



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 of 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; Kazancıoğlu & 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 *Acropora* or *Pocillopora* 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 \pm 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

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