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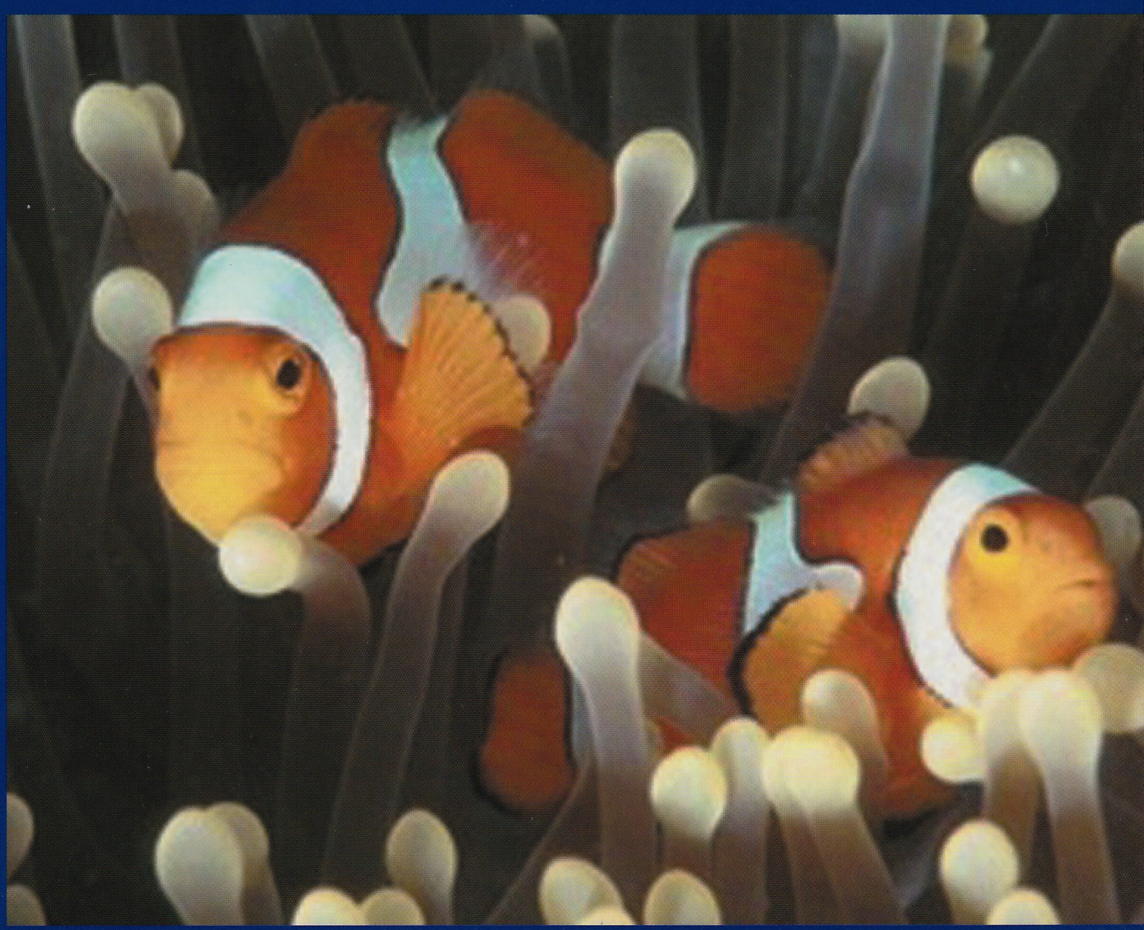

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Are clownfish groups composed of close relatives? An analysis of microsatellite DNA variation in *Amphiprion percula*

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Abstract

A central question of evolutionary ecology is: why do animals live in groups? Answering this question requires that the costs and benefits of group living are measured from the perspective of each individual in the group. This, in turn, requires that the group's genetic structure is elucidated, because genetic relatedness can modulate the individuals' costs and benefits. The clown anemonefish, *Amphiprion percula*, lives in groups composed of a breeding pair and zero to four nonbreeders. Both breeders and nonbreeders stand to gain by associating with relatives: breeders might prefer to tolerate nonbreeders that are relatives because there is little chance that relatives will survive to breed elsewhere; nonbreeders might prefer to associate with breeders that are relatives because of the potential to accrue indirect genetic benefits by enhancing anemone and, consequently, breeder fitness. Given the potential benefits of associating with relatives, we use microsatellite loci to investigate whether or not individuals within groups of *A. percula* are related. We develop seven polymorphic microsatellite loci, with a number of alleles (range 2–24) and an observed level of heterozygosity (mean = 0.5936) sufficient to assess fine-scale genetic structure. The mean coefficient of relatedness among group members is 0.00 ± 0.10 (n = 9 groups), and there are no surprising patterns in the distribution of pairwise relatedness. We conclude that *A. percula* live in groups of unrelated individuals. This study lays the foundation for further investigations of behavioural, population and community ecology of anemonefishes which are emerging as model systems for evolutionary ecology in the marine environment.

Keywords: *Amphiprion*, cooperation, group living, larval dispersal, marine fish, relatedness

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Introduction

Trying to understand why animals live in groups has been one of the major emphases of evolutionary ecology research for more than 30 years (Alexander 1974; Wilson 1975; Pulliam & Caraco 1984; Krebs & Davies 1993; Alcock 2001). The general approach has been to investigate the economics, the costs and benefits, of group living (e.g. acorn woodpeckers, Mumme *et al*. 1983; Koenig *et al*. 1995; Haydock *et al*. 2001; lions, Packer *et al*. 1990; Packer *et al*. 1991; Pusey & Packer 1994; cichlid fish, Taborsky 1985; Balshine *et al*. 1998; Brouwer *et al*. 2005; Stiver *et al*. 2005). This approach is based on the principle that natural selection will have favoured those individuals who behaved in ways that maximized their genetic contribution to future generations. If this is true, then selection will have produced animals that are basically efficient, attempting to maximize their benefits while minimizing their costs. Ideally, the costs and benefits are investigated from the perspective of each individual in the group. An individual's costs and benefits can be modulated by its behaviour, social and ecological factors and the genetic structure of the group (Keller & Reeve 1994; Emlen 1997). Thus a complete understanding of individual behaviour

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within any animal group requires elucidation of the group's kin structure.

Many terrestrial animals have been shown to form groups composed of kin, and the degree of relatedness has been shown to influence individual behaviour (Sherman *et al*. 1995; Bourke 1997; Griffin & West 2003). In contrast, kin groups seem to be relatively rare in marine animals (Grosberg & Quinn 1986; Duffy 1996; Moller *et al*. 2006) and completely absent in marine fishes. Although it is possible that the absence of kin groups in marine fishes is a real phenomenon (e.g. Avise & Shapiro 1986; Kolm *et al*. 2005), the absence could also result from a sampling bias. Historically it has been assumed that marine fish larvae are swept far from their birth site by currents (see Leis 1991 for a review) and as a result few studies have looked for the existence of kin groups. It is becoming increasingly apparent, however, that some reef fish larvae either return to, or are retained at, their natal reef, and that larval mixing is less extensive than previously believed, creating the potential for the formation of kin groups in some marine fishes (Jones *et al*. 1999; Swearer *et al*. 1999; Taylor & Hellberg 2003; Selkoe *et al*. 2006; Carreras-Carbonell *et al*. 2007; Gerlach *et al*. 2007).

The 28 species of anemonefishes (Pomacentridae, *Amphiprion* spp.) found on Indopacific coral reefs (Allen 1972; Fautin & Allen 1992) are good candidate species for the formation of kin groups in the marine environment. Anemonefishes form groups composed of a breeding pair and a small number of nonbreeders (Fricke & Fricke 1977; Fautin 1992; Elliott & Mariscal 2001; Buston 2003a); groups which bear a striking resemblance to the kin-based cooperative breeding systems seen in terrestrial vertebrates (Emlen 1991): breeders tolerate the presence of nonbreeders even though nonbreeders provide no obvious benefits (Fricke 1979; Mitchell 2003; Buston 2004a); nonbreeders tolerate their position because they stand to inherit the territory in the future (Ochi 1989; Hattori 1994; Buston 2004b; Mitchell & Dill 2005). In the anemonefishes, both breeders and nonbreeders stand to gain additional benefits by associating with relatives: breeders might prefer to tolerate nonbreeders that are relatives because there is little chance that relatives will survive to breed elsewhere (Brown & Brown 1984; Kokko & Johnstone 1999; Ragsdale 1999; Buston 2003b); nonbreeders might prefer to associate with breeders that are relatives, because of the potential to accrue indirect genetic benefits by enhancing anemone fitness and, consequently, breeder fitness (Hamilton 1964; Schmitt & Holbrook 2003; Porat & Chadwick-Furman 2004, 2005; Holbrook & Schmitt 2005; Buston & Cant 2006). Finally, intriguingly, anemonefishes have a remarkably short larval phase (8–12 days) compared to other reef fishes (Wellington & Victor 1989; Jones *et al*. 2005).

Given the ecological and evolutionary plausibility of the hypothesis that anemonefishes will form kin groups, we developed microsatellites for the clown anemonefish *Amphiprion percula* and used these markers to determine whether or not individuals within groups are genetically related. We define relatedness as the probability that two individuals from the same group share an allele relative to the probability that two individuals from the same reef share the allele (Queller 1994; Griffin & West 2002). We define relatedness in this way because of the possibility that each reef represents a distinct population (Bell *et al*. 1982; Wellington & Victor 1989; Doherty *et al*. 1995; Jones *et al*. 2005). We show that *A. percula* forms groups composed of unrelated individuals. This leaves us with the perplexing questions of why individuals do not form kin groups and why breeders tolerate multiple nonbreeders, and we propose several fitness-effects hypotheses that might provide the answers. The microsatellites and ideas developed here lay the foundation for further investigations of the behavioural, population and community ecology of anemonefishes, which are emerging as model systems for the study of evolutionary ecology in the marine environment (Holbrook & Schmitt 2005; Jones *et al*. 2005; Porat & Chadwick-Furman 2005; Buston & Cant 2006; Ollerton *et al*. 2007; Santini & Polacco 2006).

Materials and methods

Study population

This study was conducted using material from a population of clownfish, *Amphiprion percula*, which had been studied for 12 months (January to December 1997), in Madang Lagoon (5°09′S, 145°48′E), Papua New Guinea (Buston 2002). Ninety-seven anemones (*Heteractis magnifica*) were located on three reefs: Sinub (Reef 1), $n = 40$; Wongad (Reef 2), $n = 31$; Masamoz (Reef 3), $n = 26$ (see Jebb & Lowry 1995, for a description of Madang Lagoon and its reefs). Each anemone was occupied by a single group of *A. percula*. Groups consisted of a breeding pair and 0–4 nonbreeders (mean number of individuals in each group ± S.D. = 3.4 ± 0.9, $n = 97$). Individuals ≥ 18 mm in standard length (residents, $n = 334$) were recognized on the basis of natural variation in their colour markings and could be reliably censused (Nelson *et al*. 1994; Buston 2003b). At the end of the field study in December 1997, 32 individuals from nine groups were collected from Wongad (Reef 2), and their tissue was frozen in liquid nitrogen. These fish came from breeding groups that had experienced no change in group membership for the entire year (Buston 2004a). Whole fish were collected because it was our original intention to carry out DNA fingerprinting, which would have required significant amounts of tissue; more fish were not collected because it was our impression that these were long-lived and highly social organisms (Moyer 1986; Fautin & Allen 1992; Buston & García 2007).

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Microsatellite loci

A genomic DNA library enriched for microsatellite loci was constructed for *A. percula*. We followed the protocols described in Hamilton *et al*. (1999) with some modifications. Approximately 100 ng genomic DNA was digested with the restriction enzymes *Alu*I and *Hae*III (in separate reactions) while simultaneously ligating a double-stranded SNX linker. Ligation products were allowed to anneal in solution to 3′-biotinylated oligonucleotides (oligos) representing the following motifs: GT, TC, GAT, GTT, GTA, TTC, GCT, GTG, GTC, TCC, GAAT, GATA, GATT, GTAT, GTTA, GTTT, TTAC, TTTC, GATG, GGTT, GCTT, GTAG, GTCA, GTCT, GTTC, TCAC, TTCC, GGGT, GCCT, GCTG, GCTC, GTGC, GTCG, GTCC and TCCC. Dimeric and trimeric oligos were 30 nucleotides in length (representing 15 and 10 repeat units, respectively), and tetrameric oligos were 28 nucleotides long (seven repeat units). Oligos were pooled in three classes of annealing temperature (52 °C, 60 °C and 65 °C) and 8 μL of a 5 μM oligo stock was annealed to linker-ligated DNA in 100 μL of 6x SSC/0.1% SDS for 45 min. Genomic DNA/oligo complexes were removed from solution with streptavidin-coated magnetic beads (New England Biolabs, Beverly, MA) and made double-stranded through Polymerase chain reaction (PCR) with an SNX primer complementary to the linker. PCR products were trimmed with the restriction enzyme *Nhe*I, ligated to pUC 19 plasmids (previously digested with *Xba*I and dephosphorylated), and these ligations were used to transform *E. coli* DH5-α cells. Colonies were further screened by replica plating to nylon membranes and hybridization in 3 molar Tetramethylammonium chloride (TMAC) buffer to the same oligos used in the initial enrichments, now 5′-radiolabeled with ^{33}P.

Plasmid DNA for sequencing was isolated either from 1.5 mL of liquid culture (Luria broth with 50 μg/mL ampicillin) and a plasmid miniprep kit (Qiagen, Valencia, CA) or by a crude 'toothpick' boiling prep and PCR with M13 primers that flank the *Xba*I cloning site in pUC 19. Sequences were trimmed of vector, and unmodified primers were designed with the program PRIMERSELECT (DNASTAR, Inc., Madison, WI) and ordered from Integrated DNA Technologies (IDT, Coralville, IA). Loci deemed promising (from PCRs of small numbers of *A. percula* individuals and agarose gel electrophoresis) had one primer re-synthesized with a 5′-fluorescent dye (6-FAM, PET, NED, or VIC) from Applied Biosystems (Foster City, CA).

PCR and genotyping

PCR reactions (10 μL total volume) consisted of 1 μL (1–10 ng) genomic DNA, 2 picomoles each primer, 2 mM $MgCl_2$, 0.2 mM each dNTP, 0.1 μL (0.5 units) Platinum Taq polymerase (Invitrogen, Carlsbad, CA) in 1× PCR buffer (20 mM Tris-HCl, pH 8.4, 50 mM KCl). Thermal cycling typically followed a 'touchdown' protocol: 95 °C for 50 s, 67 °C– 55 °C for 1 min (the annealing temperature was reduced 2 °C/cycle for the first seven cycles), 72 °C for 1 min, followed by 28 cycles of 95 °C-50 s, 53 °C-1 min, 72 °C-1 min.

Fluorescent PCR products were diluted in water (dilution factors were determined empirically for each locus, and ranged from 1:15 to 1:40), combined with formamide and GENESCAN LIZ-500 size standard (Applied Biosystems) and allele sizes were determined with an ABI 3100 DNA analyzer and GENEMAPPER version 3.5 software (Applied Biosystems).

Summary statistics, tests of Hardy–Weinberg equilibrium and linkage disequilibrium

Summary statistics (number of alleles, observed and expected levels of heterozygosity) were generated with the program Microsatellite Analyser (MSA) (Dieringer & Schlötterer 2002). Tests of Hardy–Weinberg equilibrium (HWE) and linkage (genotypic) disequilibrium were performed with GENEPOP on the web (Raymond & Rousset 1995; http://wbiomed.curtin.edu.au/genepop/index.html). Here, we considered our sample of 32 individuals a single population. For HWE, we used the Probability test (suboption 3) of the null hypothesis ('random union of gametes') as well as the score test for the alternative hypotheses of heterozygote deficiency (suboption 1) or excess (suboption 2), all through Markov chain methods. For genotypic disequilibrium (the diploid case), we tested the null hypothesis that 'genotypes at one locus are independent from genotypes at the other locus', through pairwise comparisons of loci. As with the HWE tests, a Markov chain was used. For Markov chain methods, we used the default settings for dememorization number (1000), number of batches (100) and iterations per batch (1000).

Genetic relatedness

We were able to analyze relatedness of 32 individuals from nine groups using the seven polymorphic microsatellite loci. We determined the coefficient of relatedness of individuals within groups and the pairwise relatedness of all individuals in the population using the program RELATEDNESS 5.0.8 (Queller & Goodnight 1989). We carried out statistical analyses using STATVIEW 5.1 (SAS Institute 1998).

Results

Summary statistics, tests of Hardy–Weinberg equilibrium and linkage disequilibrium

PCR primers, cloned repeat motifs and summary statistics are shown for seven polymorphic microsatellite loci in

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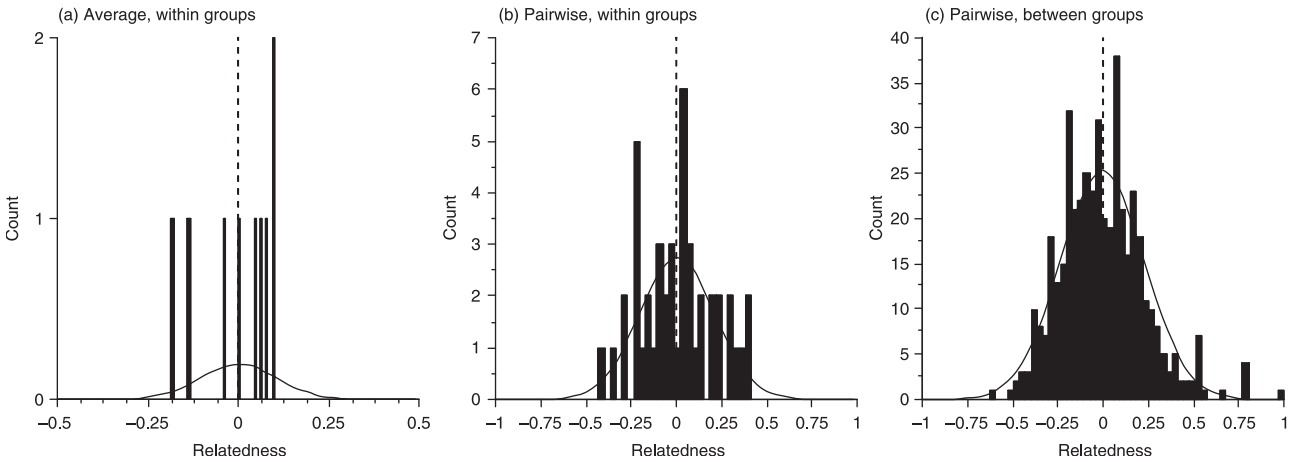

Fig. 1 No evidence of any unusual patterns in the relatedness of the clownfish *Amphiprion percula*: (a) average relatedness among group members (32 individuals, nine groups); (b) pairwise relatedness of individuals from the same group (44 pairwise comparisons, nine groups); (c) pairwise relatedness of individuals from different groups (452 pairwise comparisons). All individuals come from the same island reef (Wongad) in Madang Lagoon, Papua New Guinea (Jebb & Lowry 1995; Buston 2002).

Table 1 Seven polymorphic microsatellite loci isolated from *Amphiprion percula*, with primer sequences and characteristics of each locus (bp, base pair). Repeat structure and length are derived from sequence of original cloned allele. Heterozygosity observed (H_O) and expected (H_E) in a sample from Madang Lagoon, Papua New Guinea (n = 32) is reported

Locus	Repeat (clone)	Primer sequences (5′–3′)	Size (bp)	No. alleles	H_O	H_E	GenBank Accession No.
Cf 4	$(ACAG)_5$	CAGAGTGTGCAGCGAGTAG CGTCCATAGAAGGTAAGGAG	187, 196	2	0.065	0.178	EF375492
Cf 8	$(ATAG)_3(ATGG)_3$ $(ACGG)_5(ACAG)_3(ATAG)_3$	CTGTTAGTATTCATCCATTTTCTTTG TTTTTACTCTGTCTTTGTGGGTTTAT	296, 300	2	0.103	0.160	EF375493
Cf 12	$(AC)_{15}$	CATGGGAGCCAAATGTAAGAAT TGTCACTTTATCCTGCAACCCAGAT	221–246	8	0.677	0.756	EF375494
Cf 21	$(AAAG)_4(ATAG)$ $(AAAG)_{17}(AGA)(AAAG)_4$	CACAGCAGAGTTTTGGATGG AAAAGACGAAGGGAGTAAGTG	148–192	14	0.844	0.834	EF375495
Cf 29	$(AC)_6(GC)(AC)_2$ $(GC)_4(AC)_{39}$	TTCTTTATCCCCTTGTTTATTTCTAA AAGCCTCCTTTCCAAAACCACTCA	244–302	24	0.733	0.831	EF375496
Cf 39	$(AC)_{10}(GC)(AC)_{26}(AGAC)_{11}$ $(AGAT)(AGAC)_2(AC)_{11}(AGAC)_2$	CCGGACAGCCAGAGCAAAGA CCTAATCGATCGGTGGTGACAT	317–387	17	0.862	0.908	EF375497
Cf 42	$(AGAT)_4(AGAC)_{18}$ $(AGCC)(AGAC)_6(AC)(AG)_2$	AAGCTCCGGTAACTCAAAACTAAT GTCATCTGATCCATGTTGATGTG	305–346	9	0.871	0.834	EF375498

Table 1. Two of the loci (Cf 4 and Cf 12) exhibit perfect repeats in the cloned sequence, the other five loci are composed of more complex combinations of dimeric and tetrameric motifs. The number of alleles per locus ranges from two (Cf4, Cf8) to 24 (Cf29), and observed heterozygosity ranges from 0.065 (Cf 4) to 0.871 (Cf 42).

Exact tests of HWE indicate that locus Cf 4 is not in HWE(P = 0.013, Probability test, P = 0.013 for H1 = heterozygote deficit); data from each of the other six loci cannot reject the null hypothesis of random mating. Pairwise comparisons of genotypic disequilibrium indicate that genotypes at these seven microsatellite loci are independent (P-values for each pairwise comparison range from 0.22 to 1.0).

Genetic relatedness

The mean coefficient of relatedness among group members is zero (mean ± s.d. = 0.00 ± 0.10), which, unsurprisingly, is not significantly different from zero (One-sample t-test: t = 0.08, P = 0.94, n = 9 groups, Fig. 1a). This indicates that the probability that two individuals from the same group share an allele is the same as the probability that two individuals from the same reef share the allele. Pairwise relatedness values of individuals from the same group are normally distributed with a mean of zero (Fig. 1b), and this does not differ significantly from the distribution of pairwise relatedness values of individuals from different

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groups (Two-way analysis of variance: $F = 0.05$, $P = 0.82$, Fig. 1b, c). The unimodal distribution of pairwise relatedness within groups indicates that our main result, that the mean coefficient of relatedness among group members is equal to zero, is not the product of some groups being more related and others being less related than expected by chance, which might have been predicted if some parts of the reef showed higher larval retention rates than others (e.g. Swearer *et al*. 1999; Jones *et al*. 2005).

Discussion

The 28 species of anemonefishes (Pomacentridae, *Amphiprion* spp.) found on Indopacific coral reefs (Fautin & Allen 1992) are good candidate species for the formation of kin groups in the marine environment. They have a remarkably short larval phase compared to other coral reef fishes (Wellington & Victor 1989; Jones *et al*. 2005). They live in groups composed of a breeding pair and a small number of nonbreeders, which bear a striking resemblance to the kin groups of cooperatively breeding birds and mammals (Emlen 1991; Griffin & West 2003; Buston 2004a, b). Finally, both breeders (Brown & Brown 1984; Kokko & Johnstone 1999; Ragsdale 1999; Buston 2003b) and nonbreeders (Hamilton 1964; Schmitt & Holbrook 2003; Porat & Chadwick-Furman 2004, 2005; Holbrook & Schmitt 2005; Buston & Cant 2006) stand to gain by associating with relatives.

Here, we develop microsatellites to determine whether or not individuals within groups of *Amphiprion percula* are related (Table 1). We demonstrate that the mean degree of relatedness among *A. percula* group members is zero, i.e. the probability that two individuals from the same group share an allele is no different from the probability that two individuals from the same reef share the allele (Fig. 1). We conclude that *A. percula* forms groups composed of unrelated individuals. The finding that groups are composed of nonrelatives confirms the conclusion that nonbreeding *A. percula* benefit from the association purely because they stand to inherit the territory in the future (Buston 2004b), but leaves us with the perplexing questions of why individuals do not form kin groups, and why breeders tolerate multiple nonbreeders (Buston 2004a).

Why don't individuals form kin groups?

Why, given the potential benefits of associating with kin, do *A. percula*, and presumably other anemonefishes (e.g. *A. polymnus*, Jones *et al*. 2005), form groups of unrelated individuals? Here, we put forward two testable hypotheses, regarding costs of associating with relatives that might offset the potential benefits. First, from the breeders' perspectives, producing larvae that do not leave their natal anemone or return to their natal anemone, would likely be selected against in the first generation because of deleterious effects associated with inbreeding, which would be inherent in the breeding system (Fricke & Fricke 1977; Buston 2004b). Although such deleterious effects could be purged after multiple generations, and such inbred breeding systems do exist (e.g. naked mole rats; Reeve 1990; Bengtsson 1978; Emlen 1997), it is difficult to see how such a system would get started in anemonefishes, especially because there is no lack of recruits from other sources (Buston 2003b; Jones *et al*. 2005) that can serve as mate replacements for widowed breeders (Fricke 1979; Buston 2004a). Second, and perhaps more importantly, from the settling larva's perspective, any larva that left and then tried to return to its anemone of birth would likely be selected against because of the costs associated with searching among anemones (Mariscal 1970; Elliott *et al*. 1995; Buston 2003b). An analysis of settler search strategies suggests that settlers probably do best to remain at the first anemone they encounter, regardless of the number or identity of residents (Buston 2002), and empirical data suggest that this is the strategy that settlers do indeed employ (Elliott *et al*. 1995; Buston 2003b). Inter- and intraspecific variation in the relatedness of group members is an obvious feature of animal societies, and understanding such variation requires that we understand the costs and benefits of both the formation and maintenance of kin groups.

Why do breeders tolerate multiple nonbreeders?

In the anemonefishes, there is no evidence that the presence of multiple nonbreeders directly enhances fitness components of breeders on shorter time scales (up to one year; *A. akallopisos*, Fricke 1979; *A. ocellaris*, Mitchell 2003; *A. percula*, Buston 2004a), but evidence is accumulating that the presence of multiple nonbreeders might enhance fitness components of the anemone on longer time scales (3–5 years; *A. chrysopterus* on *Heteractis magnifica*, Schmitt & Holbrook 2003; Holbrook & Schmitt 2005; *A. bicinctus* on *Entacmaea quadricolor*, Porat & Chadwick-Furman 2004, 2005) and thereby indirectly enhance the fitness of breeders on longer time scales (Buston 2004a; Buston & Cant 2006) — and that breeders live long enough to reap these rewards [in *A. percula*, expected breeding tenure, conditional on obtaining breeding status, is 22 years (Buston & García 2007); see also, Moyer 1986; Fautin & Allen 1992; Srinivasan, unpublished]. Specifically, it has been shown that the number of fish present in the anemone can influence the survival, growth and asexual reproduction of anemones (Schmitt & Holbrook 2003; Porat & Chadwick-Furman 2004, 2005; Holbrook & Schmitt 2005). The survival of breeders is completely dependent on the survival of the anemone (Mariscal 1970; Elliott *et al*. 1995; Buston 2003b,c). The growth of breeders is positively related to anemone size (Buston 2002) and the size of breeders likely influences the number of eggs laid and hatched (Fricke 1979; Buston

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2004a). Finally, the fate of breeders' offspring depends on the availability of habitat (Buston 2003b) and asexual reproduction of anemones may result in there being more locally available habitat (Holbrook & Schmitt 2005) for locally dispersing larvae (Jones *et al*. 2005). Thus, it is plausible but as yet untested, that the presence of multiple nonbreeders can enhance the fitness of breeders on longer time scales because of indirect effects mediated by the anemone. Documentation of such effects would be a remarkable case of group augmentation mediated through an interspecific mutualism (Brown 1987; Emlen 1997; Kokko *et al*. 2001; Clutton-Brock 2002).

How far do larvae go?

This study, which shows that anemonefish larvae leave their natal anemone, naturally leads us to the questions of how far do anemonefish larvae go and why do they go that far? That is, what is the shape of the larval dispersal kernel [probability of larvae settling as a function of distance from source (Nathan & Muller-Landau 2000)] and why does it have that shape? The answers to these questions are crucial to a complete and integrated understanding of the behavioural, population and community ecology of these fish. The microsatellites developed here and elsewhere (Quenouille *et al*. 2004) will help to provide the answers. Here, we show that zero larvae of *A. percula* travel zero distance (see also Jones *et al*. 2005), which helpfully restricts the number of functions that can describe the dispersal kernel (Nathan & Muller-Landau 2000). In addition, Jones *et al*. (2005) reported that at least some larvae of *Amphiprion polymnus* travel less than 1 km and can be traced back to their parents, which demonstrates that the questions are tractable. In any given population of anemonefish, all anemones can be located and all fish can be genotyped (e.g. this study; Jones *et al*. 2005), and every larva that recruits to the anemones can be collected and genotyped (e.g. Buston 2003b; Jones *et al*. 2005). Such data can be used to create *actual* dispersal distance and direction distributions and *potential* dispersal distance and direction distributions (which are dependent on the spatial distribution of anemones; e.g. García *et al*. 2007). If *actual* and *potential* dispersal distributions are statistically different, then this difference likely has a cause. The cause of such a difference can be abiotic, such as current speed and direction, or biotic, such as larvae tending to travel particular distances or directions, or a combination of the above (e.g. Gerlach *et al*. 2007). Understanding why the larval dispersal kernel has a particular shape will be challenging and require full integration of behavioural, population and community ecology, as well as physical oceanography. In the anemonefishes, at least, these questions are tractable and the answers will reinforce the status of these fishes as model systems for the study of evolutionary ecology in the marine environment.

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Peter M. Buston, most broadly, my interests are in the behavior, ecology, and evolution of animals. More specifically, I am interested in how ecological, social, and genetic factors combine to influence the evolution of individual strategies within social groups. As a natural extension of this, I have become interested in how these individual strategies influence population dynamics, and the conservation implications of this relationship. Steven M. Bogdanowicz is interested in the molecular/genetic bases of reproductive isolation and species fromation, patterns of introgression and genealogical exclusivity among distinct yet hybridizing populations and higher taxa, genealogical and phylogenetic relationships within and among species, molecular forensics as a tool to identify cryptic and/or invasive taxa, identification of loci linked to or responsible for reproductive barriers, linkage mapping of phenotypic traits involved in reproductive isolation, and the development of molecular markers in non-model organisms for assays of variation and kinship. Alex Wong is a graduate student interested in the molecular basis of adaptation. Richard G. Harrison is an evolutionary biologist with broad interests in the genetics of natural populations.

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