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SOCIAL TRANSMISSION OF BEHAVIOURAL TRADITIONS IN A CORAL REEF FISH

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Abstract. Traditional behaviours involve the non-genetic transmission of social information across age classes or generations. French grunts (*Haemulon flavolineatum*) exhibit social traditions of daytime schooling sites and twilight migration routes. Individuals transplanted to new schooling sites and allowed to follow residents at the new sites used the new migration routes and returned to the new sites in the absence of resident fish. Control fish with no opportunity to learn showed no such directionality or return. This is the first demonstration of apparent pre-cultural behaviour in free-living fish. Our observations suggest additional classes of behaviour and taxonomic groups in which pre-cultural activities are likely to have evolved.

Traditions are subpopulation-specific social behavioural patterns maintained across age classes or generations. Information necessary to maintain traditions may be acquired through inheritance or may be transmitted socially via learning from other, usually older, individuals. Social transmission permits the rapid acquisition of advantageous behavioural traits and is intimately related to the evolution of sociality.

Behavioural traditions and their social transmission are common phenomena in birds, mammals and insects, but have been shown in few lower vertebrates and invertebrates other than insects (Bonner 1980). Although evidence of social transmission has been found in captive fishes (Radakov 1973; Mainardi 1980), it has not been documented in free-living fishes. We have investigated the possibility that social traditions are maintained by learning in aggregating fishes of the family Haemulidae (grunts).

The traditions investigated involve the daytime schooling sites and twilight migratory routes of juvenile French grunts (*Haemulon flavolineatum*) in Tague Bay, St. Croix, U.S. Virgin Islands. Large juveniles (40-120 mm total length, 80-700 days old) form coral-head-specific daytime resting schools that persist for as long as 3 years, although members of these schools do not exceed 2 years in age (Brothers & McFarland 1981; Helfman et al. 1982). At dusk, these fish migrate along featureless (to human observers) routes into nearby grassbeds to feed on invertebrates; at dawn, return migrations to the same coral heads by the same individuals occur along identical routes (Ogden & Ehrlich 1977;

McFarland et al. 1979; McFarland & Hillis 1982; Meyer et al. 1983). Migration routes remain relatively fixed over at least 3 years (Helfman et al. 1982). Medium juveniles (15-30 mm long, 30-50 days old), the size class investigated here, are generally spatially separated from large juveniles; they form daytime schools over coral or sea urchins and perform twilight migrations. The migration routes used by medium juveniles are essentially constant over the 2-3-week time scale of the present study, although the locales and routes change in the course of a few months (Helfman et al. 1982).

It has been suggested that the traditions of schooling sites and migration routes in juvenile grunts are maintained because age cohorts overlap (McFarland 1980; Helfman et al. 1982). New members recruited to a school presumably learn the location of the school site and the migratory route associated with that site by following larger individuals during dusk and dawn migrations. To test this postulate, we transplanted medium juveniles from a home site to another medium juvenile site. We hypothesized that if transplanted fish were capable of learning the migratory route at the new, resident site, they should follow resident fish during twilight migrations and subsequently migrate along the resident route and return to the site in the absence of resident fish. Controls — transplanted fish that had no opportunity to learn from residents — should take a different route and should not return to the site.

Methods

Subjects

Three categories of test fish were used in the experiments:

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(1) Residents were fish at a site with an established migration route where experiments were conducted;

(2) Transplants were moved from their home site to the resident site and tested for learning of the migration route at the resident site after having an opportunity to follow residents during migration; and

(3) Controls were fish taken from the same home site as the transplants and moved to the resident site after removal of residents and transplants. Controls were therefore not given an opportunity to learn the resident route and their migrations should indicate whether migration routes at particular sites were the result of factors other than learning.

Protocol

After capture from the home school, transplants and controls were placed in 14-litre clear plastic boxes and fed twice daily. They were marked by fin clipping or by injection of acrylic paints (Thresher & Gronell 1978). Transplants were held at the resident site for 3–7 days ($\bar{X}=5.3$, $SD=1.6$) prior to release into the resident school. On the evening of release of transplants, migrating groups consisted of one or more residents followed closely by transplants. Fish migrated as a group and therefore each group — not each individual fish — was treated as a single migration. Two days later (two evenings and two mornings), all fish in the school were captured, only the remaining transplants were released, and their migration that evening was mapped. Controls were placed at the resident site after all residents and transplants had been removed. Controls were released after 1–7 days ($\bar{X}=2.5$, $SD=2.3$) of acclimation, and their migration on the evening of release was mapped. Transplant and control groups initially contained 10–20 individuals, although mortalities occurred during acclimation. Home and resident sites were separated by 0.2–1.0 km ($\bar{X}=0.65$ km, $SD=0.36$) and were 1–4 m deep. We chose resident sites that were isolated from nearby grunt schools by at least 25 m, to reduce the possibility of inter-school mixing during daytime (see Helfman et al. 1982) and to prevent transplants from encountering and following grunts at dawn that were from another school.

Migrations were mapped by divers who dropped markers at ≈ 1 -m intervals. Resident and home school routes were followed two to three times at each site. Between evenings, a 5–10° variation in common terminal distance

(Table 1) was not unusual, although replicated measurements of migration headings with an underwater compass also varied by ≈ 5 degrees. Fourteen transplant experiments were conducted in August and December 1981. The resident route analysed for comparison was that used during the evening of release of the transplants from the holding box, although resident migrations on other evenings were similar. The results shown here are from the six trials during which transplants were still present in the resident school 2 days after release. We observed no handling-induced differences in the behaviour of transplants and controls.

Results and Discussion

Migration of Transplants and Controls

Results from transplant experiments at the six sites are shown in Fig. 1. A qualitative indication of the degree to which migration routes can be learned is particularly evident at sites 1, 2 and 3 (Fig. 1), where transplants tended to zigzag across the established migratory route. Fairly accurate learning apparently took place in the 2-day period allotted. Although there was obvious variability, the migrations of transplants at the six sites in Fig. 1 were statistically indistinguishable from those of residents, whereas controls migrated differently from residents (Table 1). Transplants migrated along headings that were different from their home migration directions, whereas control migrations were not distinguishable from home migration directions (Table 1). The overall conclusion that can be drawn from the experiment is that the opportunity to learn from residents accounts for the change in migratory behaviour of the transplants. Controls, which had no comparable learning opportunity, either migrated randomly or were perhaps influenced by the direction they would have migrated had they remained at the home site.

Site 5 was unique in that residents did not migrate from the daytime site; individuals or pairs drifted away along different headings for short distances. This is the only such non-migratory group of juvenile grunts that we have seen during more than 200 observations of more than 50 different schools. Notably, transplants at site 5 similarly failed to migrate. Instead they slowly moved 1 m and stopped, whereas controls appeared to migrate actively (Fig. 1). One suggested advantage of social learning is that it allows for flexibility in otherwise stereotyped behavioural patterns (Galef 1976; Bonner 1980; Mainardi 1980). Non-migration by transplants

Table I. Resultant Headings of French Grunt Residents, Transplants and Controls at the Six Experimental Sites and at their Home Locations*

	Resultant angle (degrees) at common terminal distance (m)†					
	Site 1 (no.)	Site 2 (no.)	Site 3 (no.)	Site 4 (no.)	Site 5 (no.)	Site 6 (no.)
Experimental migrations						
Residents	347° @ 14 m (10)	233 @ 19(100+)	218 @ 13 (10)	171 @ 3.5 (8)	none (13)	194 @ 14 (50+)
Transplants	349 (3)	235 (2)	217 (3)	223 (2)	none (3)	232 (7)
Controls	33 (4)	260 (3)	168 (8)	9 (12)	355 @ 6.5 (3)	313 (12)
Home site migrations						
Transplants and controls	263 @ 6.5 (200+)	263 @ 6.5 (200+)	281 @ 19 (150+)	281 @ 19 (150+)	263 @ 6.5 (200+)	281 @ 19 (150+)

*A rank-sum test for directional data (Batschelet 1965) was used to compare resultant heading angles at the common terminal distance at sites 1, 2, 3, 4 and 6: transplants versus residents, $U = 7.5$, $P > 0.12$; controls versus residents, $U = 0$, $P < 0.04$; transplants versus home, $U = 0$, $P < 0.04$; controls versus home, $U = 3$, $P = 0.16$.

†The resultant angle was measured on graph paper at the same distance from the origin for all three groups at each site. This common terminal distance (= a point along the actual migratory path measured as the straight-line radial distance from the origin) was determined by the nearest point to the origin at which one of the groups divided or was lost. Migrations often continued for 10–20 m beyond the common terminal distance. Headings during actual migrations were rounded to the nearest 5° to allow for measurement error. The number of fish in the migrating group at each site is given in parentheses.

at this site may indicate the importance of social learning in the development of these twilight migrations.

The successive migrations observed at site 6 may demonstrate how the migration routes of medium juveniles develop or change (Fig. 1). The route of transplants without residents but

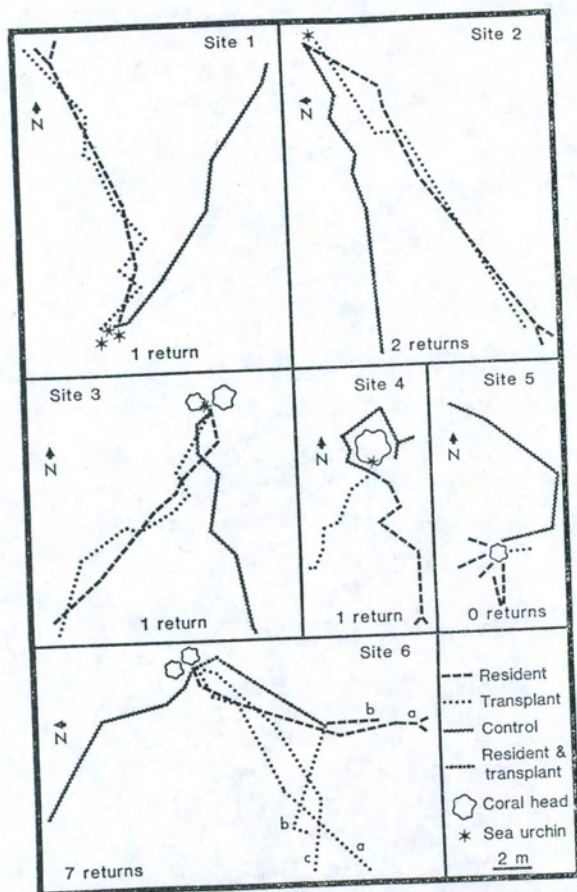


Fig. 1. Evening migration routes of French grunt residents, transplants and controls at six sites, Tague Bay, St. Croix, U.S. Virgin Islands. All migrations originated at a daytime schooling site, which included a coral head and/or *Diadema* sea urchin. Migration routes as mapped represent the direction of movement of resident, transplant or control groups. The transplant migration shown is for the first evening when transplants migrated without residents and after presumed learning took place. The number of transplants that returned in the absence of residents is shown for each site. Bifurcated ends of lines indicate that a group split and moved in different directions; other end points indicate the final heading of migration or the point at which fish were lost in the darkness (common terminal distance of Table I). First, second and third migrations at site 6 are denoted by a, b and c (see text).

after presumed learning was southwest of the resident route. We then returned residents to this site for 2 days. On the second evening, both residents and transplants initially moved together along the resident route for the first 8 m (resident and transplant line, Fig. 1). A group of residents continued along the resident route, whereas another group, which included the two remaining transplants, turned sharply to the southwest and crossed the route previously taken by the transplants when alone. The next evening, all fish were captured and the sole remaining transplant was released. It performed a migration that was intermediate between the resident route and the route used by transplants the previous evenings. Elements of both routes had apparently been incorporated into the migration of this individual. Events at this site are additional evidence that the migration route characterizing a particular site is not strictly determined by topographic features but is instead modifiable. Such flexibility would be adaptive if directions of migrations were influenced by selection pressures such as predator distribution and activity.

Return of Transplants and Controls

We visited resident school sites the morning after we released unaccompanied transplants or controls. A mean of 53% (SD=40%) of the transplants returned at least once to all sites in the absence of residents (Fig. 1); no controls were seen at any sites following the post-release migration (Mann-Whitney *U*-test on number of returned transplants versus controls, $P < 0.01$). This suggests that transplants learned the social tradition of daytime site location by following residents during migrations.

The non-return of some transplants to the resident sites — both in the six trials analysed here and in the eight additional trials during which transplants vanished — can be attributed to a number of causes besides inaccurate learning. After following residents on the evening of release, transplants may have attempted to return to their home site (Ogden & Ehrlich 1977); or they may have associated with individuals from different schools in the grassbed during the night and migrated with them the following morning (G.S.H., personal observation); or they may have been subjected to predation, perhaps owing to the conspicuousness of paint marks or erratic swimming because of clipped fins (M. J. Shulman, personal communication). In addition, resident fish actively repel newcomers in a school (W. N. McFarland, personal communication), and may

thereby discourage the establishment of transplants in a resident school.

Grunt Migrations as Possible Pre-cultural Phenomena

To be considered a socially-transmitted behavioural tradition, a behaviour pattern should meet several criteria (Galef 1976; Mainardi 1980). It should (a) lead to an increase in the homogeneity of behaviour within the social group; (b) be maintained after the termination of interactions between demonstrators and learners; (c) be distinguishable from imprinting, in that the acquisition of information is not limited to a short developmental period, and the presumed learning can be reversed or unlearned; and (d) differ among subpopulations of a species. Characteristics of grunts that are compatible with these criteria are that different developmental stages and even groups within a stage use different migration routes and daytime schooling sites (Helfman et al. 1982), and the present findings that transplanted individuals are apparently able to conform to a route at a new site.

A major advantage of the capacity for imitative learning of social traditions is its increased efficiency over trial-and-error learning, particularly when environmental changes mandate the rapid acquisition of behaviourally adaptive traits (Galef 1976; Bonner 1980; Mainardi 1980). Aggregating is an adaptive social response common to many taxa and serves multiple functions. In fishes, schooling is most often considered an adaptation to predation: this has been a postulated function of both daytime schools and group twilight migrations of grunts and other fish species (Shaw 1970; Hobson 1973; Morse 1980).

The adaptiveness of predictable behaviour in a predator-dense situation is not immediately obvious. If predators can learn the whereabouts of migration routes and can anticipate the timing of movements of their prey (as suggested by McFarland et al. 1979 and Helfman et al. 1982), selection pressures should favour individual prey that adopt novel, unpredictable activities and thereby avoid predators. If, however, group membership rather than solitary activity reduces a prey individual's risk to predators (Neill & Cullen 1974; Kenward 1978), then individuals that deviate from the route used by all other members of the group may expose themselves to nearby predators as a consequence of leaving the group. Evidence for such increased predation pressure on stragglers amongst migrating grunts

was discussed by Helfman et al. (1982). Social transmission of the traditions of site fidelity and migration route may function to establish and maintain group cohesion, to the possible benefit of both newly recruited and older school members.

The social traits of grunts that led us to suspect social transmission — traditional schooling sites, consistently used, precise migration paths, and overlap in age cohorts — are found in other marine and freshwater fish species (Hobson 1972; Gladfelter 1979; Helfman 1981). Social transmission in birds and mammals functions in the maintenance of traditional breeding migrations and areas, and has often evolved in conjunction with extensive parental care (Galef 1976; Bonner 1980; Mainardi 1980). Traditional breeding activities and/or parental care are also characteristic social traits in some fishes (Colin 1978; Loiselle & Barlow 1978; Keenleyside 1979; Baylis 1981; Johannes 1981), reptiles and amphibians (Burghardt et al. 1977; Houck 1977; Wells 1977; Shine & Bull 1979), and several invertebrate groups (Herrnkind 1969; Wilson 1971; Baker 1978; Ridley 1978; Keegan 1981). Social transmission of behavioural traditions is the common denominator of most non-anthropocentric definitions of cultural behaviour (Galef 1976; Bonner 1980; Mainardi 1980; Cavalli-Sforza & Feldman 1981). To our knowledge, this is the first demonstration of apparent pre-cultural behaviour in a free-living fish species. Pre-cultural behaviour may be a more widespread phenomenon than is commonly thought, and may even be the anticipated evolutionary result where strong selection pressures, such as predation, have produced distinct social adaptations.

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