



Relationships between pair formation, site fidelity and sex in a coral reef cardinalfish



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ABSTRACT

Coral reef fishes are characterised by extreme site fidelity and are often socially monogamous, forming pair bonds within larger social groups. Despite this, the strong link between reproductive behaviour and site fidelity in such social species is poorly understood. We examine these relationships in the cardinalfish *Ostorhinchus cyanosoma* on the central Great Barrier Reef. We tagged and followed over 100 individuals for 5 weeks to investigate pair fidelity, and behavioural differences between pairs and singles and between sexes, and we experimentally tested the strength of site and mate fidelity. Tagged pairs were typically highly site attached, and lasted throughout the study period. Sex had very little effect on pairing behaviour or habitat use. Paired individuals showed three times higher site fidelity than single ones, with singles frequently relocating. There was a two-fold increase in the movement of individuals that had their partners experimentally removed. Paired individuals exhibited greater homing success, and homed regardless of whether their mate had been displaced with them or was left on the home site. These results suggest that individuals of this species form at least seasonally stable monogamous pair bonds within larger groups, and that pair formation is closely associated with site fidelity.

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1. Introduction

Different social and mating systems arise in animals as a result of variation in the types of relationships among individuals, and between individuals and their living space. In many birds and mammals, mate fidelity is strongly associated with site fidelity, and it has been suggested that the evolution of monogamy and site fidelity are coupled (Cézilly et al., 2000). The tendency to return to a specific nest or colony site is often strongly linked to mate fidelity (Cézilly and Johnson, 1995; Cuthbert, 1985; Morse and Kress, 1984) and a change in mating partner is often associated with a shift to different mating or nest sites (Mills, 1973; Pietz and Parmelee, 1994; Thibault, 1994; Williams and Rodwell, 1992). For species that show the highest breeding site fidelity, such as colonially breeding seabirds, there is an extremely high prevalence of monogamous mating systems (Danchin and Wagner, 1997). In contrast, those move among sites, individuals are less likely to re-mate with the same partner in subsequent breeding seasons (Cézilly and

Johnson, 1995; Cuthbert, 1985; Harris, 1979). Many birds and mammals also exhibit sex differences in site fidelity (Paton and Edwards, 1996), which may be due to differing mating strategies. However, in monogamous species, whether individuals are most faithful to their partner or their breeding site is often not known.

Relationships among mate fidelity, site fidelity and sex have received less attention in other animal groups. Coral reef fishes are characteristically extremely site attached (Sale, 1977; Warner, 1988) and can be found in small social groups associated with particular patches of habitat (Wilson and Burgess, 2008). A large number of coral reef fishes are socially monogamous, either living in pairs or maintaining pair bonds in larger social groups (Barlow, 1984; Kuwamura et al., 1993). Most fish families in which monogamy has been reported are highly site attached and closely associated with habitat features such as coral colonies or rubble patches (Whiteman and Côte, 2004). Barlow (1984, 1986) suggested a close connection between the formation of lasting pair bonds and a species' site fidelity. However, the relationships between pair formation and site attachment are not well understood, and it is not known whether restricted movement is associated with pair formation.

In several monogamous coral reef fish species, groups consist of both paired and single individuals (Fricke, 1986; Kuwamura et al., 1993; Pratchett et al., 2006; Whiteman and Côte, 2004). Differences

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in the behaviour of paired and single individuals can provide clues about links between social status and movement. For example, in the goby *Gobiodon histrio*, single individuals had 34% less fidelity to coral colonies than paired individuals (Wall and Herler, 2008). For reef fish, pairing appears to be size-assorted, with male and female partners of similar size, and some smaller immature individuals single (Okuda, 2001; Pratchett et al., 2006). The likelihood of being single may be sex-related, and results from a skewed sex ratio and inability of individuals of one sex to find a partner (Jones et al., 2000; Sogabe and Yanagisawa, 2007). While socially monogamous reef fish species usually have similar social roles in males and females (Sogabe and Yanagisawa, 2007), in some species males may be dominant and exhibit lower mate fidelity, while in others females may be more aggressive and larger than their male partners (Kuwamura, 1985; Sogabe and Yanagisawa, 2007; Thresher, 1984). Mate fidelity varies among species, with some unable to re-mate once their partner is removed (Fricke, 1986), while others finding new partners almost immediately after mate removal (Nakashima et al., 1996). Many socially monogamous fish exhibit such strong site fidelity, that when displaced, are able to return to home sites over considerable distances (Marnane, 2000). However, whether this association with a home site is primarily related to the site itself, or the presence of a long-term partner is unknown.

Cardinalfishes (family Apogonidae) represent an interesting focal group to tease apart the relationships between site fidelity and mating systems in coral reef fishes. They are known to exhibit high site fidelity in their choice of towards their daily resting spots (Gardiner and Jones, 2005; Greenfield and Johnson, 1990) and can home to these sites over hundreds of metres (Marnane, 2000). All species documented so far are obligate mouthbrooders (Vagelli, 1999), and in all but two species, the male is responsible for incubation (Ridley, 1978). The mating systems are poorly understood, but it has been suggested that many species are monogamous for at least one breeding cycle, even when in larger groups (Fishelson, 1970). Since males are the predominant caregivers and cannot re-mate while tending to the brood, female cardinalfish could potentially increase their reproductive success by changing partners between broods. Females may therefore move between sites more than males. This can be associated with a scarcity of receptive males in some cardinalfish species (Okuda and Yanagisawa, 1996a) and females may become the predominant competitor for mates (Kuwamura, 1985). It has also been suggested that males of some species move less than females in order to conserve energy for the highly costly oral brooding (Okuda, 2000). However, for cardinalfishes, differences in the movement of paired and single individuals, and between males and females have received little attention. Importantly, it is not known whether the strong site fidelity of cardinalfish is related to dependence on a familiar site or to strong pair bonds between mating partners at these sites.

The overall goal of this study was to investigate the link between pair formation, site fidelity, and sex in a common species of cardinalfish from Indo-Pacific coral reefs. *Ostorhinchus cyanosoma* is a common fish on Indo-Pacific coral reefs. It is known to live in groups and to be very site attached (Marnane, 2000), but individuals within these groups potentially form pairs. We began with an intensive tagging and observational study to determine if males and females in aggregations form pairs, and to compare the behaviour and site fidelity of single and paired individuals, and the behaviour of males and females. This was followed by a mate removal experiment to examine whether site fidelity is related to the presence of a mate and if individuals are capable of forming new pair bonds. Finally, a displacement experiment in which individuals relocated with and without their mates, was carried out to determine if strong site attachment and homing were related to the site or to the presence of a mate.

The following specific questions were addressed: (1) Do males and females in larger social groups form stable pairs and do they exhibit site fidelity? (2) Are there differences in the behaviour and site fidelity of males and females in pairs, and is there any evidence of female dominance? (3) Are there differences in the behaviour of paired and single individuals, with pairing associated with greater site fidelity? (4) When mates are experimentally removed, does this affect the level of site fidelity and can individuals of either sex form new pair bonds? (5) When individuals are displaced, is the tendency to home associated with the site itself or the presence of their mating partner?

2. Methods

2.1. Study site and species

The study was conducted on a fringing reef at Orpheus Island in the central Great Barrier Reef, Australia (18°35' S, 146°28' E). The study site was located in Cattle Bay, on the leeward side of the island. Observations and experiments were performed over 5 weeks through September and October, 2011, just prior to the breeding season. Diurnal resting sites of cardinalfish were located on the reef flat and slope between 2 and 9 m depth. Cardinalfish were found in aggregations within branching *Porites cylindrica* colonies, often with multiple species in each group. *O. cyanosoma* was one of the most abundant cardinalfish species at this location. Six aggregations of 7–47 individuals each were selected as focal study groups. All of these were situated in an area 150 m in breadth and aggregations were approximately 20–50 m apart.

2.2. Observational studies

All 105 individuals of *O. cyanosoma* within each of the six groups were tagged for behavioural observations (between 7 and 47 in each group). Fish were captured using hand nets and diluted clove oil (50 ml in 100 ml 95% ethanol with 350 ml sea water (Munday and Wilson, 1997)). Clove oil effects fish for only 10–20 min and has been shown to have minimal negative impacts (Munday and Wilson, 1997). Anaesthetised individuals were sized and tagged using visible implant elastomer tags (North-West Marine Technologies), injected subcutaneously into the dorsal musculature. Unique identification tags were created for each of the 105 individuals by using a combination of five colours and five positions on the body were used to create a unique identification for each of the 105 captured fish. Elastomer tags are known to persist over at least several months and have minimal effect on fish behaviour (Marnane, 2000). Tagged fish were retained for 10–20 min in mesh containers to allow them to recover from the anaesthetic, and then released back onto their home sites. No adverse effects of the tagging process were observed.

The location and partnerships of all tagged fish in the focal aggregations were monitored six times over a period of 12 days (approximately every second day). To minimise the influence of capture and handling on fidelity data, such as increased predation losses, monitoring of tagged fish began at least 24 h after tagging occurred. Monitoring was carried out by two divers simultaneously visually relocating tagged fish on the study sites. The position of each fish was recorded in relation to its original 'home' coral colony, this being whether it was at home, in another colony nearby, or was missing. Data records for each survey were later compiled and locations categorised such that each tagged fish was either "Present" in the original coral colony (i.e. home), "Relocated" if it had changed from one site to another, "Reappeared" if it was missing on one or more days of monitoring but resighted on a subsequent day, or "Died/lost" if it was not seen again. The social status of each

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