, Barré LM, Van de Casteele T, Mann J, Brooks R. 2003. Contrasting relatedness patterns in bottlenose dolphins (*Tursiops sp.*) with different alliance strategies. Proc Biol Sci. 270:497–502.

Langergraber KE, Mitani JC, Vigilant L. 2007. The limited impact of kinship on cooperation in wild chimpanzees. Proc Natl Acad Sci USA 104:7786–7790.

McDonald DB, Potts WK. 1994. Cooperative display and relatedness among males in a lek-mating bird. Science. 266:1030–1032.

Mulder RA, Langmore NE. 1993. Dominant males punish helpers for temporary defection in superb fairy-wrens. Anim Behav. 45:830–833.

Noë R. 1992. Alliance formation among male baboons: shopping for profitable partners. In: Harcourt AH, Waal FBM, editors. Coalitions and alliances in humans and other animals. Oxford (UK): Oxford University Press. p. 285–321.

Noë R, Hammerstein P. 1994. Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. Behav Ecol Sociobiol. 35:1–11.

Noë R, Hammerstein P. 1995. Biological markets. Trends Ecol Evol. 10:336–339.

Oliveira RF, Carvalho N, Miranda J, Gonçalves Emanuel J, Grober M, Santos Ricardo S. 2002. The relationship between the presence of satellite males and nest-holders' mating success in the Azorean rock-pool blenny *Parablennius sanguinolentus parvicornis*. Ethology. 108:223–235.

Ortega J, Arita Héctor T. 2002. Subordinate males in harem groups of Jamaican fruit-eating bats (*Artibeus jamaicensis*): satellites or sneaks? Ethology. 108:1077–1091.

Packer C, Gilbert DA, Pusey AE, O'Brieni SJ. 1991. A molecular genetic analysis of kinship and cooperation in African lions. Nature. 351:562.

Packer C, Pusey AE. 1982. Cooperation and competition within coalitions of male lions: kin selection or game theory? Nature. 296:740.

Stiver KA, Alonzo SH. 2013. Does the risk of sperm competition help explain cooperation between reproductive competitors? A study in the ocellated wrasse (*Symphodus ocellatus*). Am Nat. 181:357–368.

Stiver KA, Wolff SH, Alonzo SH. 2013. Sharing of potential nest sites by *Etheostoma olmstedi* males suggests mutual tolerance in an alloparental species. PLoS ONE. 8:e56041.

Taborsky M. 1994. Sneakers, satellites, and helpers: parasitic and cooperative behavior in fish reproduction. In: Slater PJB, Rosenblatt JS, Snowdon CT, Milinski M, editors. Advances in the study of behavior. p. 1–100. San Diego: Academic Press.

Taborsky M, Hudde B, Wirtz P. 1987. Reproductive behaviour and ecology of *Symphodus (Crenilabrus) ocellatus*, a European wrasse with four types of male behaviour. Behaviour. 102:82–118.

Warner RR, Lejeune P. 1985. Sex change limited by paternal care: a test using four Mediterranean labrid fishes, genus *Symphodus*. Mar Biol. 87:89–99.