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Initiators, Leaders, and Recruitment Mechanisms in the Collective Movements of Damselfish

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abstract: Explaining how individual behavior and social interactions give rise to group-level outcomes and affect issues such as leadership is fundamental to the understanding of collective behavior. Here we examined individual and collective behavioral dynamics in groups of humbug damselfish both before and during a collective movement. During the predeparture phase, group activity increased until the collective movement occurred. Although such movements were precipitated by one individual, the success or failure of any attempt to instigate a collective movement was not solely dependent on this initiator's behavior but on the behavior of the group as a whole. Specifically, groups were more active and less cohesive before a successful initiation attempt than before a failed attempt. Individuals who made the most attempts to initiate a collective movement during each trial were ultimately most likely to lead the collective movement. Leadership was not related to dominance but was consistent between trials. The probability of fish recruiting to a group movement initiative was an approximately linear function of the number of fish already recruited. Overall, these results are consistent with nonselective local mimetism, with the decision to leave based on a group's, rather than any particular individual's, readiness to leave.

Keywords: collective decision-making, local interactions, shoaling.

To maintain the benefits of sociality, grouping animals need to coordinate their behavior. Collective movements, in which multiple individuals travel relatively synchronously and coherently as a group between two points, are an important facet of group living. The establishment and maintenance of collective movement is dependent on information transfer, mimetism, and social feedback between

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group members (Couzin and Krause 2003; Sueur and Deneubourg 2011). Hence, studying the behavior of individuals within the group and the dynamics of the interactions between those individuals before and during such movements provides an excellent opportunity to understand collective behavior and decision making.

The period before a group's departure from a particular location can be crucial in determining the timing and characteristics of a subsequent cohesive group movement (Trillmich et al. 2004; Stueckle and Zinner 2008; Petit and Bon 2010). In many cases, the buildup to a collective movement is characterized by increased activity (Black 1988; Ramseyer et al. 2009*a*, 2009*b*). Once the group reaches a certain state of arousal, or readiness, then a collective move may be triggered (Petit and Bon 2010). Any group movement must be set in train by a single group member (an "initiator") making the first move (King 2010). However, this initiator will only be a leader if other group members follow; as Lamprecht (1991) put it, there is no leader without followers. Previous studies have shown that an initiator may be more likely to succeed in an attempt to instigate a collective movement if it is socially dominant and has close affiliations with other group members (Byrne et al. 1990; Sueur and Petit 2008) and if it is in close proximity to other group members (Ramseyer et al. 2009*b*) or in a central position (Leca et al. 2003). In addition, the behavior of the initiator before and during an initiation attempt may play an important role in determining the outcome of the initiation attempt (Ramseyer et al. 2009*a*). Often, however, several initiation attempts may fail before one is successful, and little is known about why some initiation attempts fail while others that involve the same individuals succeed.

What fundamentally distinguishes a failed initiation at-

tempt from a successful one is whether the initiator manages to recruit followers. To be considered successful, an initiation attempt must induce a mimetic response within the group and ultimately must recruit most, if not all, group members (Petit and Bon 2010). If individuals are selective in regard to which group members they will follow and which they will not, then it is likely that the social hierarchy and/or affiliations within the group will play an important role in the departure process; this is the so-called selective mimetism seen in many primate collective movements (Sueur et al. 2009, 2010; Jacobs et al. 2011; King et al. 2011; Sueur and Deneubourg 2011). Alternatively, the identity of the initiator and its affiliations within the group may be relatively unimportant in the recruitment process, as occurs with white-faced capuchins *Cebus capucinus* (Meunier et al. 2006). In such cases, it may be the proximity of individuals to the initiator when it actually makes its move to depart that is of primary importance in determining the sequence of departures. Local mimetism, in which individuals nearest to the initiator follow first and the decision proliferates topologically throughout the group, is a key driving force underlying the collective behavior of many species (Couzin et al. 2005; Ame et al. 2006; Faria et al. 2010b). Furthermore, recruitment may be relatively linear, whereby the probability of a group member being recruited to the new movement initiative is directly proportional to the number of individuals who have already been recruited, or group members may apply a quorum rule and wait to respond until a threshold number, or quorum, of individuals have been recruited (Ward et al. 2008, 2012; Sumpter and Pratt 2009).

To examine the dynamics of collective movement, we used the humbug damselfish *Dascyllus aruanus*, which is a tropical marine pomacentrid fish that grows to a typical maximum length of approximately 7 cm, as our model species. The humbug damsel is a social species and lives in colonies that can consist of up to 20 individuals but that most commonly consist of 3–6 members (Forrester 1991). Each humbug damselfish colony is highly territorial, and residents often actively repel unfamiliar conspecifics (Jordan et al. 2010). This aggression limits migration between colonies and so has the effect of stabilizing group membership over time (Forrester 1991). Individuals are capable of recognizing colony members and form linear, size-based dominance hierarchies whereby the largest individual in the colony is dominant to all other colony members, the second-largest individual is subordinate to the largest but is dominant to all other group members, and so on (Jordan et al. 2010; L. A. Jordan, unpublished data). As with many social species that live in close proximity to their predators, humbug damselfish are highly attentive and responsive to the behavior of others in their group. This is particularly noticeable in the context of their

movement decisions within their territories in the wild (A. J. W. Ward, personal observation).

We examined the process of collective movement in groups of humbug damselfish in an arena containing two habitat patches. Specifically, we examined the influence of group-level properties, including mean activity (in this case, mean distance swum per unit time) and cohesion, on the timing of collective movement and the influence of individual group members' size, activity, and proximity to other group members on collective movement. We contrasted the activity and mean neighbor distance of initiators and other group members in instances of failed and successful initiation attempts. Finally, we investigated for patterns of selective and local mimetism in the initial recruitment to the collective movement and determined whether the recruitment was a linear process, or a nonlinear process indicative of quorum formation.

Methods

Study Animals

Humbug damselfish (*Dascyllus aruanus*) were collected using hand nets from the first lagoon at One Tree Island (23°30′29″S, 152°5′30″E) on the Great Barrier Reef, Australia, in September 2009. To facilitate their capture, we applied a localized dose of clove oil to sedate the fish. We caught 5 fish from each of 16 discrete colonies. The fish were then transferred to one of sixteen 40-L containers in the aquarium facilities at the research laboratories at One Tree Island. Each colony was allocated to its own container, which was furnished with a piece of coral to provide shelter for the fish. To maintain water quality, all containers were set up on a flow-through system so that the water in the container was gradually replaced with water taken from the lagoon. The fish were closely observed for any signs of stress or illness after their capture; none were apparent. The fish were fed with plankton collected in the lagoon each evening by torchlight using fine mesh nets. Experiments commenced 48 h after capture.

Experimental Setup and Protocol

The experimental arena was a white opaque container measuring 110 cm × 50 cm × 60 cm (l × w × h) that was filled to a depth of 35 cm with water pumped from the lagoon. The tank was bare except for a single 15-cm strip of coral sand and pebbles ("the strip") at one end of the arena (fig. 1). All members of a single colony were then carefully netted and transferred to the arena. Although the strip offered little refuge, damselfish obligatorily associate with coral, and hence the group would
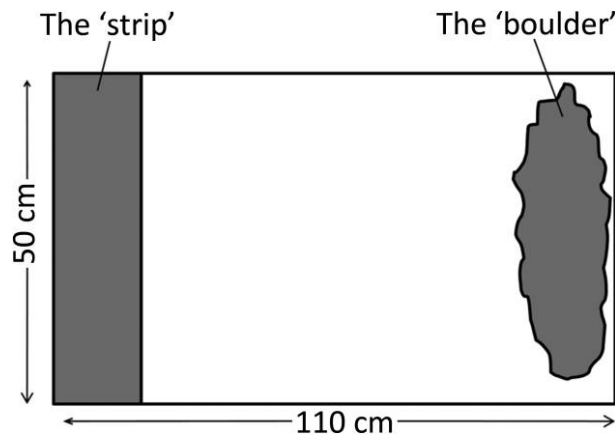
The 'strip'   The 'boulder'

Figure 1: Experimental setup.

always take up residence on this poor habitat patch. After
15 min had elapsed, we gently introduced a single, large
piece of coral ("the boulder") measuring 46 cm ×
15 cm × 29 cm (l × w × h, largest dimensions) to the
opposite end of the arena to the strip. The boulder was
attractive to the fish, because it offered multiple refugia.
However, the fish had to balance their motivation to cross
against their reluctance to leave their existing patch and
to cross open water to reach it. The fish were then left
undisturbed for an additional 20 min. The entire sequence
of 35 min was filmed at a resolution of 640 × 480 pixels
using a Canon G7 camera suspended approximately 1 m
above the arena. The trial was completed once the group
had crossed to the boulder or the 20-min period had
elapsed, whichever happened first. We conducted two trials
for each group with approximately 48 h between trials.
After the completion of the trials, the fish were removed
one by one, their flanks were photographed to provide
morphological information, and they were returned to
their original holding tanks. No attempt was made to sex
the fish; humbug damselfish are sequentially hermaph-
roditic, and external sex characteristics are not readily ap-
parent to human observers. The boulder was removed and
rinsed with fresh seawater, and the arena was completely
emptied and refilled before the beginning of the next trial.
After completion of the experiments, all fish were released
at their site of capture.

Data Collection and Analysis

The films of each experiment were processed into image
stacks using ImageJ, and these image stacks were then used
for manual tracking. Each individual fish was tracked sep-
arately throughout the full course of the experiment at a
frequency of 6 frames per second to obtain its *x, y* co-

ordinates. From this we were able to determine the activity
of each individual in terms of the distance that it swam
and the distance between all fish throughout the trial.

In all but one of the 16 trials in the first batch, the fish
crossed from the strip to the boulder within the time of
the experiment. The group that failed to cross was sub-
sequently excluded from the analysis. All groups crossed
to the boulder in the second batch of trials. Fish were
deemed to have crossed to the boulder once they had
swum more than halfway from the strip to the boulder.
This definition was based on pilot data collected the pre-
vious year and was robust in this series of experiment,
because fish remained at the boulder and did not return
to the strip once they had crossed. Before the crossing,
fish spent a mean of 96.7% of their time on the strip.

Statistical analysis was performed using R, version 2.13.0
(R Development Core Team 2011). Statistical models were
examined for normality by inspection of quantile-quantile
plots and for heteroscedasticity by inspection of standard-
ized residuals against fitted values and were log trans-
formed if necessary. Differences between groups in indi-
vidual body size, log(time taken to cross), mean activity,
and mean cohesion were examined using ANOVA.

For each trial, we investigated changes in log(group ac-
tivity) and log(cohesion) over the time period between the
addition of the boulder and crossing using general linear
mixed effects models using the lme4 package in R (Bates
et al. 2011). We included group identity as a random factor
and allowed for intercepts and slopes to vary between
groups. Exploratory analysis revealed significant autocor-
relation effects for most groups; this was controlled for by
adding an autocorrelation factor with a lag of one time
step to the mixed effects model. A model incorporating
random slopes and intercepts and autocorrelation was a
significantly better fit to the data than models in which
one or more of these factors were not included (assessed
using the Akaike Information Criterion). We then ex-
tracted the slopes and intercepts for the random effects
(groups) to assess the influence of these factors and their
interaction on crossing time using general linear models.
The intercept value gives an indication of the initial level
of activity or cohesion in the group, and the slope value
indicates the rate at which the measure increased over
time. The interactions effect was nonsignificant and so was
removed from the model, and only main effects are pre-
sented here.

We investigated differences and correlations between the
first and second trial in activity, cohesion, and crossing
time using mixed effects models with individual identity
nested within group identity as random effects. As fish
tended to cross in groups (see "Results"), we investigated
whether fish size, activity, and the mean distance to the
other four fish predicted its crossing lag; that is, the dif-

ference between the time taken for a given fish to cross and the time taken for the first fish in the group to cross. We therefore used mixed effects models to test for effects of size, activity, and distance to group mates (and their two- and three-way interactions) on log(time lag + 1), with group identity as a random factor. Nonsignificant interactions were removed following the stepwise procedure in Crawley (2007).

To examine the difference between a failed and a successful initiation of group movement, we first identified trials in which the individual fish that ultimately led a successful crossing had previously also attempted and failed to initiate a group movement in the trial. We defined a failed initiation attempt as one in which a fish left the strip and swam into open water for a distance of a minimum of one body length before abandoning the attempt and returning to the strip. We examined the behavior of this initiator and the behavior of other group members in the 10 s immediately before the initiator left the strip. We then used these metrics to compare behavior before failed versus successful initiation attempts.

To determine consistency in leadership, we examined the frequency with which the fish that led the first crossing also led the second crossing using a randomization goodness-of-fit test (McDonald 2009). In addition, we used the randomization goodness-of-fit test to examine whether leadership was related to rank and also to examine the use of local mimetism in the early stages of recruitment to the collective movement. In the latter case, we determined the distance between the initiator and all other fish in the last second before the initiator's departure. We ranked fish according to their proximity to the initiator from 1 (nearest) to 4 (farthest) and examined the ranked proximity to the initiator of the first fish to follow, hypothesizing that, if local mimetism was occurring, then the first fish to follow would be most likely to be a near neighbor.

Finally, to examine the possibility of selective mimetism, in which higher ranked (i.e., larger) fish may be more likely to successfully initiate a crossing, we calculated the probability of success as the number of successful initiations divided by the total number of initiations for each rank. To analyze this, we used the proportional goodness-of-fit test described by Zar (1999).

Recruitment Process: A Markov Chain Model

The process of crossing from the strip to the boulder involves fish moving both away from and back to the strip before finally crossing to the boulder. Assuming no or only weak differences between individuals, we can use a Markov chain to model how the fishes' decision to return to the strip or to leave it and cross to the boulder depends on the number of fish that are not on the strip (i.e., are in open water). Such a model will reveal whether there is a recruitment process (i.e., whether the probability of leaving increases with the number that have already left) and reveal the relationship between the number that have already left and crossing probability. The assumption underlying any Markov chain is that the state at the next second of time depends only on the current state.

The Markov chain has 6 states (i.e., 0–5 fish in open water, being more than one body length from the strip). If p_i denotes the probability that individual fish will leave the strip to enter open water at the next step when there are i fish already in the open area at present step, q_i denotes the probability that individual fish will remain in open water when there are i fish already in open water, and we assume each fish has the same p_i and q_i. We can write an $(n + 1) \times (n + 1)$ matrix **P** where element $P_{i,j}$ gives the probability that when there were i fish in open water at the previous step (i.e., $n - i$ fish on the strip), there j of these $n - i$ fish will go out to the open area from the strip. Thus, for each i, $P_{i,j}$ is binomially distributed among j, namely

$$P_{i,j} = \binom{n-i}{j} p_{n-i}^j (1 - p_{n-i})^{n-i-j}, \; j \leq n - i, \qquad (1)$$

$$P_{i,j} = 0, \; j > n - i, \qquad (2)$$

where $i = 0, \dots, n - 1$, and $j = 0, \dots, n$. Similarly, an $(n + 1) \times (n + 1)$ matrix **Q** can be written where element $Q_{i,j}$ denotes the probability when i fish were in open water at the previous step, j of these i fish will stay in open water. $Q_{i,j}$ is also binomially distributed among j,

$$Q_{i,j} = \binom{i}{j} q_i^j (1 - q_i)^{i-j}, \; j \leq i, \qquad (3)$$

$$Q_{i,j} = 0, \; j > i, \qquad (4)$$

where $i = 1, \dots, n$ and $j = 0, \dots, n$. Intuitively, when there are no fish on the strip, then no additional fish can leave the strip, which means $P_{n,0} = 1$. Similarly, when there are no fish already in open water, no fish can remain in open water; thus, $Q_{0,0} = 1$.

We obtained parameters from the experimental data by calculating the proportion of times that individual fish went out from the strip when there were i fish in open water at the previous time step (each time step is 1 s) and also the proportion of times that individual fish remained in open water when there were i fish in the open area. Because the result is obtained from 16 trials, the sample
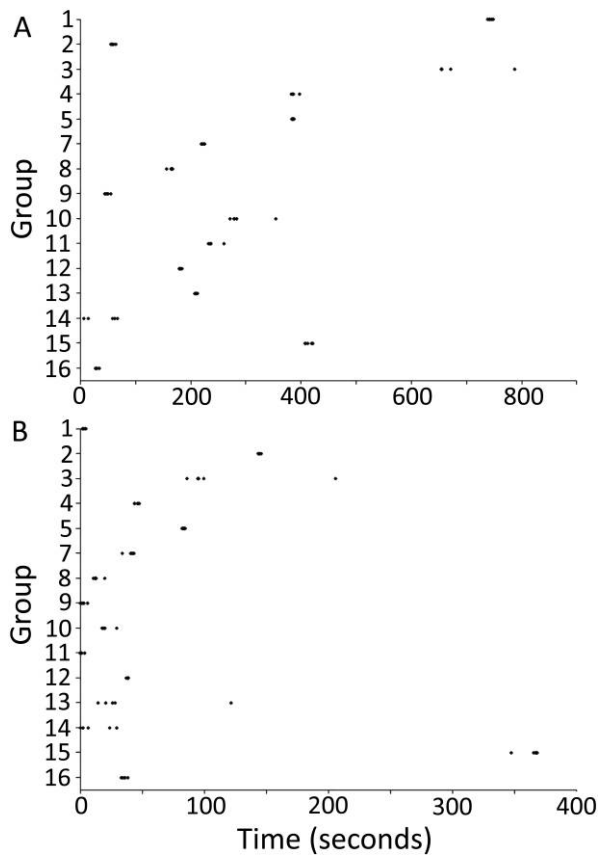
Figure 2: Crossing times for each group of fish for the first crossing trial (*A*) and the second crossing trial (*B*).

size is large enough to obtain reasonable estimates of p_i and q_i from the data.

The transition matrix, **T**, combines leaving and joining probabilities. Specifically, when there are i fish in open water, then $T_{i,j}$ is the probability that j fish will be in open water at the next time step. For each row, T_i, elements in it are a convolution of row i in P and Q, namely,

$$T_{i,j} = \sum_{k=0}^{j} P_{i,k} Q_{i,j-k},\qquad(5)$$

where $i = 0, \ldots, n$ and $j = 0, \ldots, n$. With p_i and q_i from the data, we can obtain the transition matrix theoretically using the procedure stated above. However, we can also get the transition probabilities from the data by calculating the proportion of times that the number of fish in the open area changed from i to j in one time step. Comparison of the two methods allows us to test the assumption that transitions in states can be represented simply in terms of independent parameters p_i and q_i. If the direct estimation of the Markov chain looks different from that obtained by putting together p_i and q_i, then it would un-

dermine the assumption that, within each second of time, fish decide independently of each other to move off or onto the strip.

For the second batch of crossing trials, we estimated the spontaneous leaving probability p_0 from the data (i.e., the probability of individual fish going off of the strip when there were zero fish in the open area). Our aim was to test whether the results of the second crossing can be predicted by the linear individual leaving and coming back probability obtained from the first batch of crossing trials (see "Results") with only one change, namely, the spontaneous leaving probability. When there are no fish in the open area, the crossing of fish can be treated as a Bernoulli trial; therefore, the maximum likelihood estimate (MLE) of the spontaneous leaving probability p_0 can be calculated by

$$\hat{p}_0 = \frac{\sum_{i=1}^{5} i \cdot t(n = i | n_{-1} = 0)}{5 \cdot t(n_{-1} = 0)},\qquad(6)$$

where $t(n = i | n_{-1} = 0)$ denotes the time length of the system being in the state that there are i fish in the open area when there were 0 fish at the previous step. We calculated p_0 for each trial in the second crossing and took the average as the final estimation.

A null hypothesis for the second crossing can be that each individual fish has a constant probability of leaving the strip and constant probability of staying in the open area regardless of the number of fish in the open area. To test this hypothesis, let $p_0 = p_1 = \ldots = p_4 = p$ and $q_1 = q_2 = \ldots = q_5 = q$; we had the MLE for p_0 by equation (8), so $p = \hat{p}_0 = p_1 = \ldots = p_4$. Similarly, the MLE of q_5 can be calculated by

$$\hat{q}_5 = \frac{\sum_{i=1}^{5} i \cdot t(n = i | n_{-1} = 5)}{5 \cdot t(n_{-1} = 5)}.\qquad(7)$$

Therefore, we have $q = \hat{q}_5 = q_1 = q_2 = \ldots q_4$. From these probabilities, we obtain the corresponding transition matrix, **T**.

Results

Group-Level Effects

There was no difference in body length between groups (ANOVA: $F_{15} = 0.56$, $P = .89$). There were significant differences between groups in time taken to cross in both trials (ANOVA, trial 1: $F_{14} = 73.69$, $P < .001$; trial 2: $F_{14} = 32.68$, $P < .001$) as well as differences between groups in activity in both trials (ANOVA, trial 1: $F_{14} = 7.77$, $P < .001$; trial 2: $F_{14} = 16.95$, $P < .001$) and differences between groups in group cohesion in both trials (ANOVA, trial 1: $F_{14} = 30.41$, $P < .001$; trial 2: $F_{14} = 6.36$, $P < .001$).

Table 1: Outcome of individual-level analysis examining the strength of fish size, activity, and mean distance to its neighbors as predictors of crossing lag

Variable	Value	df	T	P
Trial 1 (no significant interaction):				
Intercept	1.488	57	1.972	.054
Size	.19	57	1.589	.118
Activity	−.092	57	−1.383	.172
Mean neighbor distance	−.001	57	−.094	.952
Trial 2 (1 significant interaction):				
Intercept	−.897	56	−.937	.352
Size	.538	56	2.096	.041
Activity	−.069	56	−2.676	.01
Mean neighbor distance	.019	56	3.548	.001
Size × mean neighbor distance interaction	−.004	56	−2.278	.027

Note: Crossing lag is defined as the difference between the time taken for a given fish to cross and the time taken for the first fish in the group to cross.

Each group typically crossed in a single, relatively cohesive, and synchronous collective movement (fig. 2). Although there were considerable differences between groups with respect to the time that each took to cross, there was very little variation within groups, because each group member crossed at a similar time. Variability among groups is indicated by the sum of squares of the group mean time taken to cross about the overall mean time taken to cross. In the first trial, this was 5.449, and in the second, it was 13.989. By contrast, the within-group variability using the same sum of squares approach was 0.074 in the first trial and 0.428 in the second. There was no difference in within-group variability in crossing times between the first and the second trial (paired t-test: $t_{14} = 0.55$, $P = .59$).

In the first trial, both mean group activity (general linear mixed effects model: $t_{3,907} = 5.3$, $P < .001$; fig. 3c) and interindividual distances increased (general linear mixed effects model: $t_{3,926} = 3.6$, $P < .001$; fig. 3d) with time, until groups finally made the crossing. Groups that were more active after the introduction of the boulder crossed sooner than groups that were less active (linear model: $F_{1,12} = 17.9$, $P = .001$), but there was no significant effect of the rate of increase in activity (linear model: $F_{1,12} = 3.96$, $P = .069$). These factors (initial activity and change in activity) were negatively correlated (linear model: $F_{1,13} = 9.34$, $P = .009$). Similarly, groups that were initially less cohesive after the introduction of the boulder crossed sooner than those that were more cohesive (linear model: $F_{1,12} = 10.4$, $P = .007$), but the rate of change in cohesion was unrelated to crossing time (linear model: $F_{1,12} = 1.02$, $P = .333$). Again, these factors were negatively correlated (linear model: $F_{1,13} = 9.62$, $P = .008$).

In the second trial, there were fewer data, because groups tended to cross much more quickly. After the introduction of the boulder, mean group activity increased with time (general linear mixed effects model: $t_{844} = 2.4$, $P = .017$; fig. 3g), although interindividual distances did not increase (general linear mixed effects model: $t_{844} = 1.8$, $P = .068$; fig. 3h). There was no effect of initial activity (linear model: $F_{1,9} = 2.1$, $P = .179$) or cohesion (linear model: $F_{1,9} = 1.97$, $P = .193$) on crossing time.

Groups were more active (mixed effects model: $t_{74} = 7.14$, $P < .001$), less cohesive (mixed effects model: $t_{74} = 4.84$, $P < .001$) and crossed more quickly (mixed effects model: $t_{74} = 11.36$, $P < .001$) in the second trial than in the first. However, although there were differences in activity between trials when the whole trial was considered, in the critical period (30 s) immediately before the collective movement, group activity was roughly consistent between trials (paired t-test: $t_{11} = 1.28$, $P = .22$). Group activity, but not group cohesion, was correlated between trials 1 and 2 (mixed effects models, activity: $t_{59} = 5.22$, $P < .001$; cohesion: $t_{59} = 1.21$, $P = .22$).

Individual-Level Effects

During the first trial, neither a fish's size, nor its activity, nor its distance to its group mates predicted its crossing time lag. In the second trial, however, more active fish tended to cross more quickly, and there was an interaction between a fish's size and its distance to its neighbors, in which larger fish that were closest to their near neighbors tended to cross more quickly (table 1).

Fish that acted as leaders in the first crossing trial were significantly more likely to lead the second crossing than expected by chance (randomization goodness-of-fit test: $\chi^2 = 6.7$, df $= 1$, $P = .019$; fig. 4A). The probability of a fish leading the crossing was unrelated to its size and therefore unrelated to its rank (randomization goodness-of-fit test; first crossing: $\chi^2 = 6$, df $= 4$, $P = .22$, second crossing: $\chi^2 = 4.67$, df $= 4$, $P = .388$; fig. 4B). The fish
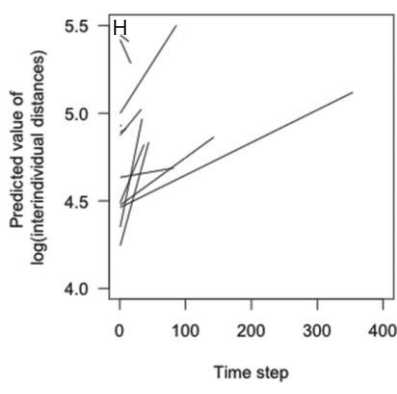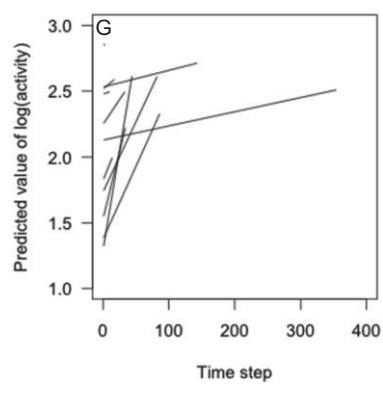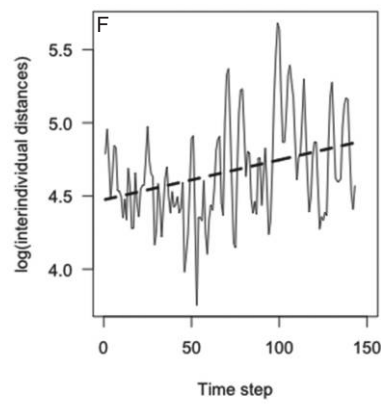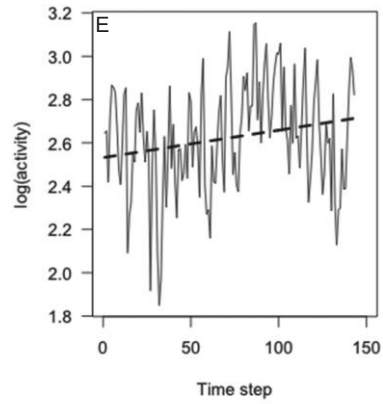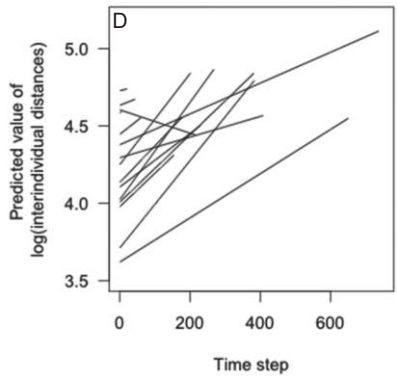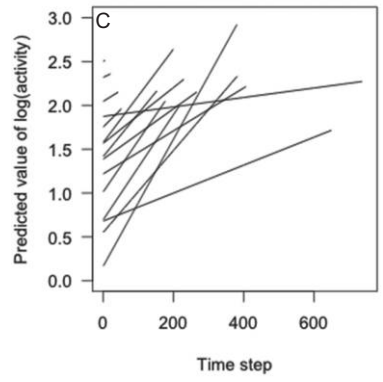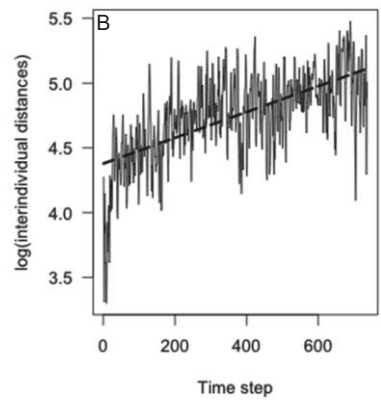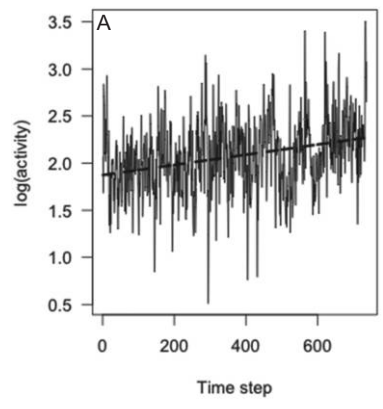
that had led the most failed initiation attempts before the final crossing was the most likely to lead the final crossing in both the first (randomization goodness-of-fit test: $\chi^2 = 11$, df $= 1$, $P = .003$) and second crossings (randomization goodness-of-fit test: $\chi^2 = 7.6$, df $= 1$, $P = .009$)

Comparison of Successful versus Failed Leadership Initiations

There was no difference in the activity of an initiator (paired t-test: $t_{12} = 1.58$, $P = .14$) or in its proximity to other group members (paired t-test: $t_{12} = 1.71$, $P = .11$) in the 10 s immediately before a failed versus successful initiation attempt. However, group members were more active (paired t-test: $t_{12} = 2.94$, $P = .01$) and less cohesive (paired t-test: $t_{12} = 3.44$, $P = .004$) before a successful initiation attempt than when compared with a failed attempt.

Initiators were significantly more active than other group members (paired t-test: $t_{12} = 4.11$, $P = .001$) and had a significantly greater mean distance to their neighbors than did other group members (paired t-test: $t_{12} = 4.11$, $P = .001$) before failed attempts, but showed similar levels of activity (paired t-test: $t_{12} = 1.13$, $P = .28$) and similar distances to neighbors (paired t-test: $t_{12} = 1.58$, $P = .14$) as other group members before successful initiation attempts.

Selective and Local Mimetism

There was no evidence that the size (or therefore rank) of an initiator influenced the probability of its being able to successfully initiate a crossing (goodness-of-fit test; first crossing: $\chi^2 = 7.49$, df $= 4$, $P = .223$, second crossing: $\chi^2 = 7.48$, df $= 4$, $P = .224$; fig. 4C). However, there was evidence for local mimetism in that the first fish to follow the initiator was likely to be a near neighbor at the point of departure (randomization goodness-of-fit test, first crossing: $\chi^2 = 8.73$, df $= 3$, $P = .037$; second crossing: $\chi^2 = 9.27$, df $= 3$, $P = .025$; fig. 4D).

Recruitment Mechanism

The leaving and returning probability by individual fish from the first crossing indicates that the number of fish in the open area is a good predictor of how likely other fish are to follow into the open area. When the number of fish i in open water increases, the probability p_i of moving to open water increases, whereas the probability of returning to the strip, $1 - q_i$, decreases (fig. 5A). The rate of change of these parameters is approximately linear in both cases. Once the number of fish in open water exceeds two, the probability of leaving the strip is greater than the probability of returning to the strip (fig. 5B).

The slope of the linear leaving probability function

$$p_i = \alpha \cdot i + p_0 \tag{8}$$

given by MLE is $\hat{\alpha} = 0.0581$. We obtained a spontaneous probability of crossing per second, $\hat{p}_0 = 0.0405$. Using p_i and q_i in figure 5, we obtained the transition matrix given by the Markov chain model. For most values of i, the p_i- and q_i-based transition matrix matches the experimental data (fig. 6a). The main difference between model and data occurs when there are one or two fish in open water. Here the probability that one fish will remain in open water is lower than predicted by the model.

In the second crossing, we obtained a spontaneous leaving probability $\hat{p}_0 = 0.0726$ by MLE. We then tested two hypotheses about the second crossing: (1) that the linear response of leaving established in the first crossing held for the second crossing, albeit with a larger value for p_0; and (2) that leaving probabilities in the second crossing were independent of the other fish.

To test hypothesis (1), and based on the linearity showed in equation (9), we calculated $p_1, \ldots, p_4$ using $\hat{\alpha} = 0.0581$ obtained from the first crossing and the new spontaneous leaving probability $\hat{p}_0 = 0.0726$. With the same q_i from the first crossing, we obtained the transition matrix (black dashed line in fig. 5B). We compared this to the transition matrix directly from the data (green solid line in fig. 6b). The transition probabilities were well predicted by the linear individual leaving (p_i) and coming back ($1 - q_i$) probability obtained from the first crossing with only an adjustment of p_0. In contrast, the transition matrix obtained from hypothesis (2), that individual fish have a constant leaving and staying probability, namely $p_i = p$ and $q_i = q$ does not provide as good fit to the data (black dotted line in fig. 6).

Figure 3: Changes in mean activity and interindividual distance within groups with time after the introduction of the "boulder." Shown are the change in mean activity over time for an example group (group 1) in crossing trial 1 and the line of best fit for this series (A); the change in mean interindividual distances for the same group, again in crossing trial 1 and with the line of best fit plotted (B); the lines of best fit for mean activity for all groups in trial 1 (C); and the lines of best fit for mean interindividual distance for all groups in trial 1 (D). We plot these data for crossing trial 2, using group 2 as our example group, in E–H.
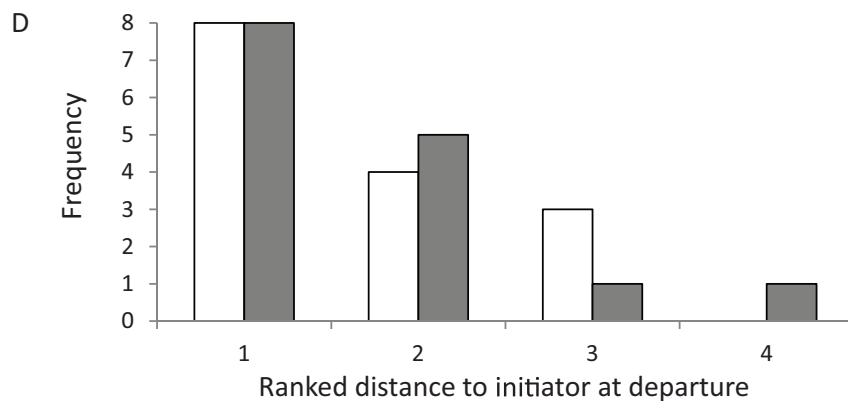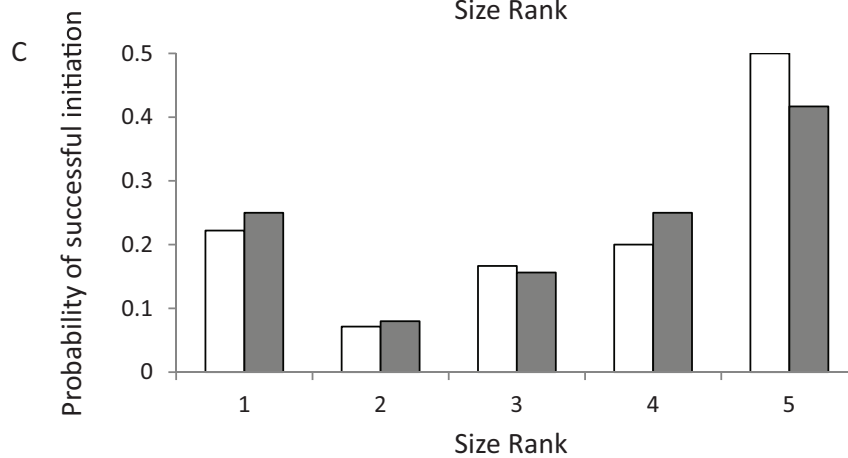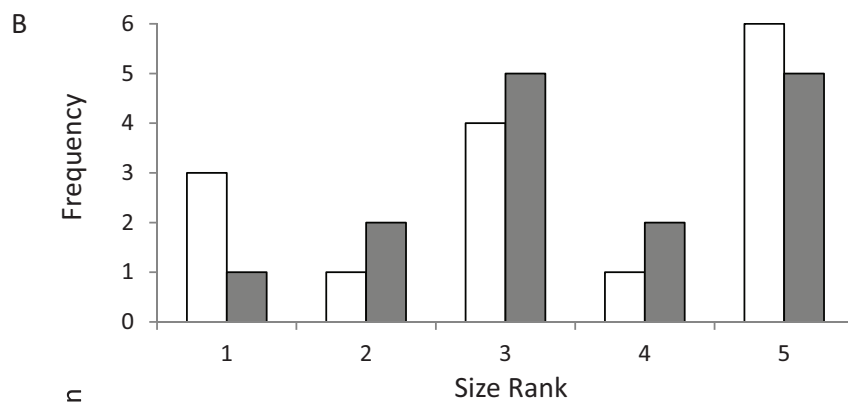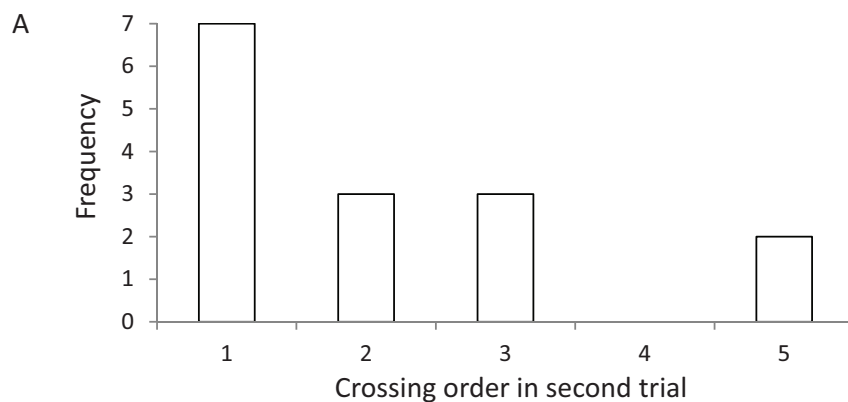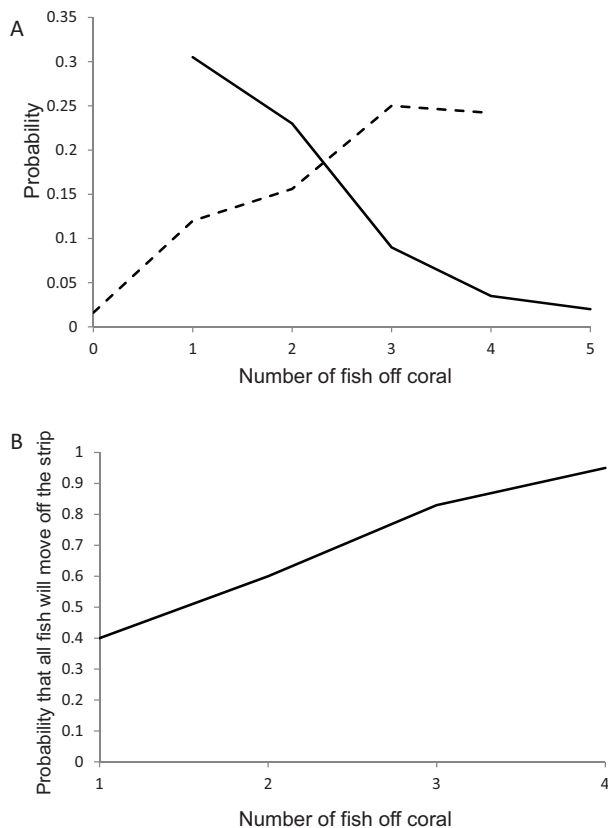
Figure 5: *A,* Number of fish in the open area versus the probability of individual fish leaving the strip (p_i) and returning to the strip $(1 - q_i)$ when there was a corresponding number of fish in the open area at the previous second. The dashed line represents p_i, and the solid line is for $1 - q_i$. The experiment was conducted for 16 sets of fish; $n = 5$ fish in each of the trials. *B,* Probability that all fish will be off the strip when starting from different system states. The calculation is based on the transition matrix from the first set of crossing trials. To calculate this, we set up 0 fish and all fish (5 fish) in the open area as two absorbing states of the Markov model with transition matrix **T** and calculated the probability for each initial condition that the system would move to the end state.

Discussion

Collective movements are a fundamentally important component of the behavior of many social species. Groups of humbug damselfish moved relatively synchronously and coherently between two habitat patches. The timing of the decision to move and the likelihood of recruitment to the move appeared to be dependent on the collective dynamics of the entire group. In the buildup to the move, group members became more active; indeed, any attempt to initiate a group movement could succeed only once the group was sufficiently active. The initial recruitment to the move was based on local mimetism, and overall, fish recruited linearly to the collective movement. Leadership was consistent between the two trials but was not related to size (or therefore to dominance).

The behavioral dynamics in this system are likely driven by conflict between attraction to the boulder on the one hand and the need for caution on the other, because crossing open water is potentially risky, and in addition, the boulder could theoretically harbor predators. To minimize these risks, the fish benefit from coordinating the timing of the group departure, because traveling as a group provides a valuable defense against predator attack (Neill and Cullen 1974; Krause and Ruxton 2002). In the second trial, in which fish had some experience of the experimental arena and of the boulder, the time taken to cross was much reduced, although group members showed the same level of coordination in the timing of their crossing. This suggests that, even when the perception of risk decreases, group members continue to exert considerable influence upon one another and remain strongly motivated to coordinate their behavior (Couzin et al. 2005; Buhl et al. 2006; Sumpter 2006).

The success or failure of an attempt to initiate a collective movement was not solely dependent on the behavior of the initiating individual; there was no difference in the behavior of the initiator between failed and successful initiation attempts. Instead, the probability of success or failure appeared to depend on whether the other group members had reached some critical level of activity or had reacted to previous (failed) start attempts, which emphasizes the importance of the predeparture period in the generation of collective movements (Petit and Bon 2010). Hence, for group movement to occur, it is a necessary requirement both that an individual act to initiate the move and that the group be ready to move. Although much research has focused on the phenotypic and behavioral attributes of leaders, our study emphasizes the primary importance of the other group members' behavior in determining the outcome of an initiation attempt. In all cases, the failure of other group members to respond to an initiation attempt by following caused an initiator to abandon the move and return to the group (Petit et al. 2009). It is possible that, even in failure, an initiator may succeed in communicating the intention to move and,

Figure 4: Position adopted in the second crossing trial by the individual that led the first crossing (*A*); frequency that each size rank adopted the role of leader (*B*); probability of successfully initiating a group movement for each size rank (*C*); and ranked proximity of the first fish to follow in relation to the initiator, where 1 is the nearest neighbor of the initiator (*D*). In *C*, *D*, and *E*, white bars represent values from the first crossing trial, and gray bars represent values from the second crossing trial. For each trial, $n = 15$.
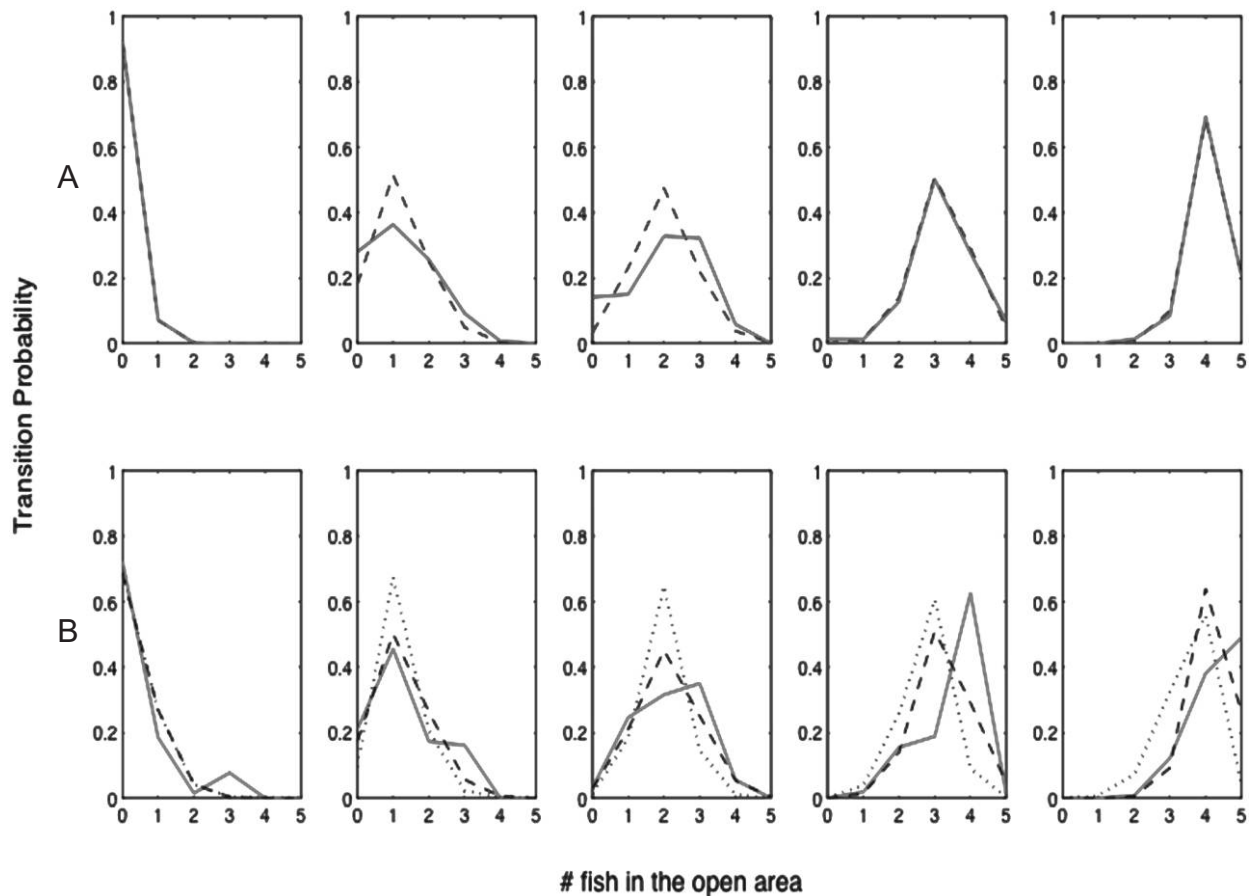
Figure 6: Comparison of data and prediction from the Markov chain model. It displays the transition matrix from the experiments. The *X*-axis is the number of fish *j* in the open area at the next step, and the *Y*-axis shows the probability that the system would transfer to the state indicated by the *X*-axis from its current state. From left to right, the current state is $j = 0, \ldots, 4$, respectively. *A*, The first round of the experiment. The dashed line indicates the prediction, whereas the solid line is the corresponding probability calculated from the data. *B*, The second round of the experiment. The dashed line indicates the prediction from the linear leaving probability model, the dotted line represents the prediction from the constant leaving probability model, and the solid line is the corresponding probability calculated from the data.

indeed, in "priming" such a move (Raveling 1969; Bourjade et al. 2009). In fact, in the small groups studied here, in which global communication among all group members is possible, such recruitment strategies may often be successful (Conradt and Roper 2005). Nonetheless, although initiators often failed to instigate a collective movement, they were the most likely to lead the collective movement when it did finally occur. Generally, the most active fish tended to attempt most initiations and ultimately to lead the group, which suggests a role for personality in determining leadership in humbug damselfish in common with other species (Ward et al. 2004; Kurvers et al. 2009; Burns et al. 2012).

There was no evidence of selective mimetism in relation to the hierarchy in terms of the probability of group members recruiting to the move. Instead, proximity to the ini-

tiator was the key determinant of which fish was the first to follow. In some ways, this is surprising, given that the social organization of the damselfish bears similarity to that of species in which selective mimetism has been observed (Sueur et al. 2009) and differs from the fission-fusion groups that are characteristic of most shoaling fish (Couzin 2006). Nonetheless, their emphasis on local mimetism displays strong similarities to other fish species (Herbert-Read et al. 2011; Katz et al. 2011) and, indeed, to human pedestrian behavior. Local mimetism was also found in humans waiting to cross a road. Single leaders who spot a gap in the traffic and move to cross are regularly followed by their nearest neighbors. However, a one-person gap in the crowd was already sufficient to disrupt this mimetic effect (Faria et al. 2010*a*). As Sueur et al. (2011) argue, there is reason to believe that the characteristics of

collective behavior and decision making may vary across different species according to the fission-fusion dynamics of their social organization.

As has been observed in other species (e.g., eusocial insects: Seeley and Buhrman 1999; birds: Raveling, 1969; mammals: Ramseyer et al. 2009*a*, 2009*b*), there was a characteristic predeparture phase in which activity increased that led up to the move. Although group cohesion also decreased during this time, this was likely a simple consequence of the increasing activity as individuals moved around the strip. The interindividual distances remained at all times within the typical values observed in fish groups (Pitcher 1993). Interestingly, although the rate of change in activity was not important, initial activity was a strong predictor of the group's latency to cross, and more active groups made the crossing sooner. Furthermore, although groups were more active in the second trial than the first, possibly reflecting the reduction in novelty and therefore neophobia, this was largely driven by the fact that groups showed higher mean activity at the outset of the second trial. Importantly, in the 30 s before crossing, groups showed roughly equivalent levels of mean activity in both trials. This appears to suggest that groups must reach some critical activity threshold before making a crossing, hence the greater initial activity in the second trial likely helped determine the lower crossing latency in that trial. This critical activity threshold seems to be group specific, however. Although each group attained an activity level before crossing in the second trial that was similar to that attained in the first, there was large variation among groups, with the most active groups being more than twice as active as the least active groups.

The probability of fish leaving the strip increased and the probability of fish returning to the strip decreased linearly as the number of fish off the strip increased. Individuals were thus more likely to move if their companions had already initiated movement. The two probability functions cross when there are two fish in the open area, which suggests that two fish might be a critical quorum threshold for making a decision to cross (Ward et al. 2008; Sumpter and Pratt 2009). Unlike in the quorum models, however, the overall probability of leaving the strip, which depends on the product of these two linear functions, also grows approximately linearly as the number of fish off the strip goes up. In the second crossing trials, the fish already had experience of the experimental setup and, having crossed the arena once previously, were twice as likely to initiate a movement in this case. Despite this increase, the fish movements were still consistent with a linear response to conspecifics. In other words, the baseline tendency to leave increases in a "safer" situation, but the form of the response remains the same. This is consistent with the fish

"tuning" their crossing decision to safer conditions (Pratt and Sumpter 2006).

In our study, we have considered the process of decision making relating to the need to reach consensus on the timing of a collective movement. The dynamics of such a decision are likely to be somewhat different compared with decisions regarding the direction of a collective movement. Reaching consensus over the timing of a collective movement may often require less of a compromise by group members than achieving consensus over the direction of a move (Conradt and Roper 2010). It would be fascinating in future work to examine the process of collective movement in this system in the context of a conflict over the direction of travel.

Acknowledgments

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