

Group stability and homing behavior but no kin group structures in a coral reef fish

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Understanding the reasons behind stable group formations has received considerable theoretical and empirical attention. Stable groups displaying homing behavior have been suggested to form as a result of, for instance, benefits from knowledge of the social or physical environment or through kin selection and the forming of kin groups. However, no one has disentangled preference for grouping in a familiar location from preference for grouping with familiar or related individuals. To investigate this, we conducted a series of field experiments and a group genetic analysis on the group-living Banggai cardinalfish (*Pterapogon kauderni*). We found homing behavior but no evidence for recognition of familiar group members. Instead, homing was based on the original location of their group rather than the individuals in that group. Moreover, we found no evidence for kin structures within these groups. We suggest that benefits from living in a known social environment drive homing behavior in this species and that homing behavior is not enough for the formation of kin group structures. Instead, our results suggest that kin recognition may be a prerequisite for the forming of kin groups. **Key words:** dispersal, group stability, kin selection, microsatellites, territory. [*Behav Ecol* 16:521–527 (2005)]

Group living is a common feature of many animal taxa and may yield fitness benefits to individuals. Such benefits may be diverse, ranging from reduced susceptibility to predation (e.g., Pitcher and Parrish, 1993) to benefits from cooperation (e.g., Hölldobler and Wilson, 1990) and cooperative breeding (Stacey and Koenig, 1990). Thus, arguments explaining the evolutionary advantages for group living are many and widely accepted. In many animal species, however, individuals not only prefer to live in groups but also to live in a *specific* group. An individual's knowledge of the location of a specific group and the physical properties of the group's local environment may be highly important for the maintenance of groups in spatially stable species. Furthermore, knowledge about the social environment of a specific group may also be important, particularly for species that form dominance hierarchies (e.g., Huntingford and Turner, 1987). Homing behavior has been observed in several taxa (e.g., Gill, 1994; Hert, 1992; Lembo et al., 2002; Meylan et al., 1990), and experimental studies have demonstrated remarkable abilities for individuals to find their way home after translocation (e.g., Gill, 1994; Hert, 1992; Lebboroni and Chelazzi, 2000).

The most advanced form of group living is that displayed by species living in groups of related individuals (i.e., kin groups). By living in kin groups, individuals may gain indirect fitness benefits from helping their relatives (Hamilton, 1963, 1964). Moreover, studies have shown that individuals within groups of kin or even familiars display less aggression (e.g., Brown GE and Brown JA, 1992, 1993; Creel S and Creel NM, 2002). As aggression can be costly, both directly due to actual injuries as well as indirectly through trade-offs between aggressive behaviors and for instance foraging (e.g., Huntingford and Turner, 1987), there may be both direct and indirect

benefits from forming groups with familiars or kin. Accordingly, kin selection can be highly important for the formation of stable groups (e.g., Baglione et al., 2003; Emlen, 1995; Stacey and Koenig, 1990; Ward and Hart, 2003).

Kin recognition has been suggested to be a prerequisite for nepotistic behavior to evolve (Gamboa et al., 1991). Such kin recognition is often based on olfactory cues, as has been shown in several taxa (Blaustein and O'Hara, 1982; Brown et al., 1993; Kareem and Barnard, 1986; Mateo, 2002; Olsén, 1989; Quinn and Busack, 1985), but could also result from a combination of visual and olfactory stimuli (Arnold, 2000). Intuitively, individuals obviously need to be able to recognize kin in order to modify their behavior in line with inclusive fitness theory. However, kin recognition does not automatically produce nepotistic behavior (Mateo, 2002).

Recent developments in molecular genetics have resulted in an explosion of studies that have investigated the genetic composition of groups to determine whether they consist of related individuals (e.g., Baglione et al., 2003; Höglund et al., 1999; Hughes, 1998; Shorey et al., 2000). It is often assumed that such kin groups have formed as a result of kin selection (e.g., Höglund et al., 1999; Shorey et al., 2000). However, the presence of related individuals within groups does not necessarily mean that kin selection is at work (e.g., Clutton-Brock et al. 1999; Creel and Waser, 1994). Limited dispersal or short-ranging dispersal strategies may also result in the formation of groups of related individuals (Coltman et al., 2003). If individuals display limited dispersal but strong homing behavior for reasons related to the benefits from being in a known location rather than for reasons related to the individuals within that location, kin groups may assemble without kin selection. Accordingly, homing resulting in stable groups could be targeted at either the individuals in the home group or the known environment of that home group or both. Disentangling the effects of location from the effects of relationships of individuals within groups in group-living

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species with homing behavior may thus provide important insights into the mechanisms underlying the formation of stable groups.

A suitable organism for the study of these issues is the Banggai cardinalfish (*Pterapogon kauderni*). This small marine species (maximum, 5.5 cm) is endemic to the Banggai Archipelago outside of East Central Sulawesi, Indonesia. It is a paternal mouthbrooder with direct development and hence no pelagic larval phase (Allen and Steene, 1995). It lives in groups of up to 500 individuals in shallow, protected lagoons. Groups are commonly found in proximity to groups of sea urchins (Kolm and Berglund, 2003), in which the fish hide when threatened. The Banggai cardinalfish, like many other day-active planktivores (Hobson, 1991), feeds on plankton that passes the group via water currents. Movements between groups have been suggested to be very limited (Lunn and Moreau, 2002). Furthermore, a previous study showed that the Banggai cardinalfish appears to engage in remarkably limited dispersal, as evidenced by high levels of population genetic structure (Hoffman et al., in press). Furthermore, when collecting fin samples for a previous study, it was apparent that the Banggai cardinalfish exhibited homing behavior; a number of individuals, from several groups, returned hundreds of meters to their groups after fin clipping (Kolm and Berglund, 2003). However, this anecdotal evidence for homing in this species needs to be verified using a replicated experimental design. Because the Banggai cardinalfish is a group-living species with limited dispersal that apparently displays homing behavior, it is a likely candidate for the formation of kin groups. Furthermore, as the species can readily be used for experimental manipulations, it is perfect for disentangling group genetic structure resulting from effects of homing for a known location versus homing for familiar individuals.

By using a combination of field experiments we tested whether the Banggai cardinalfish exhibits homing behavior, whether it can recognize individuals from its own group, and whether the homing behavior of the Banggai cardinalfish is based on the location of the group or on the individuals in the group. We also performed a group genetic analysis using 10 polymorphic microsatellite markers to determine whether the strong group structure of the Banggai cardinalfish has resulted in high relatedness of individuals within groups (Hoffman et al., in press). By using this combination of behavioral experiments and genetic analysis, we could elucidate the effects of homing for location and familiars on the genetic composition of stable groups in an unprecedented way.

METHODS

Field experiments and sampling for genetic analysis were conducted in November, 2002, in a shallow lagoon of Peleng Island, Sulawesi, where Banggai cardinalfish are abundant and protected from the fishery. The lagoon had some coral cover, sand, and seagrass. Water depth ranged between 1 and 3 m depth. Sea urchins, which provide the main microhabitat of the Banggai cardinalfish, were highly abundant within the lagoon. All the groups that were used in the study were in close proximity to some coral and at least 1 m² of sea urchins and were separated from one another by at least 30 m (see below for separate descriptions of each experiment) of open patches of sand. This ensured that groups really were distinct from each other because one rarely encounters this species in open sandy areas (Kolm N, personal observation; Vagelli and Erdmann, 2002). Fishes in experiments were between 30 and 50 mm standard length.

Table 1

Results from homing experiment; * = $p < .05$ (see text for details)

Group	Number of translocated fish	Number of returned fish	Percentage of returned fish	Expected number of returned fish
1	20	0	0	0.2
2	30	10	33	0.4
3	16	13	62	0.2
4	20	10	50	0.4
5	20	3	15	0.1
6	20	8	40	0.2
Average	21	7.3*	33*	0.25

Homing experiment

To investigate homing behavior in the Banggai cardinalfish, we fin-clipped 20–30 individuals from each of six different groups (30–75% of the total number of fishes in each group). The groups selected for this experiment were separated by at least 50 m. By using a unique combination of fin clips for each group (i.e., six different combinations), we avoided any unnoticed mixing between groups. Directly after fin clipping at 0600 h in the morning, we released the fin-clipped fishes together, 50 m from their original group in a random direction. We checked an area (10 m by 50 m) between the location of the group and the place of release, for potential alternative suitable sea urchin groups. Under the assumption that the number of sea urchin groups per square meter found within this area would be representative for the entire 50-m radius, we calculated the number of potential sea urchin groups for the entire 50-m radius. This procedure allowed us to calculate the probability of fishes returning to their original location by chance alone, assuming that fishes would swim in a random direction, using the following formula:

$$E = \frac{R}{TA/CA \times PL}$$

E equals the expected number of returned fish by chance alone, R equals the number of transferred fish, TA equals the maximum total area of the potential 50-m radius area that fish would potentially pass to end up in their old location by chance, CA equals the area checked for potential alternative sea urchin groups, and PL equals the number of potential alternative sea urchin groups found in that area (see Table 1). All original groups were visited and scored for number of returned fish at 10 h (1600 h in the afternoon) and 24 h (0600 h the next day) after translocation for total number of returned fish.

Familiarity experiment

To test whether or not Banggai cardinalfish recognize members of their own group, we used a cage design in which we allowed individuals to choose between members of their own group and individuals from other groups (Figure 1). The experimental cage was situated at a depth of 1 m, at least 50 m from the closest group of Banggai cardinalfish. Twelve focal fish from six different groups were used in the experiment (i.e., 6 replicates with 12 trials, total $N = 72$). Sexing of the individuals used in the experiment was not possible due to time constraints as this species can only be sexed on the bases of behavioral differences between the sexes (Kolm, 2004). However, because all focal fish were randomly chosen, and we expect a 50/50 sex ratio within groups, it is unlikely that any of our results will be biased due to the sex of the focal or

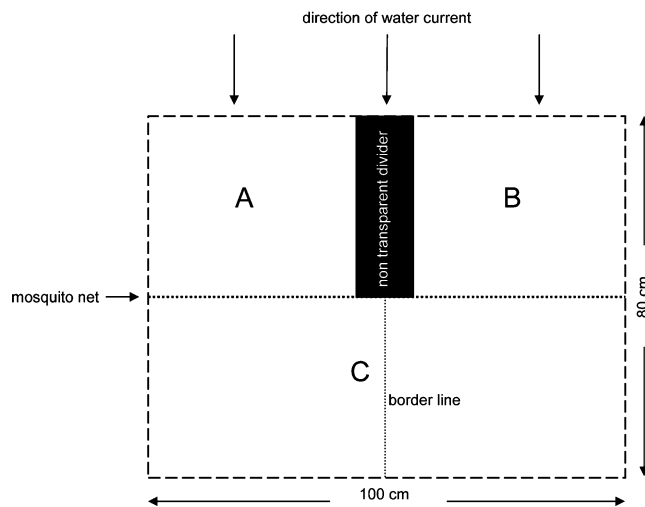


Figure 1

The experimental cage was constructed of plastic net with a mesh size of 8 mm. A mosquito net separated the stimulus compartments (A and B) and the compartment in which the focal fish was placed (C). A strip of tape was placed on the outside of the cage in the middle of compartment A and B so that the observer was able to decide whether the focal fish was closer to compartment A or B. See text for details.

stimulus fish. For each experimental trial, 12 fishes from the same group as the focal fish were put into one of the compartments A or B (Figure 1), and 12 fishes from another group were placed into the other compartment. The minimum distance between original locations of these groups was 50 m. The focal fish was then put into compartment C and allowed to acclimatize for 5 min. Immediately after the release of the focal fish, we noted to which stimulus group it first swam. After the acclimation time, we measured the time spent in front of each group for 5 min. All observations were made using snorkeling from a distance of 1 m from the cage. Prior to each experimental replicate, we positioned the cage so that any water current, and hence any olfactory cues, would flow from the stimuli fish towards the focal fish. To control for potential side effects, we switched the stimuli groups between compartments A and B after six trials of each replicate. Data were also collected on whether focal fish actually visited both compartments, and if so, how many times they crossed between the two compartments. These data could be important to establish whether focal fish actually had knowledge about both stimulus groups in the cage as well as to provide information on stress levels of the focal fish (Warburton and Lees, 1996).

Location versus familiars experiment

To disentangle any location effect from the effect of familiars, we performed a cage experiment where we allowed fish to choose between their old location, which we caged in and reinhabited with unfamiliar, and a new, caged in location inhabited by familiars (Figure 2). The cages were box shaped (80 × 80 × 50 cm) and made from a tree frame covered in mosquito net, allowing both visual and olfactory stimuli. In order to make the new location (cage B) as similar as possible to the original location (cage A), we added rocks and the same number of sea urchins as found on the original location. We caught all individuals on the original location, took out those fishes that we used as focal fish, and put the rest in cage B. We then caught fishes from another group and put

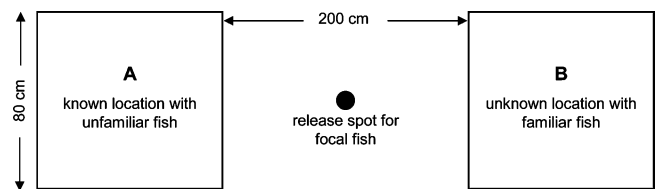


Figure 2

Two cages constructed by wood frames covered with mosquito net were used. Cage A was a familiar location with unfamiliar fish, and cage B an unfamiliar location with familiar fish. The focal fish was introduced in the middle of the experimental cages.

them in the cage over the original location (cage A) after matching the number of individuals to those put in cage B. The minimum distance between original locations of these groups was 30 m. We allowed 20 single focal fish from five different groups (total $N = 100$) to choose between their old location inhabited by unfamiliar and the new location inhabited by familiars. Each trial was performed by releasing the focal fish in the middle of the two cages and observing where it would swim. As soon as a focal fish was within 10 cm of either cage, it was considered to have chosen that cage. If a focal fish had not chosen a cage within 10 min of release, it was discarded from the experiment and replaced by another individual until 20 focal fish from each group actually had made a choice. If a fish changed cages within 10 min of each trial, it was considered to have chosen the cage where it was at the end of the trial. One person released the focal fish and another person observed the focal fish using SCUBA. In order to ensure that these single fish trials were not confounded due to stress caused by the solitude of the focal fish, we replicated the experiment for three of the five groups using groups of three fish as the focal unit (total $N = 60$).

Genetic analysis

For the molecular genetic analysis, we sampled tail-fin clips (approximately 3×2 mm in size) of 20 fishes, each from 10 different groups (total $N = 200$) prior to any behavioral experiments conducted on those groups. All fishes appeared unharmed by the sampling procedure and were released in their original groups after sampling. Given the high levels of genetic divergence observed among different populations of Banggai cardinalfish (Hoffman et al., in press), we collected these samples from distinct groups within a single population. Because homing to such groups was established for this population prior to sampling, we considered that they were indeed distinct groups. Tail-fin clips were stored in 95% ethanol and transferred to the laboratory for genetic analysis. We extracted DNA from each tail-fin clip by following a standard chelex extraction protocol (Miller and Kapuscinski, 1996). Each fish was then genotyped at 11 microsatellite markers according to the conditions of Hoffman et al. (2004).

Statistical analysis

For the Homing Experiment, a dependent t test against a reference constant was used (Statistica 6.0), where the constant (i.e., the expected return rate by random) was calculated using the formula described above. For the Familiarity Experiment, a dependent t test was performed where the average time (average based on $N = 12$ for each of the six groups, i.e., total $N = 72$) spent in front of familiars for each of the six groups was compared to the expected time under the null hypothesis that focal fish should spend half the experimental time (150 s) in front of familiars. For the Location Versus Familiars

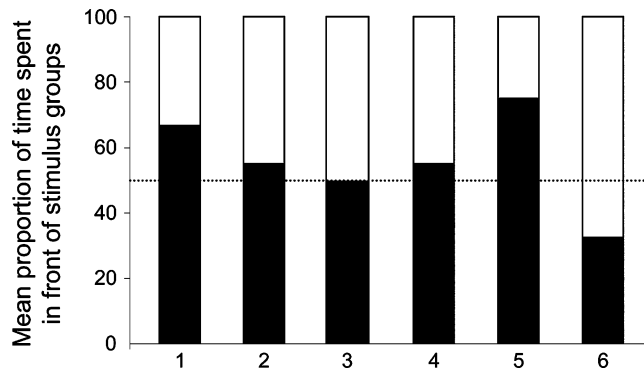


Figure 3

Each bar represents the mean proportion of time that the focal fish of that group ($N = 12$ for each group) spent in front of the familiar stimulus group (shaded area) or the unfamiliar stimulus group (white area). The line represents the expected frequency (50%) under the null hypothesis that there would be no difference between stimulus groups.

Experiment, we used G tests separately for each of the five single focal fish trials ($N = 20$ in each trial) as well as for the three trials including three focal fish ($N = 20$ groups of three fish in each trial). The results from these separate analyses were then further analyzed using a Fisher's combined probability test with χ^2 distribution and $2k$ degrees of freedom (k = number of separate tests; Sokal and Rohlf, 2000). For the Genetic Analysis, average within-group relatedness was estimated using the program Relatedness 5.0.8 (Queller and Goodnight, 1989). We used all genotyped fish to calculate the background population allele frequencies. Groups were weighted equally, and standard errors were calculated by jackknifing over loci. The relatedness estimate was considered to be statistically different from zero if the 95% confidence intervals of the estimate ($r \pm 1.96$ (SEM)) did not overlap zero. All the abovementioned parametric analyses were checked for and displayed normally distributed residual errors.

RESULTS

Homing experiment

After 10 h, no translocated fishes had returned to their original groups. However, after 24 h, an average of 33% (Table 1) of the translocated fish within groups had returned to their original group. Only in one group did we not observe any returning fish.

This return rate was significantly higher than would be expected if fishes just swam in a random direction and stayed in the first group of sea urchins they could find (dependent t test against reference constant: $t_5 = 3.6$, $p = .016$). No translocated fishes were found in any of the other groups involved in this experiment. Thus, no mixing took place between these groups during the experiment.

Familiarity experiment

Focal fish did not spend more time in front of familiars as compared to individuals from another group (Figure 3). On average, 56% (mean seconds \pm SD = 167 s \pm 44) of the total experimental time of 5 min (300 s) was spent in front of familiars and 44% (133 s \pm 44) was spent in front of fishes from another group (dependent t test: $t_5 = 0.94$, $p = .39$). More than 90% of the focal fish tried to enter the compartments of the stimulus fish, suggesting that focal fish indeed responded to the stimulus fish and that they actively tried to reach a group of fish. Most focal fish also visited both stimulus groups (mean number of times the border between the compartments was crossed \pm SD = 2.2 \pm 3.3). There was no difference in time spent with familiars between focal fish that visited both experimental groups (mean time spent with familiars \pm SD = 159.8 \pm 115.0) and those that did not (176.5 \pm 149.9) (t test: $t_{70} = 0.53$, $p = .6$). Furthermore, focal fish did not visit familiars first more often. On average, 60% of the focal fish visited familiars first and 40% of the focal fish visited individuals from another group first (χ^2 test: $\chi^2_6 = 2.0$, $p = .85$).

Location versus familiars experiment

Focal fish preferred their home location with unfamiliars over an unknown location with familiars in both the single focal fish trials and the group of three focal fish trials (Figure 4). On average, 77% of the single focal fish chose their home location, whereas only 23% chose their familiars in the new location (Fisher's combined probability test: $\chi^2 = 27.6$, df = 10, $p < .005$). For the group of three focal fish trials, 93% of the focal fish groups chose their home location, whereas only 7% chose their familiars in the new location (Fisher's combined probability test: $\chi^2 = 38.1$, df = 6, $p < .0001$). All focal fish actively tried to enter the stimulus cages by swimming through the net. A total of nine focal fish in the single focal fish trials altered their decisions after their first

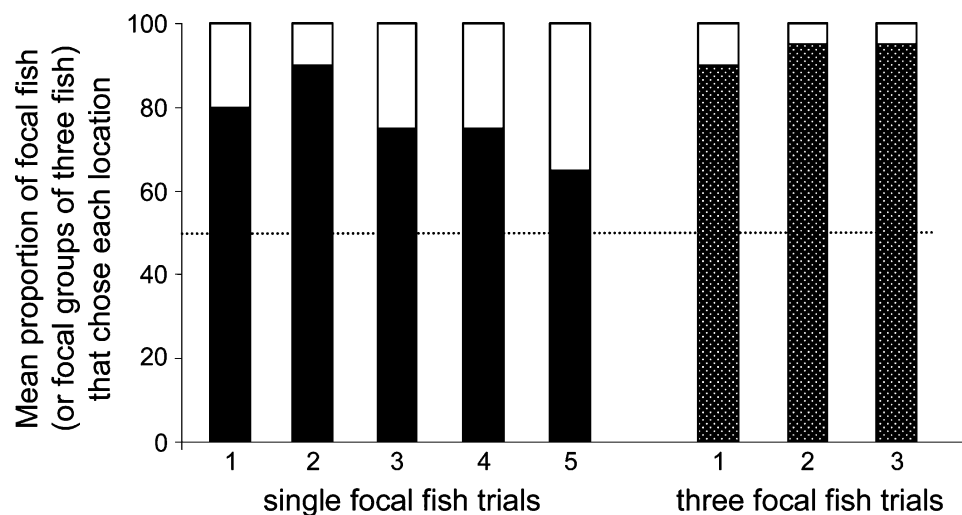


Figure 4

Each bar represents the mean proportion of fish that chose location (shaded area) or familiars (white area) for the five single focal fish trials and the three focal fish trials where three focal fish were used ($N = 20$ for each group). The line represents the expected frequency (50%) under the null hypothesis that there would be no difference between stimulus groups.

Table 2

Average relatedness (R) of individuals within 10 groups of Banggai cardinalfish calculated from 10 polymorphic microsatellite loci. Average number of individuals genotyped across all loci in a group is designated by n . None of the R values are significantly greater than zero (95% confidence ranges of R overlaps with zero for all groups)

Group	1	2	3	4	5	6	7	8	9	10
N	16.7	16.2	14.6	16.9	15.5	17.8	19.1	18.4	17.4	17.4
(\pm SEM)	(1.5)	(0.8)	(1.0)	(1.2)	(1.6)	(0.7)	(0.6)	(0.7)	(0.7)	(0.6)
R	0.06	-0.004	0.002	-0.008	0.02	0.02	0.01	-0.02	0.02	-0.03
(\pm SEM)	(0.04)	(0.03)	(0.02)	(0.01)	(0.02)	(0.02)	(0.02)	(0.02)	(0.01)	(0.01)
Range of 95% confidence limits	-0.01 to 0.13	-0.05 to 0.05	-0.03 to 0.03	-0.03 to 0.02	-0.03 to 0.06	-0.02 to 0.06	-0.02 to 0.04	-0.06 to 0.02	-0.004 to 0.04	-0.05 to -0.009

choice. Interestingly, eight of these nine focal fish returned to their home location with unfamiliar after having visited the unknown location with familiars, whereas only one fish altered its decision in the other direction (binomial test: 8 versus 1, $p = .04$). For the groups of three focal fish trials, four focal groups returned to their home location after initially having visited familiars, whereas no fish altered their decisions in the other direction (binomial test: 4 versus 0, $p = .12$). These observations suggest that the focal fishes indeed had knowledge about both cages in the experimental setup and that some of the focal fish first sampled the different locations and groups.

Genetic analysis

Only 10 of the microsatellite loci were used for the relatedness calculations because one locus (Pka11) was monomorphic in all groups and therefore was removed from the relatedness calculations. Of the 10 loci used in the relatedness calculations, the number of alleles per locus ranged from 2 (Pka06) to 19 (Pka16) with an average (\pm SEM) of 11.5 (± 1.57). The number of individuals genotyped per locus within a group ranged from 10 to 20. The average number of individuals genotyped within groups across loci was 17 (Table 2). Surprisingly, none of the relatedness values were significantly greater than zero (Table 2).

DISCUSSION

Our experimental results show that Banggai cardinalfish indeed form stable groups and display homing behavior. Interestingly, we found no evidence for recognition of familiars and homing in this species was targeted to the location of the home group rather than to the individuals in that group. Furthermore, we found no evidence for kin structures within groups.

Homing in the Banggai cardinalfish appears to be a quick response as returning of individuals was observed within 24 h. Nevertheless, we believe that, given more time, additional individuals would have returned to their original groups. Such a pattern was evident, for example, in an experimental study on cichlids, where translocated individuals returned after as long as 7 days (Hert, 1992). Homing behaviors have been shown also in other species of cardinalfish (Marnane, 2000; Usuki, 1977). In three different species of cardinalfish, Marnane (2000) showed that the spatial distribution of individuals was highly stable. Furthermore, Marnane (2000) showed that high numbers of fish (33–63%), initially translocated as far as 2 km, returned within 3 days. Hence, group stability and homing appear to be common features in the family of Apogonidae.

But how does an individual find its way back to its original site? And what potential disturbances can cause displacement of individuals from their homesites and hence select for the

ability to return? Because we translocated fish above the water, we can rule out navigation through memory of the outward route. Instead, a recent study showed that such homing abilities can be driven by olfactory cues, enabling orienteering toward the original group of residence (Atema et al., 2002), a possibility also in the Banggai cardinalfish. Displacement of individuals is probably relatively common in shallow lagoons like the ones inhabited by the Banggai cardinalfish due to oceanic disturbances (e.g., storms). A selective pressure on homing abilities may hence be present if fitness benefits are derived from living in a familiar group or location.

We found no evidence for recognition of or preference for familiar group members. This is unlikely to be caused by lack of information of the stimulus groups because most focal fish visited both treatment groups. Furthermore, stress levels, measured as number of crossings between the stimulus groups, were low (Warburton and Lees, 1996). But there was no significant difference as to which group the focal fish first visited or in the time spent in front of the familiar compared to the unfamiliar group. Although we cannot strictly exclude that Banggai cardinalfish are able to recognize familiars at any life stage, due to our use of relatively large fish and relatively low statistical power, we can at least conclude that preferences for group members (or kin recognition) is not a particularly strong behavioral feature of this species. Furthermore, the results from the location versus familiars experiment show that the location rather than the familiar group members is the cue that elicits the homing behavior in the Banggai cardinalfish.

Interestingly, the homing behavior in this species does not result in the formation of kin groups. Individuals within groups were not more related than individuals between groups. The formation of kin groups has been shown in many taxonomic groups, such as birds (e.g., Greenwood, 1980; Höglund et al., 1999; Shorey et al., 2000; Stacey and Koenig, 1990), mammals (e.g., Creel and Waser, 1994; Greenwood, 1980; Spong et al., 2002), fish (reviewed by Griffiths, 2003), and amphibians (e.g., Nicies, 1999). Moreover, kin-recognition mechanisms have been suggested to be a prerequisite for Hamiltonian kin selection (Gambao et al., 1991), and in most of the examples mentioned above, kin-recognition mechanisms have been observed. Our results support this view as the Banggai cardinalfish does not appear to recognize familiar group members (and hence most likely not kin) and does not form kin groups, despite homing behavior and group stability. Hence, the inability to recognize relatives may well constrain the evolution of kin selection and the formation of kin groups in the Banggai cardinalfish.

In light of the lack of population-level mixing, as evidenced by unusually high genetic structure over short distances between bays (Hoffman et al., in press), it was surprising to find that panmixis prevails among groups within a population of Banggai cardinalfish. Apparently, there is sufficient interchange of individuals between groups within populations

to dilute any group kin effects. Exactly how this takes place is unknown. Theory predicts that such dispersal may take place when group size reaches a threshold with regard to available resources (e.g., review by Goss-Custard and Sutherland, 1997). One such resource could be the number of sea urchins available for refuge. Interestingly though, there is only a very weak positive correlation between sea urchin area and number of fishes within groups in the Banggai cardinalfish (Kolm and Berglund, 2003). This pattern suggests that the number of sea urchins is not the limiting factor. As inbreeding may have deleterious genetic consequences in most species (Keller and Waller, 2002), inbreeding avoidance may be another potential factor leading to dispersal between groups. The question of when dispersal takes place and by who between groups in the Banggai cardinalfish is certainly a very interesting question that calls for further research.

But what are the benefits of staying in a particular group if kin-selection benefits can be ruled out? We suggest that there may be benefits from staying in a known social or physical environment that has led to the evolution of homing in this species. Based on an experimental study on five species of cichlids, Hert (1992) hypothesized that translocated individuals suffered greater costs from establishing new territories in new locations as compared to returning to an established territory. Although they do not display as much aggression as most cichlids, Banggai cardinalfish are still territorial within groups in aquaria and form dominance hierarchies (Kolm N, personal observation). Furthermore, spawning territories, which usually form in the vicinity of the main group, are aggressively defended in the wild (Kolm and Berglund, 2004). Hence, we suggest that Banggai cardinalfish may benefit from being in a known social environment where their social rank does not have to be reestablished through costly aggressive interactions. However, benefits may also be gained by staying in a known physical environment, if such behavior facilitates feeding and/or increase protection from predators. For the planktivorous Banggai cardinalfish staying in a known location where the water currents follow known patterns may be advantageous. Furthermore, as predatory fish may be highly stationary (Lembo et al., 2002), a known environment may be beneficial also with regard to predation risks.

To conclude, in this study we disentangled site affinity from affinity for group members behind the homing behavior in a homing species. Our results suggest that homing behavior is not sufficient to produce kin group structures, which supports the view that kin recognition may be an important prerequisite for kin selection and the formation of kin groups. It is obvious that the structure of groups and interactions between groups can be very complicated even in species with limited dispersal such as the Banggai cardinalfish and that many prerequisites need to be fulfilled prior to the formation of kin groups.

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