Discrete and continuous reproductive tactics in a hermaphroditic society

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An important step towards understanding conflicts in animal societies lies in identifying socioecological predictors of individual reproductive tactics. In gonochoristic species, individuals can choose to adopt breeding or nonbreeding tactics, and if they breed, how large a share of reproduction they acquire. In hermaphroditic species, individuals can also adopt male or female breeding tactics. Hermaphrodites' wider suite of reproductive options makes them interesting models for investigating predictors of reproductive tactics. We used molecular and ecological data to determine socioecological correlates of discrete (breeding versus nonbreeding; males versus female) and continuous (share of reproduction) reproductive tactics in the hermaphroditic coral-dwelling fish, *Dascyllus aruanus*. The number of potential competitors within groups was positively related to coral size, and the amount of total reproduction over which they competed was associated with the size of the largest individual (i.e. the parental male). Discrete and continuous reproductive tactics were strongly influenced by rank and body size: high-ranking and large individuals were more likely to breed and attain larger reproductive shares and output. High-ranking breeders also obtained a larger reproductive output if they adopted male tactics, whereas low-ranking breeders obtained a larger share if they adopted female tactics, which can explain why these fish show protogynous sex change. Genetic analysis also revealed that subordinates could attain a larger reproductive share than dominants, and that extragroup individuals could contribute to reproduction. Our results shed new light on the causes of variation in reproductive tactics, the payoffs from group membership and the nature conflict in hermaphroditic societies.
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A fundamental challenge in social behaviour research lies in determining the causes of intraspecific variation in the partitioning of reproduction in animal societies (Keller & Reeve 1994; Sherman et al. 1995; Emlen 1997; Clutton-Brock 1998). Or, to put the focus firmly on the individual, the determinants of reproductive tactics that individuals adopt within animal societies. The solution is important, because if we can understand the conditions under which individuals will gain only a small amount of reproduction, then we can understand the conditions under which individuals are likely to forgo their reproduction and engage in alternate activities, such as cooperation, that exemplify complex societies (Jennions & MacDonald 1994; Keller & Reeve 1994; Cockburn 1998; Wong & Balshine 2010).

The majority of research in this area has been conducted on societies of gonochores, animals that exhibit one sex over their lifetime, such as social insects, mammals and birds (e.g. Alexander et al. 1991; Keller & Reeve 1994; Sherman et al. 1995; Bourke 1997;

Emlen 1997; Ratnieks 2001; Kokko & Ekman 2002). In societies of gonochores, total reproduction is split into two separate pools and individuals compete with other members of the same sex for a share of reproduction. Reproductive tactics can vary in a discrete fashion (e.g. breeder versus nonbreeder) or in a continuous fashion, with breeders varying in the proportion of current reproduction they obtain relative to other breeders (Sherman et al. 1995) and some nonbreeders standing to gain more of the future reproduction than others (Kokko & Johnstone 1999; Ragsdale 1999). Natural selection will favour individuals that adopt the tactic that maximizes their own reproductive success, taking into account conflicts with others.

For hermaphrodites, animals that change sex, a large body of theoretical and empirical studies has addressed the evolution of sex allocation strategies, specifically, the conditions determining why sex change occurs, in what direction, and at what time (Ghiselin 1969; Warner 1975, 1988; Charnov 1986; Ross 1990; Muñoz & Warner 2003a; Munday et al. 2006; Kazancioğlu & Alonzo 2010). Even so, there has been relatively little emphasis on understanding individual-level decisions regarding male versus female reproductive tactics in societies of hermaphrodites (but see Sakai et al. 2001), as seen in many species of coral-reef fish (Buston 2004;

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Wong et al. 2005; Munday et al. 2006). In hermaphrodites, the total reproduction is not split into two separate pools. Rather, individuals compete with all other group members for a share of total reproduction. In hermaphroditic societies, the set of reproductive tactics available to individuals is greater than for gonochores: individuals that opt for a breeding tactic can also choose between a male or female tactic. Thus, individuals have more tactics at their disposal with which to maximize their own reproductive success, taking into account the actions of other individuals.

Theory and data suggest that both social and ecological factors can influence the type of reproductive tactics adopted. Traits that are related to competitive ability, such as body size and dominance rank, could determine whether or not individuals breed (Creel et al. 1997; Clutton-Brock et al. 2001; Beekman et al. 2003), whether they function as breeder males or females (Ross 1990; Kuwamura & Nakashima 1998; Sakai et al. 2003), and if they do breed, how much of a share they obtain (Lundy et al. 1998; Haydock & Koenig 2002; Griffin et al. 2003; Bradley et al. 2005). The number of group members could also play an important role in explaining variation in reproductive tactics. For example, the presence of more potential breeders in a group can mean increased competition over reproductive shares, which may result in a decreased per capita share of reproduction compared to small groups (Webster et al. 2004; Boesch et al. 2006). Finally, ecological factors, such as resource limitation at the scale of the group, could also explain variation in reproductive tactics. For example, if there is insufficient food to support multiple reproductive individuals in a group, the most dominant individual may suppress the reproduction of others (Woodroffe & MacDonald 1995; Fitzpatrick et al. 2006; Wong et al. 2008).

The humbug damselfish, *Dascyllus aruanus*, presents an interesting system for investigating the causes of variation in reproductive tactics within societies of hermaphrodites. *Dascyllus aruanus* are found in close association with *Acroporan* or *Pocilloporan* corals (Sale 1972; Holbrook et al. 2000). Within each coral, there is a single group of *D. aruanus* (mean group size <10 individuals; Sale 1972; Forrester 1990; Holbrook et al. 2000). Group members are generally unrelated (Buston et al. 2009), thus relatedness is not likely to be a factor governing reproductive tactics used (i.e. neither kin selection nor inbreeding avoidance will influence reproductive tactics). Within each group, there is a size-based dominance hierarchy (Coates 1980; Forrester 1991). *Dascyllus aruanus* is primarily a protogynous hermaphrodite; histological analyses of gonads have indicated that individuals begin as undifferentiated individuals and then differentiate into immature females. Subsequently, they mature to become either adult females or male-active hermaphrodites. Both females and male-active hermaphrodites can then later change sex to become adult males (Cole 2002; Asoh 2003). The social mating system is highly plastic, and is thought to change from monogamy to harem polygyny to polygynandry with increasing group size (Fricke 1980).

Here, we combine field observations of *D. aruanus* ecology with multilocus microsatellite DNA fingerprinting to address the following three questions. (1) What are the predictors of the number of individuals in a group and the total reproductive output of the group (this defines the number of competitors and the resources over which they compete)? (2) What are the predictors of discrete reproductive tactics (breeder versus nonbreeder tactics and male versus female tactics)? (3) What are the predictors of continuous tactics (reproductive shares and output)? The use of genetic markers to assign parentage to offspring has revolutionized our understanding of mating system variation in various taxa (Birkhead & Møller 1992; Avise et al. 2002; Gardner et al. 2002; Walker et al. 2002). Hence, by using this invaluable tool, we can build on observations of the social mating system (Fricke 1980; Cole 2002; Asoh 2003), accurately quantify the genetic mating system of *D. aruanus*, and unveil the likely causes of variation in reproductive tactics in a hermaphroditic society.

METHODS

The study was conducted at the Northwestern tip of Moorea in Moorea lagoon, French Polynesia (17°32′S, 149°50′W) during July–August 2007 and February 2010. All field data were collected using snorkel or SCUBA.

Socioecological Correlates of Group Size and Reproductive Output

We investigated correlates of group size and reproductive output to examine (1) whether ecological and social factors would predict the number of potential competitors and (2) whether the number of competitors would predict total group reproductive output. In July–August 2007, we investigated the relationship between group size, coral size and body size of the largest group member. A total of 309 groups of *D. aruanus* and their corals were located throughout the study site and mapped using a compass and measuring tape. For each group, we measured the longest length (L), width (W) and height (H) of the coral colony and calculated average diameter $(L + W + H/3)$ (Kuwamura et al. 1993). We also recorded the genus of the coral (*Acropora, Montipora, Pocillopora, Porites*). The number of fish in each group was estimated as the mean of a visual census made by two observers (observers rarely differed in their counts). Although immatures (fish less than 19 mm standard length, SL; Cole 2002) are not direct reproductive competitors, we included them in our counts of group members because they do act as competitors of resources such as food and shelters, which are important for successful reproduction (Coates 1980).

We also conducted a more detailed investigation using 34 groups found in *Pocillopora*. We focused this detailed investigation on groups inhabiting *Pocillopora* because these groups were spatially well defined, enabling us to be certain of group membership. We collected all group members from these groups by spraying a 1:4 clove oil solution (Munday & Wilson 1997) into the coral and using hand nets to herd the fish into a fence net. We then placed the fish into Ziploc bags, brought them to the surface and measured the standard length of each fish to the nearest 0.1 mm using callipers.

Next we investigated the relationship between total reproductive output and group size. In February 2010, we returned to the same study site and located 64 groups of *D. aruanus*. Once again, we restricted our survey to groups inhabiting *Pocillopora*. Each group was surveyed at least once every 3 days to look for signs of spawning and egg clutches. Egg clutches were successfully collected from 13 groups (mean group size ± SE = 9.8 ± 1.65). The presence and location of egg clutches was inferred by parental behaviour of the largest, nest-tending individual (the parental male). When tending eggs, these parental males stayed very close to a specific location in or around the coral colony, vigorously chased other group members and heterospecifics away, fed less and were occasionally observed fanning eggs. Eggs were found deposited on coral branches or on rocks and rubble near the coral. When eggs were found, the coral branch or substrate on which eggs were present was collected, taken to the surface, and preserved in 95% ethanol. Wherever possible, egg clutches were collected during the latter half of egg development to ensure sufficient DNA would be available for later extraction (described below). Egg stage could be inferred from the colour of eggs, which turn from white (first day) to grey (second day) to silver (third day) prior to hatching (Mizushima et al. 2000). After clutches were collected, they were

transported back to the laboratory, where the number of eggs was counted under a dissecting microscope. After the entire clutch had been counted, a 'targeted subsample' (mean ± SE = 172.2 ± 19.5 eggs) was reserved for later genetic analysis (described below), by dividing the egg clutch into quarters and haphazardly sampling individual eggs from within each quarter.

Genetic Analysis of Reproductive Tactics, Shares and Output

To investigate the socioecological correlates of individual reproductive tactics, shares and output, we collected all group members from each of the 13 groups from which egg clutches had been collected (described above). Fish were collected by placing a large, transparent plastic bag over the coral and injecting clove oil into the bag. Anaesthetized fish were caught with hand nets and placed individually in mesh bags. We measured the body size of each fish using callipers while the fish were still inside the bag. We also took a fin clip from each fish and placed the samples into vials containing 95% ethanol for later genetic analysis (described below). All fish recovered from clove oil within 5 min and were safely released back into the coral head. We waited until the fish were fully awake and capable of maintaining their position in the coral head before we left to ensure that none were taken by passing predators. We measured the size of each coral as previously described. Dominance rank of fish was assigned based on an individuals' size relative to other members of the group, with rank N being dominant over rank $N + 1$ (Wong et al. 2007); in fish societies, relative size has always been shown to be the most important indicator of dominant–subordinate relationships (e.g. Buston 2003; Hamilton et al. 2005; Wong et al. 2008; Ang & Manica 2010). All procedures described above were conducted in accordance with Boston University Institutional Animal Care and Use Committee (Protocol number 10-036) and caused minimal distress to the animals.

Genetic Protocol

For each collected egg clutch, a random sample of eggs (mean ± SE = 47.2 ± 2.6 eggs) from the targeted subsample was genotyped. Nine out of the 13 egg clutches were successfully genotyped (Table 1). Four clutches could not be genotyped, possibly because the eggs were too young (PCR was conducted but no amplifications were obtained for the entire clutches). All group members from each of the nine groups were genotyped (Table 1). Group sizes ranged from 6 to 27 individuals (mean ± SE = 10.8 ± 2.2 individuals). Sex (male or female) and status (breeder or nonbreeder) of individuals was directly determined based on the following genetic analysis of parentage. Females and

males were identified among parents using the simple rule, based on previous reports of *D. aruanus* mating behaviour, that a dominant parental male breeds polygynously with multiple females and the dominant parental male is typically the largest individual in the group (Fricke 1977, 1980; Mizushima et al. 2000; Cole 2002).

Genomic DNA was isolated from fin clips using QIAxtractor DX reagent (Qiagen, Germantown, MD, U.S.A.) following the manufacturer's protocol. Forward primers of specific microsatellite loci (Fauvelot et al. 2009) were labelled with ABI fluorescent dyes and 10 loci were successfully amplified into two multiplex PCRs as follows: Multiplex1: NED: Da331/NED, Da589/NED, Da593/PET, Da590/ VIC and Da494/6-FAM; Multiplex2: Da304/NED, Da360/NED, Da523/PET, Da565/VIC and Da542/6-FAM. These 10 loci were chosen as none of them deviated from Hardy–Weinberg analysis in a previous study (Buston et al. 2009). Each multiplex was amplified in a single 10 μl multiplex PCR reaction using the Type-it Microsatellite PCR Kit (Qiagen) according to the manufacturer protocol, and using an annealing temperature of 60 °C. Amplified fragments were sent to DNAVision (Charleroi, Belgium), where they were separated on an ABI 3730XL sequencer, with a GeneScan® LIZ-500 internal size standard (Applied Biosystems, Foster City, CA, U.S.A.). The GeneMapper software (Applied Biosystems) was used to genotype all individuals screened. Finally, GMConvert (Faircloth 2006) was used to convert the GeneMapper table of genotypes into a GENEPOP (Raymond & Rousset 1995) input file.

One locus, Da589, could not be unambiguously scored and was therefore discarded. Among the nine loci left, the number of alleles ranged from seven (in Da331) to 37 (in Da542), with a mean number of alleles per locus of 20 for the adults and 16 for the eggs. Observed and expected heterozygosities were, respectively, 0.819 and 0.839 for the adults ($N = 147$), and 0.792 and 0.811 for the eggs ($N = 469$).

Statistical Analyses

A parentage analysis was performed using FAMOZ (Gerber et al. 2003) for which all genotyped parents were chosen as possible parents for all clutches. The program is based on the calculation of LOD (log of the odds ratio) scores for parentage relationships and the construction of statistical tests for parentage assignment. These tests are based on simulations that generate offspring from genotyped parents (Ho: the most likely parent is the true parent) or from allele frequencies in the population (Hi: the most likely parent is not the true parent). The error rate of the LOD score was set to 10^{-3} (Saenz-Agudelo et al. 2009).

An additional analysis was conducted using a maximum likelihood analysis in COLONY (Jones & Wang 2010). Several runs were performed independently on each colony, selecting solely the

Table 1
Group structure and parentage analyses of the hermaphroditic coral-dwelling fish *D. aruanus*

Group ID	Total no. group members	No. male breeders (mean mm SL)	No. female breeders (mean mm SL)	No. adult nonbreeders (mean mm SL)	No. juveniles (mean mm SL)	No. extragroup breeders	Total clutch size	No. eggs typed in TS
6	9	1 (42.8)	4 (34.5)	4 (39.6)	0	0	1398	53
56	13	3 (43.2)	3 (36.3)	7 (30.8)	0	1	2471	49
54	11	2 (47.2)	2 (40.4)	7 (37.4)	0	1	2364	51
2a	27	1 (52.8)	3 (37.6)	23 (29.6)	0	1	1343	53
24	7	2 (41.1)	3 (38.3)	2 (39.1)	0	1	5617	50
57	10	2 (35.4)	2 (29.3)	5 (28.4)	1 (17.7)	0	2825	48
58	7	2 (49.9)	3 (40.5)	2 (46.7)	0	2	2062	50
61	9	2 (38.1)	3 (34.0)	4 (23.7)	0	2	1632	28
15	6	1 (39.0)	2 (28.5)	1 (22.5)	2 (13)	0	1026	43

Shown are the total number of group members, the numbers of male breeders, female breeders, nonbreeding adults, juveniles (<19 mm standard length) and outsider breeders, the total clutch size and the number of eggs in the targeted subsample (TS) genotyped.

adults genotyped on a single colony as likely fathers and mothers of the eggs. Results of the two methods were then compared and discrepancies were resolved by conducting manual checking of the multilocus genotypes.

To investigate the socioecological determinants of group size, we performed an ANCOVA to analyse the relationship between coral size (continuous predictor) and coral genus (categorical predictor) on group size (continuous response) for all 309 groups. In the more detailed investigation, we conducted a multiple regression to analyse effects of coral size and body size of the largest group member (continuous predictors) on group size (continuous response) for the 34 groups in *Pocillopora*.

To investigate the socioecological predictors of discrete reproductive tactics, we began by performing a logistic regression with backward stepwise elimination to analyse the effect of body size (continuous predictor), rank (continuous predictor), group size (continuous predictor) and coral size (continuous predictor) on whether or not an individual bred (binary response, with $0 =$ nonbreeder and $1 =$ breeder). At each step, the predictor variable with the lowest F value and highest nonsignificant P value ($P > 0.05$) was removed first from the model. Even though rank is determined on the basis of body size, both factors were included separately in the analyses because rank is an indicator of relative size and dominance at the group level, whereas SL is an indicator of absolute size, and these variables may influence reproductive tactics in different ways. Since nonbreeders could comprise mature adults that refrained from breeding during this particular reproductive bout as well as immature individuals that were incapable of breeding (i.e. juveniles), we conducted this analysis excluding immature individuals (less than 19 mm SL; Cole 2002) because they are not opting for a nonbreeding tactic in behavioural time (note: when we conducted this analysis including immature individuals we found no significant change to the results, so we report here only the analysis excluding immature individuals). We defined mature individuals that did not breed in the focal breeding attempt as nonbreeders, recognizing that such nonbreeders may include individuals that skipped a breeding attempt to restore energy (i.e. costs of maturing new gametes) or to avoid conflict (i.e. social suppression). Since we could not distinguish between these two alternatives in the current study, we choose the overall term 'nonbreeders' because this was essentially their action during a given breeding attempt.

Subsequently, we focused solely on mature breeders and performed a logistic regression with backward stepwise elimination to analyse the effect of the same suite of predictors on whether an individual bred as a male or as a female (binary response, with $0 =$ female and $1 =$ male).

To investigate the socioecological predictors of continuous reproductive tactics, we used a general linear model (GLM) with backward stepwise elimination to test the effects of body size, rank, group size, coral size, total reproductive output (all continuous predictors), breeder sex (categorical predictor) and group ID (random factor) on the proportion of eggs sired or mothered (continuous response). At each step, the predictor variable with the lowest F value and highest nonsignificant P value ($P > 0.05$) was removed first from the model. To investigate the correlates of individual reproductive output, we performed the same analysis but with the proportion of eggs sired or mothered multiplied by total clutch size as the continuous response variable.

In the preceding analyses, body size and rank exhibited collinearity, so we repeated the analyses omitting either rank or body size from the model to create 'body size' and 'rank' models, respectively. If both rank and body size significantly predicted reproductive tactics, then we determined which was the better predictor by comparing the goodness of fit of the rank model to the goodness of fit of the body size model using a likelihood ratio test.

RESULTS

Socioecological Correlates of Group Size and Reproductive Output

First, we tested the hypothesis that group size would be related to coral size and coral type, as has commonly been demonstrated in other social fishes (e.g. Wong et al. 2005; Thompson et al. 2007). Group sizes ranged from 1 to 44 individuals (mean $\pm$ SE $= 8.1 \pm 0.46$, $N = 309$). Group size was positively related to coral diameter, controlling for coral genus (ANCOVA: $F_{1,304} = 36.5$, $P < 0.0001$; Fig. 1). Coral genus was also a significant predictor of group size ($F_{3,304} = 9.9$, $P < 0.01$), with groups being, on average, larger in *Acropora* (11.4 ± 1.6, $N = 25$ groups), followed by *Pocillopora* (8.3 ± 0.5, $N = 226$ groups), *Montipora* (6.1 ± 2.1, $N = 15$ groups) and *Porites* (5.6 ± 1.2, $N = 43$ groups). However, post hoc tests revealed that only the difference between group sizes on *Porites* and *Acropora* was significant (Tukey HSD test: $P = 0.02$).

Second, we tested the hypothesis that group size would be related to coral size and body size of the largest group member, as has been shown in other social fishes (Buston & Cant 2006; Ang & Manica 2010; Awata et al. 2010; Wong 2011). Group sizes in this subset ranged from 3 to 18 individuals (mean $\pm$ SE $= 7.5 \pm 0.4$, $N = 34$). Group size was positively related to coral diameter (multiple regression: $F_{1,32} = 5.4$, $P = 0.03$) but was unrelated to the size of the largest group member ($F_{1,30} = 0.08$, $P = 0.8$).

Third, we tested the hypothesis that group reproductive output would be related to coral size, group size and the body size of the largest group member, all of which have been shown to influence reproductive success in other social fishes (e.g. Awata et al. 2010; Buston & Elith 2011). Total clutch size ranged from 38 to 5617 eggs (mean $\pm$ SE $= 2393 \pm 475$ eggs, $N = 13$ clutches). Total clutch size was positively related to the size of the parental male (multiple regression: $F_{1,11} = 4.8$, $P = 0.05$) but was unrelated to group size ($F_{1,11} = 3.03$, $P = 0.11$) and coral size ($F_{1,11} = 0.3$, $P = 0.59$).

Finally, we investigated whether the significant positive relationship between parental male size and clutch size was due to large males mating with more or larger females in the group than small parental males did. The size of the parental male was not significantly related to the number of breeding females within the group (Pearson correlation: $r_{1,7} = 0.6$, $P = 0.1$) but was significantly positively related to the average size of breeder females within the group ($r_{1,7} = 0.92$, $P < 0.001$).
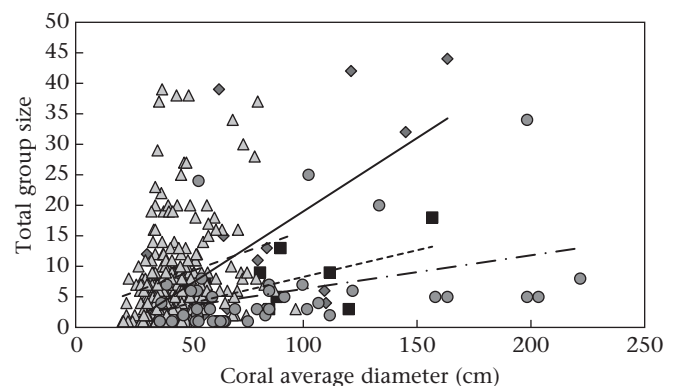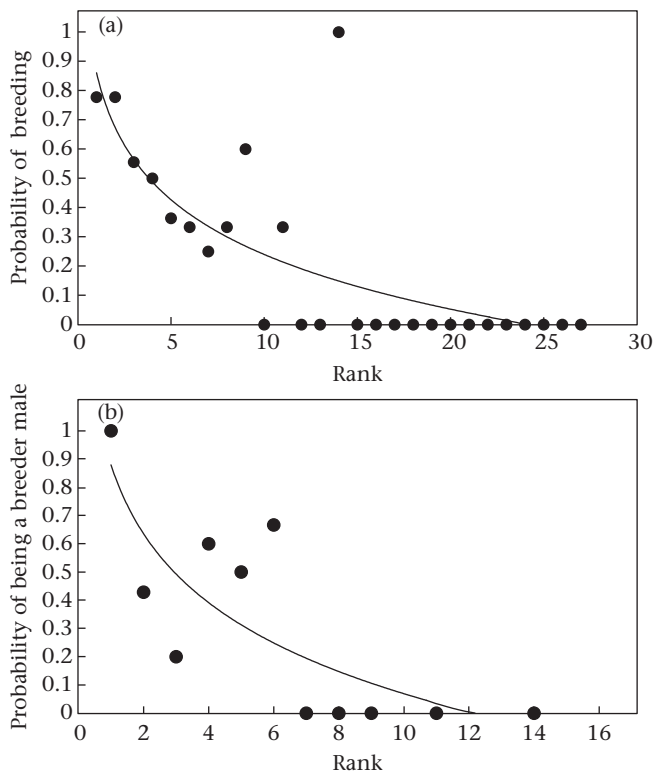

Figure 1. Ecological correlates of group size in *D. aruanus*. Relation between coral size (average diameter) and total group size (including immature individuals <19 mm standard length, SL) for each coral genus (*Acropora, Montipora, Pocillopora* and *Porites*) ($N = 309$ groups). Plotted points are observed data and plotted lines are linear regression lines fitted through these data. Diamonds, solid line: *Acropora*; triangles, dashed line: *Pocillopora*; squares, small dashed line: *Montipora*; circles, dash-dot line: *Porites*.
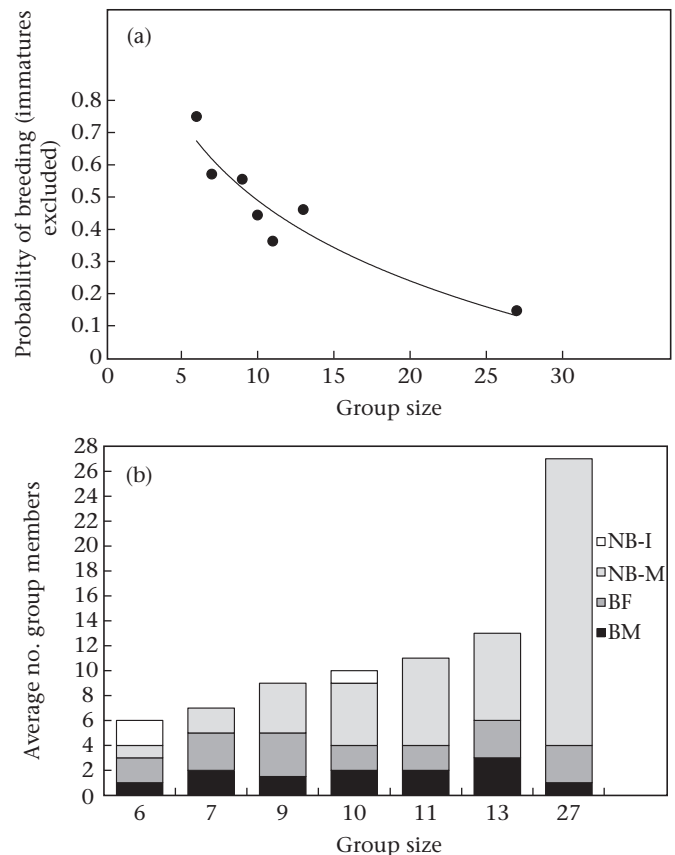
Socioecological Correlates of Discrete Reproductive Tactics

We tested the hypothesis that, among mature individuals, an individual's decision to adopt a breeder versus nonbreeder tactic and a male versus female tactic will be dependent on rank, body size, group size and coral size. A logistic regression with backward stepwise elimination revealed that the likelihood of an individual being a breeder increased with dominance ($\chi_1^2 = 12.8$, $P < 0.0003$; Fig. 2a); a similar result was found when immature individuals (<19 mm SL; Cole 2002) were included ($P < 0.005$). Repeating the analysis with rank omitted from the model revealed that SL was a significant predictor of breeding ($\chi_1^2 = 12.2$, $P = 0.0005$). However, a likelihood ratio test indicated that the model incorporating rank had a significantly better fit than the model incorporating SL ($\chi_1^2 = 11.1$, $P < 0.001$), suggesting that rank was a better predictor of breeding. Similarly, the logistic regression with backward stepwise elimination revealed that the likelihood of a breeder being a male as opposed to a female increased with dominance ($\chi_1^2 = 8.06$, $P = 0.0045$; Fig. 2b). Repeating the analysis with rank omitted from the model revealed that SL was a significant predictor of breeding ($\chi_1^2 = 9.45$, $P = 0.0021$). However, a likelihood ratio test indicated that the model incorporating rank had a significantly better fit than the model incorporating SL ($\chi_1^2 = 5.45$, $P < 0.01$), suggesting that rank was a better predictor of being a breeder male.

The likelihood of breeding was unrelated to group size ($\chi_1^2 = 2.37$, $P = 0.12$; Fig. 3a) or coral size ($\chi_1^2 = 0.06$, $P = 0.81$). While it appears that the probability of breeding decreased with group size (Fig. 3a), this was not because individuals of high rank

Figure 3. Relation between group size and discrete reproductive tactics in *D. aruanus*. (a) Proportion of mature individuals (>19 mm standard length, SL) that adopted a breeding tactic versus a nonbreeding tactic in relation to group size. (b) Group composition in relation to group size. BM: breeder male; BF: breeder female; NB-M: nonbreeding mature individuals; NB-I: nonbreeding immature individuals.

were less likely to breed in larger groups, but because the number of nonbreeding individuals increased in larger groups (Fig. 3b). Finally, the likelihood of breeding as a male was not related to group size ($\chi_1^2 = 0.19$, $P = 0.67$) or coral size ($\chi_1^2 = 0.66$, $P = 0.42$).

Socioecological Correlates of Continuous Reproductive Tactics

First, we assessed overall patterns of reproductive partitioning and output between different categories of males and females. Breeding males could be split into three types: parental male, nonparental males and extragroup males. With respect to reproductive shares, parental males sired an average ± SE of 54.7 ± 16.3% of the eggs laid ($N = 9$), nonparental males sired an average of 43.3 ± 16.1% of the eggs laid ($N = 9$) and extragroup males sired the remaining 1.9 ± 1.3% of the eggs ($N = 3$). With respect to reproductive output, parental males ($N = 9$) sired an average of 1475.6 ± 561.8 eggs (range 0–5504.7 eggs), nonparental males ($N = 9$) an average of 791.4 ± 375.7 eggs (range 0–2271.8) and extragroup males ($N = 3$) an average of 36.8 ± 27.1 eggs (range 0–247.4). In four of nine groups, a nonparental male sired a larger fraction of reproduction than did the parental male, and in one of nine groups, a nonparental male sired all the eggs.

Breeding females could be split into two types: intragroup and extragroup females. Intragroup females mothered an average ± SE of 89.5 ± 6.4% ($N = 25$) while extragroup females mothered 10.5 ± 6.4% ($N = 5$) of the eggs laid. Average reproductive output of intragroup females ($N = 25$) was 1951.7 ± 319.9 eggs (range

Figure 2. Relation between dominance rank and discrete reproductive tactics in *D. aruanus*. (a) Proportion of mature individuals (>19 mm standard length, SL) that adopted breeding versus nonbreeding tactics in relation to dominance rank. In (a), probability of 1 represents adoption of breeding tactics, and probability of 0 represents adoption of nonbreeding tactics. (b) Proportion of mature individuals that adopted male tactics versus female tactics in relation to dominance rank. In (b), probability of 1 represents adoption of male tactics, and probability of 0 represents adoption of female tactics.

1026–3931.9) and that of extragroup females ($N = 5$) was 352.7 ± 217.9 eggs (range 0–1685.1). In three of nine groups, a smaller (subordinate) female obtained a larger fraction of reproduction than the largest breeding female.

We tested the hypothesis that continuous variation in reproductive shares would be explained by dominance rank, body size, group size, coral size, total reproductive output and breeder sex. The GLM revealed that rank ($F_{1,37} = 14.5$, $P < 0.01$) and an interaction between rank and sex ($F_{1,37} = 5.1$, $P = 0.03$) were significant predictors of reproductive shares (Fig. 4a). Repeating the analysis with rank omitted from the model revealed that SL was a significant predictor of shares ($F_{1,38} = 17.4$, $P < 0.001$). A likelihood ratio test indicated that the model incorporating rank did not have a significantly better fit than the model incorporating SL (chi-square test: $\chi_1^2 = 3.8$, $P > 0.05$), suggesting that rank and SL are equally good predictors of individual shares. None of the other factors significantly predicted reproductive shares ($P > 0.05$).

In a similar vein, we tested the hypothesis that continuous variation in individual reproductive output (proportion of eggs sired or mothered multiplied by total clutch size) would be explained by dominance rank, body size, group size, coral size, total reproductive output and breeder sex. The GLM revealed that rank ($F_{1,36} = 13.7$, $P < 0.001$), total reproductive output ($F_{1,36} = 12.5$, $P = 0.001$) and an interaction between sex and rank ($F_{1,36} = 7.4$, $P < 0.01$) were significant predictors of individual reproductive output (Fig. 4b). When rank was omitted from the model, SL became a significant predictor of output ($F_{1,37} = 10.7$, $P = 0.002$), and there was no significant difference between the goodness of fit between the rank model and the SL model ($\chi_1^2 = 2.36$, $P > 0.05$), suggesting that SL and rank are equally good predictors of individual reproductive output. None of the other factors significantly predicted reproductive output ($P > 0.05$).

DISCUSSION

Here we investigated the causes of intraspecific variation in the reproductive tactics in a hermaphroditic society, the humbug damselfish, *D. aruanus*. The number of potential competitors over resources and reproduction (defined by the size of the social group) increased with coral size, and the amount of reproduction over which they competed (defined by the total clutch size) increased with the size of the largest individual. In terms of discrete reproductive tactics, individuals were more likely to adopt a breeder tactic rather than a nonbreeder tactic if they were high ranked, large in size and lived in smaller groups, and breeders were more likely to adopt a male rather than a female tactic if they were high ranked and large in size. In terms of continuous reproductive tactics, breeders gained a larger proportional reproductive share and overall reproductive output if they were high ranked and large in size. Furthermore, high-ranked breeder males obtained a larger reproductive share and output than high-ranked breeder females. We now consider plausible ultimate explanations for the causes of these observed correlative relationships.

The Number of Competitors and the Amount of Reproduction

The number of competitors over resources and reproduction was positively related to the size of the coral colony. This positive relationship is a common feature of the social organization of many group-living fishes (e.g. Kuwamura et al. 1994; Munday et al. 2002; Mitchell & Dill 2005; Wong et al. 2005; Thompson et al. 2007) and suggests that critical resources associated with a territory, such as food, space and breeding sites, generally limit group size. In addition, group size was related to coral genus irrespective of coral size, with groups, on average, being largest in *Acropora*, followed by *Montipora*, *Pocillopora* and then *Porites*. This suggests that the quality of the habitat or territory also influences group size, as has been reported for other social animals (Beukers & Jones 1998; Holbrook et al. 2000; Balshine et al. 2001). In contrast, the number of competitors in a group was unrelated to the size of the largest group member (the parental male), suggesting that social conflicts over rank do not place an upper limit on group size in *D. aruanus*, as seen for other social fishes (Buston & Cant 2006; Ang & Manica 2010; Awata et al. 2010; Wong 2011). Therefore, ecological factors at the group level appear to play the key role in defining the number of competitors over reproduction within groups of *D. aruanus*.

Total reproductive output (or clutch size) was positively related to the size of the largest group member (the parental male). Since the average size of breeding females was also positively related to the size of the parental male, the most likely explanation for this relationship is that large parental males mated with large females, and these large females produced more eggs than small females (i.e. size-limited fecundity; Bagenal 1967; Heg 2008).

Breeding versus Nonbreeding Tactics

In many animal societies, reproduction is monopolized by just one or a few individuals (e.g. Woolfenden & Fitzpatrick 1978;
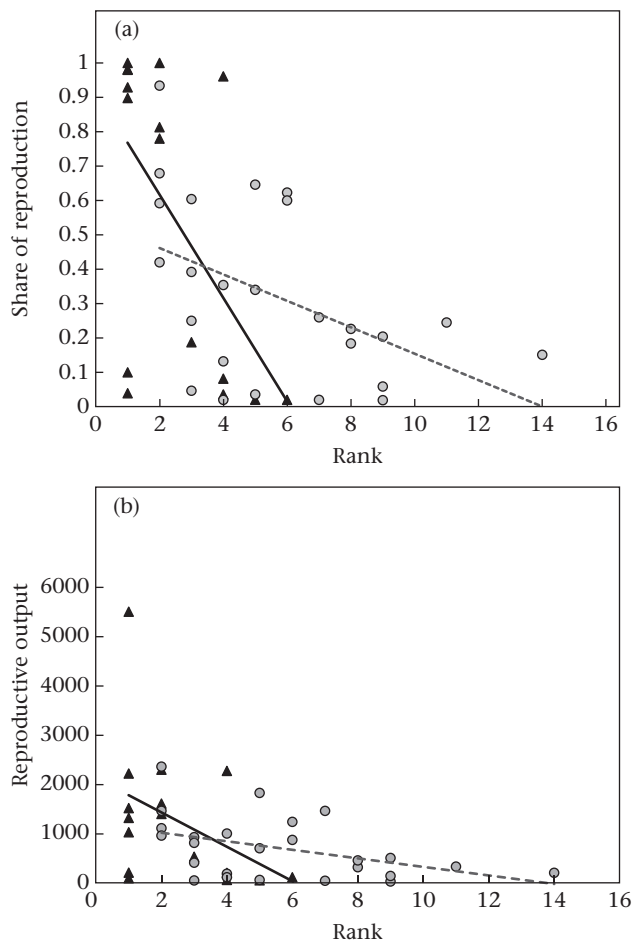
Figure 4. Relation between dominance rank and continuous reproductive tactics in *D. aruanus*. (a) Reproductive shares of mature breeders (expressed as the proportion of genotyped eggs that were assigned to each individual) in relation to rank. (b) Reproductive output of mature breeders (expressed as individual reproductive share multiplied by total clutch size) in relation to rank. Triangles: breeder males; circles: breeder females.

Clutton-Brock et al. 2001; Faulkes & Bennett 2001; Reeve & Keller 2001; Stiver et al. 2009). In *D. aruanus*, breeding tactics were strongly related to individual dominance rank and body size within the group. Group members were more likely to function as breeders if they were of high rank (more dominant) and large in size, and as nonbreeders if they were of low rank (more subordinate) and small in size. From the dominant's perspective, it is clearly in their best interest to breed and suppress the reproduction of their smaller subordinates as much as possible, as seen in other species (Fitzpatrick et al. 2006; Gilchrist 2006; Wong et al. 2008; Clutton-Brock et al. 2010). Thus, the conundrum lies in explaining why subordinates tolerate being nonbreeders (Woolfenden & Fitzpatrick 1978). Since nonbreeders were small and of low rank, it could be that these individuals had simply not reached a size or age at which they could mature and commence breeding. However, in only three cases did we find group members that were less than 19 mm SL (considered juveniles; Cole 2002), and inclusion of these immature individuals into our analyses did not alter the overall relationships. Therefore, it is more likely that a lack of suitable outside options, arising because of habitat saturation or high risks of movement for example (Koenig et al. 1992), or benefits of remaining in their group, arising because of high habitat quality, for example (Stacey & Ligon 1987), results in greater payoffs from remaining in their current group as nonbreeding group members (Creel & Waser 1994; Buston 2004; Wong 2010). Surprisingly, however, some nonbreeders were of high rank, equivalent to the rank of breeding individuals, suggesting that these nonbreeding mature adults showed plasticity in their breeding tactics between reproductive bouts. Indeed, mature adult females show spawning intervals of 2–7 weeks (Mizushima et al. 2000). Future work investigating the correlates of temporal variation in spawning patterns would be interesting for determining the payoffs or constraints involved in such reproductive plasticity.

Male versus Female Reproductive Tactics

With respect to sexual tactics, individual *D. aruanus* were more likely to function as breeder males if they were of high rank and large in size, and as breeder females if they were of low rank and small in size. This pattern can be understood in light of the size-advantage hypothesis, a key component of sex allocation theory (Ghiselin 1969; Warner 1975; Muñoz & Warner 2003a). In a species where large individuals can potentially monopolize and mate with multiple small individuals (i.e. where there is an environmental potential for polygyny; Emlen & Oring 1977), the relationship between male reproductive success and size will often be steeper than the relationship between female reproductive success and size (if males benefit more from multiple partners than do females). In these cases selection will favour individuals that adopt female tactics when small (when they can obtain more reproductive success as a female than as a male) and male tactics when large (when they can obtain more reproductive success as a male than as a female). This is precisely the scenario that we observed in *D. aruanus*: plotting the relationship between rank and reproductive shares and output for male tactics and female tactics separately, we defined the shape of the fitness curves for male and female tactics with respect to rank and, hence, relative size, and we found that large individuals that adopted male tactics attained greater reproductive success than large individuals that adopted female tactics, thus explaining the occurrence of protogynous hermaphroditism. Furthermore, using our plotted size-advantage curves, we can predict the optimal rank at which individuals should switch tactics (Munday et al. 2006; Kazancioğlu & Alonzo 2010). (Note, we choose to assess the optimal rank rather than size of sex change because in site-attached species, an individual's relative size (i.e. its rank) will likely be a biologically more relevant indicator of reproductive opportunities/success than will its absolute size.) We show that the population-wide male and female fitness curves intersect at approximately rank 3, indicating that this should be the optimal rank at which females should change sex to males (on average). The precise rank of sex change will, however, be driven by social conditions within individual groups (e.g. Muñoz & Warner 2003b), and this is the scale at which the social determinants of sex change should now be studied in *D. aruanus* and other hermaphroditic fishes (Munday et al. 2006).

Large Share versus Small Share of Total Reproduction

Among males, reproductive shares were monopolized by the largest group member (the parental male), who fathered the majority share of offspring (54.7%), on average. Indeed, dominance rank and body size were predictors of both variation in male reproductive shares and output, supporting the widespread consensus that high rank and large size confer benefits in the form of enhanced reproductive allocation and success (Lundy et al. 1998; Gerloff et al. 1999; Griffin et al. 2003; Bradley et al. 2005; Neff & Clare 2008; Townsend et al. 2009; Nichols et al. 2010). Reproductive shares and output amongst female group members were also positively related to their dominance rank and body size. Genetic analyses of maternity in other social species from a range of different taxa also support the conclusion that dominant and large females tend to monopolize the majority of the available female reproduction (Lundy et al. 1998; Griffin et al. 2003; Stiver et al. 2009; Townsend et al. 2009).

Despite these overall trends, our genetic analysis of parentage also revealed that subordinates can sometimes obtain a surprisingly large share of total reproduction (in 4/9 groups, a subordinate male obtained a larger share than the parental male, and in 3/9 groups, a subordinate female obtained a larger share than the largest breeding female). From the subordinate's perspective, it is clearly in their best interest to attain some proportion of the total available reproduction. Subordinate males could achieve this by sneaking fertilizations while the parental male is spawning with females or chasing away intruders (Fu et al. 2001; Östlund-Nilsson 2002; Neff & Clare 2008). Thus, the conundrum lies mainly in explaining why dominant males and females would tolerate sometimes significant amounts of subordinate reproduction. On the one hand, dominants may experience a net benefit from allowing subordinates to breed, for example, if it enhances the survival of the parental male's own offspring (Taborsky & Grantner 1998; Lissåker & Kvarnemo 2006). Similarly, dominant females may benefit from the reproduction of subordinates through enhanced offspring survival, for example, if eggs laid in nests containing those from other females have increased hatching success or survival probability (Knapp & Sargent 1989; Goldschmidt et al. 1993; Forsgren et al. 1996; Mizushima et al. 2000; Stiver & Alonzo 2011). Alternatively, dominants may experience high costs from suppressing the reproduction of subordinates (Clutton-Brock et al. 2010; Bell et al. 2011). Further work is clearly needed to uncover the payoffs of reproductive sharing. Whatever they turn out to be, we have shown here that subordinate reproduction can be more substantial than previously expected in this species, comparable with the levels of subordinate paternity revealed by parentage analysis of social birds, mammals and invertebrates (e.g. Haydock & Koenig 2002; Webster et al. 2004; Bradley et al. 2005; Spiering et al. 2010; Pettinger et al. 2011).

The natural question to follow from this is: what factors, above and beyond relative competitive ability within the group, determine the precise share a subordinate *D. aruanus* obtains from the total reproductive pie? Theoretical models indicate that if

dominant group members benefit from the presence of subordinate group members, then factors operating beyond the group may influence reproductive shares. Specifically, subordinates will be able to negotiate a share of the reproduction that is at least equal to what they are expected to obtain elsewhere (i.e. equal to their outside option; Johnstone & Cant 1999; Johnstone 2000; Buston et al. 2007; Buston & Zink 2009; Cant & Johnstone 2009). Future work quantifying and manipulating the outside options of *D. aruanus*, in terms of local habitat saturation and costs of movement (e.g. Wong 2010), would be useful for assessing this hypothesis. Alternatively, the share of reproduction a subordinate can attain may be explained by variation in the costs and benefits to dominants of suppressing subordinate reproduction, without invoking any reproductive transactions between dominants and subordinates (Clutton-Brock et al. 2010; Bell et al. 2011). Hence, having quantified outside options, manipulations of outside options under varying costs of reproductive suppression would be invaluable for teasing apart the relative effects of these factors on the partitioning of reproduction in hermaphroditic societies.

Social versus Genetic Mating Systems

The use of microsatellites to assign parentage has brought about significant changes to our understanding of mating system evolution ever since its inception over 20 years ago (Burke 1989; Hughes 1998). Early work on birds revealed that social monogamy, based on observations of breeding, is not always an accurate reflection of true monogamy, based on genetic analyses, and that extrapair reproduction occurs in a wide variety of socially monogamous species (Birkhead & Møller 1992; Møller & Birkhead 1993 and references therein). Here, using genetic analyses, we have not only confirmed previous field reports of polygynandry within groups of *D. aruanus* (Fricke 1980), but we have also revealed the occurrence of extragroup reproduction in a species that has typically been thought of as highly sedentary. Extragroup reproduction has also been reported in other species (e.g. Vigilant et al. 2001; Sefc et al. 2008; Townsend et al. 2009) and suggests that floating could be a viable reproductive strategy for males and females of *D. aruanus*. Not only can individuals move to other groups, but they can also clearly breed successfully within those groups. This adds an extra layer of complexity to our understanding of the costs and benefits of group living for individuals, and further work identifying these extragroup breeders would be enlightening for our appreciation of the diversity of reproductive tactics in site-attached social fishes.

Acknowledgments

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