



## Context-dependent group size choice in fish

D. J. HOARE\*, I. D. COUZIN\*†, J.-G. J. GODIN‡ & J. KRAUSE\*

\*Department of Biology, University of Leeds

†Department of Ecology and Evolutionary Biology, Princeton University

‡Department of Biology, Mount Allison University, Canada

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The costs and benefits of group membership vary with the size of groups, and individuals are expected to modify their choice of groups in response to ecological factors such as food availability and predation risk. We experimentally examined context-dependent group size choice in a shoaling fish, the banded killifish, *Fundulus diaphanus*, by using nondirectional odour cues to simulate a food source or a successful attack by a predator (food or alarm treatments) in the laboratory. Group sizes were significantly smaller in the food treatment and larger in the alarm treatment than in control trials. When presented with food and alarm cues together, fish formed groups that were larger than control groups but smaller than those seen with alarm cues alone. These results are consistent with theoretical predictions based on the known benefits and costs of grouping and with previous laboratory work examining the individual shoal choice behaviour of single fish. To examine possible mechanisms of group formation, we developed an individual-based model of shoaling behaviour in which simulated fish were allowed to modify the area over which they interacted with neighbouring individuals. Group size distributions produced by the model were a good approximation of our experimental data. We suggest that local behavioural interaction rules of this type are a potential mechanism by which fish may individually adjust grouping behaviour without requiring extensive information on the position and movement of all possible shoalmates.

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For group-living animals, individual fitness varies as a function of group size, so that individual group choice reflects a dynamic trade-off between the costs and benefits of membership (Pulliam & Caraco 1984). Typically, competition for resources increases, whereas predation risk and certain foraging costs decrease with increasing group size (Alexander 1974). This trade-off has been extensively investigated for shoaling fish (Pitcher & Parrish 1993), in which changes in both shoal size and composition may be common under natural conditions (Pitcher et al. 1996; Mackinson et al. 1999; Krause et al. 2000; Svensson et al. 2000), providing the opportunity for individuals to use shoaling behaviour as a flexible strategy in response to changes in environmental conditions or internal state.

Laboratory studies have shown that individual fish generally prefer to join the larger of two available groups, and that these preferences are stronger when perceived predation risk is high (e.g. Keenleyside 1955; Hager &

Helfman 1991; Ashley et al. 1993; Krause & Godin 1994a; Svensson et al. 2000). In these studies, an individual fish was presented with a simple binary choice of associating with one of two stimulus shoals which were restrained in tanks or bottles, so that the group sizes available were controlled by the experimenter. These observations reveal the 'ideal' choices of individual fish, and are consistent with the concept that individuals join larger groups to benefit from reduced predation risk (Godin 1986, 1997; Magurran 1990; Pitcher & Parrish 1993).

By definition, however, natural group sizes reflect the behaviour of all group members, and it is not always easy to predict how individual membership decisions interact to produce stable outcomes. Predicted 'optimal' group sizes, for example, are generally exceeded because solitary individuals continue to join (Sibly 1983; Pulliam & Caraco 1984). It is thus important to ask what group sizes are actually observed when all individuals are free to make membership decisions, although few studies have examined such free choice situations (but see Pitcher et al. 1983).

We examined group size choice in the banded killifish, *Fundulus diaphanus* (see Fig. 1), when individuals were free to join and leave shoals. We tested whether frequency

Correspondence: J. Krause, Department of Biology, University of Leeds, Leeds LS2 9JT, U.K. (email: [jens.krause@leeds.ac.uk](mailto:jens.krause@leeds.ac.uk)). I. D. Couzin is now at the Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08540, U.S.A. J.-G. J. Godin is now at the Faculty of Science, Carleton University, 1125 Colonel By Drive, Ottawa, ON K1S 5B6, Canada.

distributions of observed group sizes were context specific, and investigated the relative importance of perceived food availability and predation risk in determining group size.

Fish were subjected to four experimental treatments: food; alarm; food + alarm; and control. We used odour cues to simulate the presence of food or a potential predatory threat without any directional information, thus avoiding aggregations resulting simply from fish moving towards or away from a particular location in the tank. Food odour was used to simulate the presence of food without direct competition for the resource itself. We simulated increased predation risk in the form of a successful predatory attack by adding a killifish skin extract to the water to evoke an alarm response in the test fish. Many aquatic organisms show antipredator behaviour in response to chemical cues from potential predators or from injured prey (reviewed in Chivers & Smith 1998; Kats & Dill 1998). Preliminary trials showed that adding killifish skin extract to the water caused a fright reaction in conspecifics, and thus functioned as an effective alarm cue for the purposes of this study.

No odour cues were added in the control treatment, which provided a reference point of normal activity in the experimental arena. We predicted that groups should be smaller on average in the food treatment than in the control treatment (as fish try to reduce potential competition), and larger in the alarm treatment than in the control (as fish seek to reduce per capita predation risk). We also predicted that group sizes among fish in the combined food + alarm treatment, with potentially conflicting cues, were likely to be intermediate between the group sizes formed with either cue alone.

The mechanisms underlying the interactions of individuals during group choice are still poorly understood. Increasingly, however, social group dynamics have been considered to arise from an interplay between 'social forces', such as attraction, alignment and repulsion, which regulate interindividual distances (reviewed by Warburton 1997). Individual-based simulations have been used to examine how local interactions between neighbouring individuals based on such a 'balance of forces' model (Breder 1954) can give rise to group level properties such as overall structure and movement (e.g. Okubo 1986; Huth & Wissel 1994; Parrish & Turchin 1997; Beecham & Farnsworth 1999). We present a simple agent-based model in which individuals adjust their position within a group using a simple behavioural rule based on local interactions with neighbours. At the mechanistic level, apparent predation risk and food availability are expected to result in changes in the interindividual distances that fish maintain. For example, fish increase nearest-neighbour distances when hungry (Morgan 1988; Robinson & Pitcher 1989a, b) and increase shoal cohesion, positioning themselves closer to other individuals, when perceived predation risk is high (Magurran & Pitcher 1987; Krause 1993a). We used a balance-of-forces model, in which individual fish vary the range over which they interact with others, to investigate whether such a mechanism can explain the grouping patterns of killifish observed in our experiment. We did not specify the functional cause of changes in interaction range within our model, as we used

it to investigate context-specific group size changes in general.

## EXPERIMENTAL SHOALS

### Methods

Several hundred juvenile banded killifish were collected under permit (from the Department of Fisheries and Oceans, Canada) from the littoral zone of Morice Lake (near Sackville, New Brunswick, Canada: 45°55'N, 64°21'W) in September 1995 using a 5-m beach seine. Fish were maintained in a fibreglass tank (200×200 cm and 15 cm high) supplied with flowing well water (18–20 °C) and exposed to overhead fluorescent lighting on a 12:12 h light:dark cycle for approximately 1 month prior to testing. They were fed freeze-dried chironomids *ad libitum* twice daily. Experiments were conducted in a Plexiglas tank (100×100 cm and 15 cm high, water depth 10 cm), surrounded by a blind of black plastic sheets to minimize external disturbance.

We conducted six replicate trials for each of four experimental treatments: (1) Food: food odour plus water; (2) Alarm: killifish skin extract plus water; (3) Food + Alarm: food odour plus skin extract plus water; (4) Control: water only. For each trial, we obtained skin extract by dissecting off the skin of a single freshly killed killifish (total body length 40 mm) and crushing the skin with a pestle and mortar (von Frisch 1942). This crushed skin was then sieved through filter paper to remove large particles and mixed with 300 ml of well water to yield an extract of a concentration similar to that of the Schreckstoff alarm substance used by von Frisch (1942). Skin extract was kept refrigerated and used within 24 h of preparation.

For each trial, we produced food odour by crushing approximately 200 mg of dried chironomid larvae (the food fish were usually given, see above) with a pestle and mortar. This was then sieved through filter paper to remove large particles and mixed with 300 ml of well water. In treatment 3, food odour and skin extract were mixed in 300 ml of well water, and unmanipulated well water (300 ml) was used as a control.

To record trials, we used a video camera mounted above the centre of the tank. Fish were not fed for 2 h before the trial started. For each trial, 10 fish were haphazardly selected from the holding tank, but were size matched to within 5 mm within each trial to avoid association biases caused by body length (Krause & Godin 1994a; Hoare *et al.* 2000). Overall, the total body length of test fish ranged from 35 to 45 mm. For each trial, the 10 test fish were introduced together into the centre of the experimental tank and left overnight to acclimate.

We filled a water vaporizer with 300 ml of well water containing the test substance and sprayed it five times (in total about 5 ml) evenly on to the water surface from above the tank. Spraying was done from outside the test tank so that fish could not perceive any overhead movement during the procedure. Pilot trials using water dyed with Alcyon Blue showed that the sprayed fluid spread evenly on the water surface and thus did not produce differences in fluid concentrations within the test tank. We began trials

when the treatment cue was sprayed over the tank, and stopped them after 60 min of recording. At the end of a trial, the test fish were removed, placed in a separate holding tank, and not reused in subsequent trials. We then emptied the experimental tank, scrubbed it and flushed it with well water for several hours to remove any residual odours. Experiments were carried out between 0900 and 1700 hours and trial order was randomized.

We collected data on group size from the video recordings. The size of all groups was recorded every 30 s, beginning 30 s after the introduction of the treatment substance. We considered two fish to be part of the same group if they were within four body lengths of each other (16 cm, measured from the head). This distance falls within the range of interindividual distances observed in natural fish shoals (Pitcher & Parrish 1993) and is a criterion previously used for defining group size in laboratory experiments (Pitcher et al. 1983). Since shoals were largely two-dimensional in the shallow experimental tank, we did not consider distances between fish in the third dimension in the analysis. A trial lasted 60 min, thus yielding 120 data points. We conducted six replicate trials of each treatment, although two trials were lost because of damaged recordings. As a consequence, the number of replicates was unbalanced across treatments, and non-parametric statistics were used in the analyses. We used Mann–Whitney  $U$  tests to test for a priori predicted differences in the median group size between each of the three odour cue treatments and the control treatment. The mean group size observed was calculated for each 30-s time interval (because group sizes are not independent within each observation), and the median of these values was calculated for each replicate trial separately.

#### Ethical note

To produce the skin extract for the alarm treatment, six individuals were killed by a single hard blow to the head and the head was crushed before we dissected off the skin. We did not use chemical methods (e.g. MS 222) to kill the subjects to avoid possible confounding odour cues in the subsequent experiment. All other fish were released at their site of capture at the end of the experimental period (after several months in captivity), and as banded killifish are abundant at the study site (Hoare et al. 2000) the loss of six individuals does not represent any significant effect on the population.

General observations indicated that increased shoal size and shoal cohesion were the primary behavioural responses to the alarm treatment (see Results), and we used a nondirectional alarm stimulus to avoid directional escape responses. No fish in this or other treatments showed 'freezing' behaviour or violent escape movements such as attempts to escape the experimental tank. Free-swimming killifish shoals at this site are frequently accompanied at close range for prolonged periods, and attacked, by predatory yellow perch, *Perca flavescens*, and respond primarily through shoaling interactions with conspecifics (personal observation). We are thus confident that this treatment did not represent an unusually high level of threat and simulated a heightened predation risk without causing undue distress to the subjects.

## Results

Grouping behaviour, measured in terms of the median group size observed, varied markedly between the four treatments (Fig. 1). Group size in all three odour cue treatments was significantly different from that of the control treatment (two-tailed Mann–Whitney  $U$  test: control versus food:  $U = 0$ ,  $N_1 = 6$ ,  $N_2 = 4$ ,  $P = 0.01$ ; control versus alarm:  $U = 0$ ,  $N_1 = N_2 = 6$ ,  $P = 0.004$ ; control versus food + alarm:  $U = 1$ ,  $N_1 = N_2 = 6$ ,  $P = 0.01$ ). As predicted, median group size was smallest in the food treatment and largest in the alarm treatment (Fig. 1). The combined treatment of both food and alarm stimuli produced an intermediate response, with the median group size falling between that of the control trials and those with the alarm cue alone.

Frequency distributions of the median group size observed across all replicate trials (Fig. 2) confirm the general pattern of results described above. In the control treatment, small groups were most common and large groups of five or more fish relatively rare. When food odour was added to the tank, solitary fish became much more common and the distribution was more strongly skewed to the left, indicating that larger groups separated. In contrast, adding killifish skin extract in the alarm treatment resulted in fish forming large groups; although small groups of one or two were still relatively common, the majority of individuals occurred in groups of 10, as indicated by the distribution of individuals across groups of each size (Fig. 2d). This highlights the need to examine the shoal choice of individuals rather than simply counting group sizes. Fish responded to the food + alarm treatment in an intermediate manner compared with the single-odour treatments. Small groups were most frequent, with 50% of observations involving groups of two or less, but individuals were evenly distributed between large and small groups (Fig. 2c).

## MODELLING SHOALING BEHAVIOUR

### Methods

Following the approach of Aoki (1982) and Huth & Wissel (1994), we simulated the behaviour of individuals as resulting from 'repulsion', 'alignment' and 'attraction'

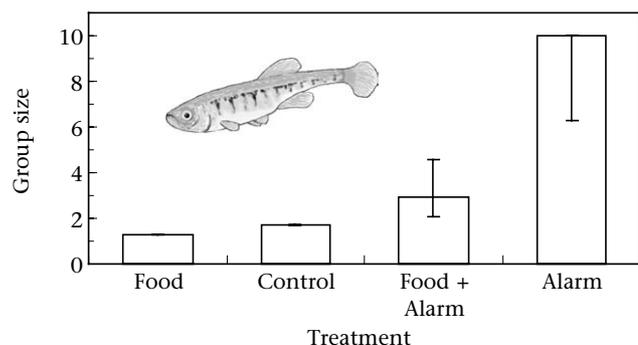
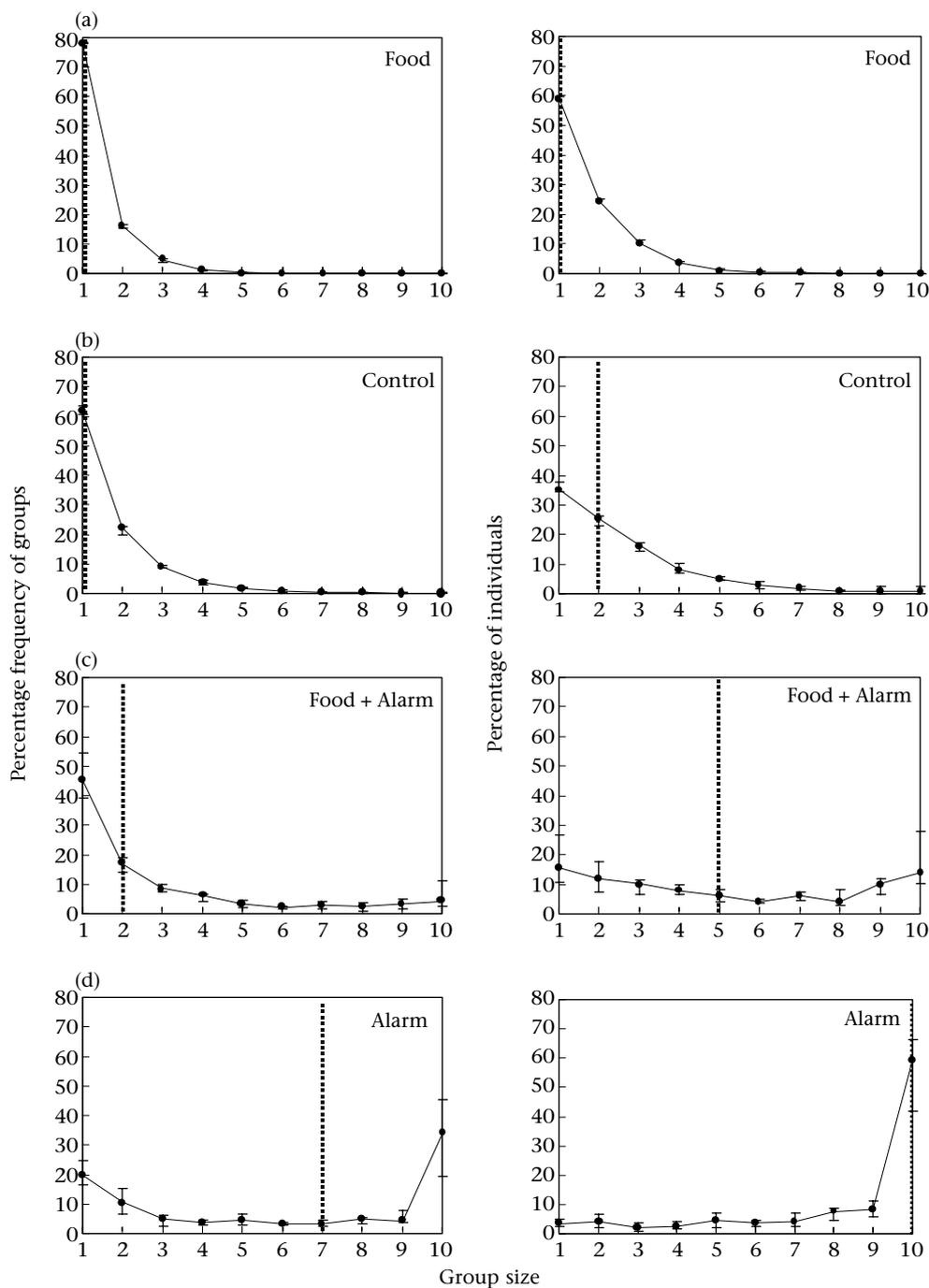


Figure 1. Median group size observed in each treatment. Vertical lines indicate quartiles; where quartiles do not appear they are identical to the median value.



**Figure 2.** Percentage frequency distributions of killfish group sizes and percentage of individuals occurring in groups of different size in the four treatments: (a) Food; (b) Control; (c) Food + Alarm; (d) Alarm. Values are the median percentage frequency across all replicate trials. Vertical lines indicate quartiles. Dotted lines represent the point above which 50% of observations lie.

tendencies based upon the position of individuals relative to one another. Vision and lateral line mechanoreception are thought to be the most important sensory modalities for coordinating collective movement in fish (Partridge 1982; Bleckmann 1993) although the relation between perception and movement tendencies is still poorly understood. For this reason, individuals in our simulation model were accorded the following simple behavioural

rules that are intended to characterize generic behavioural tendencies to approach or avoid other fish.

(1) Individuals attempt to maintain a minimum distance  $\delta$  between themselves and other individuals at all times. This represents the tendency of fish to avoid collisions, and is consistent with interindividual distance regulation in real fish schools (Partridge 1982; Huth & Wissel 1994; Couzin et al. 2002; Krause & Ruxton 2002).

This rule is assumed to have the highest priority since collisions with neighbours, even during rapid avoidance manoeuvres, are known to be rare. Furthermore, if they occur, they may create a localized disturbance that can result in individuals becoming misaligned, and therefore prone to predation (Radakov 1973; Partridge 1982). For simplicity, here we assume  $\delta$  is constant. See Couzin et al. (2002) for a similar model in which this parameter is varied.

(2) If individuals are not making an avoidance manoeuvre (1), they tend to be attracted towards and to align themselves with neighbours. Individuals respond in this manner to all other individuals within a local interaction zone of radius  $\rho$ , which is equal to or larger than the zone of repulsion. This zone of interaction is variable and subject to changes in grouping motivation. Increasing the radius ( $\rho$ ) of the zone of interaction increases the number of neighbours to which a fish is attracted, and thus serves to increase group cohesion. Conversely, reducing the radius of the interaction zone decreases the number of near neighbours to which a fish is attracted, effectively reducing shoal cohesion.

(3) Individuals also tend to maintain a minimum distance  $\delta$  between themselves and environmental obstacles, such as simulated arena walls in this case. This represents avoidance of collisions with such obstacles.

In our model, there are  $N$  simulated fish, with individual  $i$  having position vector  $\mathbf{c}_i(t)$  and direction vector  $\mathbf{v}_i(t)$ . Fish are simulated in a domain measuring  $1 \times 1$  m with a reflective boundary.

Time is partitioned into discrete steps  $t$  with spacing  $\Delta t = 0.01$  s chosen to approximate the response latency of shoaling fish to external stimuli (Partridge & Pitcher 1980). At each time step, the direction vectors and then the position vectors of all fish are updated in parallel.

The updating of the direction vectors is as follows. If there are other fish  $j$  within a distance  $\delta$  of fish  $i$  it avoids them by turning towards a desired vector

$$\mathbf{d}_i(t + \Delta t) = - \sum_{j \neq i} \frac{\mathbf{c}_j(t) - \mathbf{c}_i(t)}{|\mathbf{c}_j(t) - \mathbf{c}_i(t)|}. \quad (1)$$

If there are no fish within distance  $\delta$ , the individual will respond to fish  $k$  within the interaction range  $\rho$

$$\mathbf{d}_i(t + \Delta t) = 1/2 \left[ \sum_{k=1} \frac{\mathbf{v}_k(t)}{|\mathbf{v}_k(t)|} + \sum_{k \neq i} \frac{\mathbf{c}_k(t) - \mathbf{c}_i(t)}{|\mathbf{c}_k(t) - \mathbf{c}_i(t)|} \right] \quad (2)$$

where the first term within brackets represents a tendency to align with neighbours, and the second term within brackets represents the tendency to be attracted to neighbours.

If there are no neighbours within distance  $\rho$ , then  $\mathbf{d}_i(t + \Delta t) = \mathbf{v}_i(t)$ .

Fish also attempt to keep a certain minimum distance  $\delta$  from the borders of obstacles: in this case the four edges of the domain. Therefore a border (each domain edge)  $B$  exerts a repulsive effect, which can be described by

$$\mathbf{f}_B(t) = - \frac{\mathbf{r}_B(t) - \mathbf{c}_i(t)}{|\mathbf{r}_B(t) - \mathbf{c}_i(t)|} \quad (3)$$

where  $\mathbf{r}_B(t)$  denotes the location of that point of the border  $B$  that lies closest to fish  $i$ . The repulsive forces are summed for all borders within distance  $\delta$  of fish  $i$ , and this cumulative force is normalized, becoming  $\mathbf{f}'_B(t)$ . Replacing  $\mathbf{d}_i(t + \Delta t)$  with  $\mathbf{d}'_i(t + \Delta t)$ , the influence of the borders is incorporated as  $\mathbf{d}'_i(t + \Delta t) = 1/2(\mathbf{d}_i(t + \Delta t) + \mathbf{f}'_B(t))$ .

In the eventuality that the social forces result in a zero vector, then  $\mathbf{d}_i(t + \Delta t) = \mathbf{v}_i(t)$ .

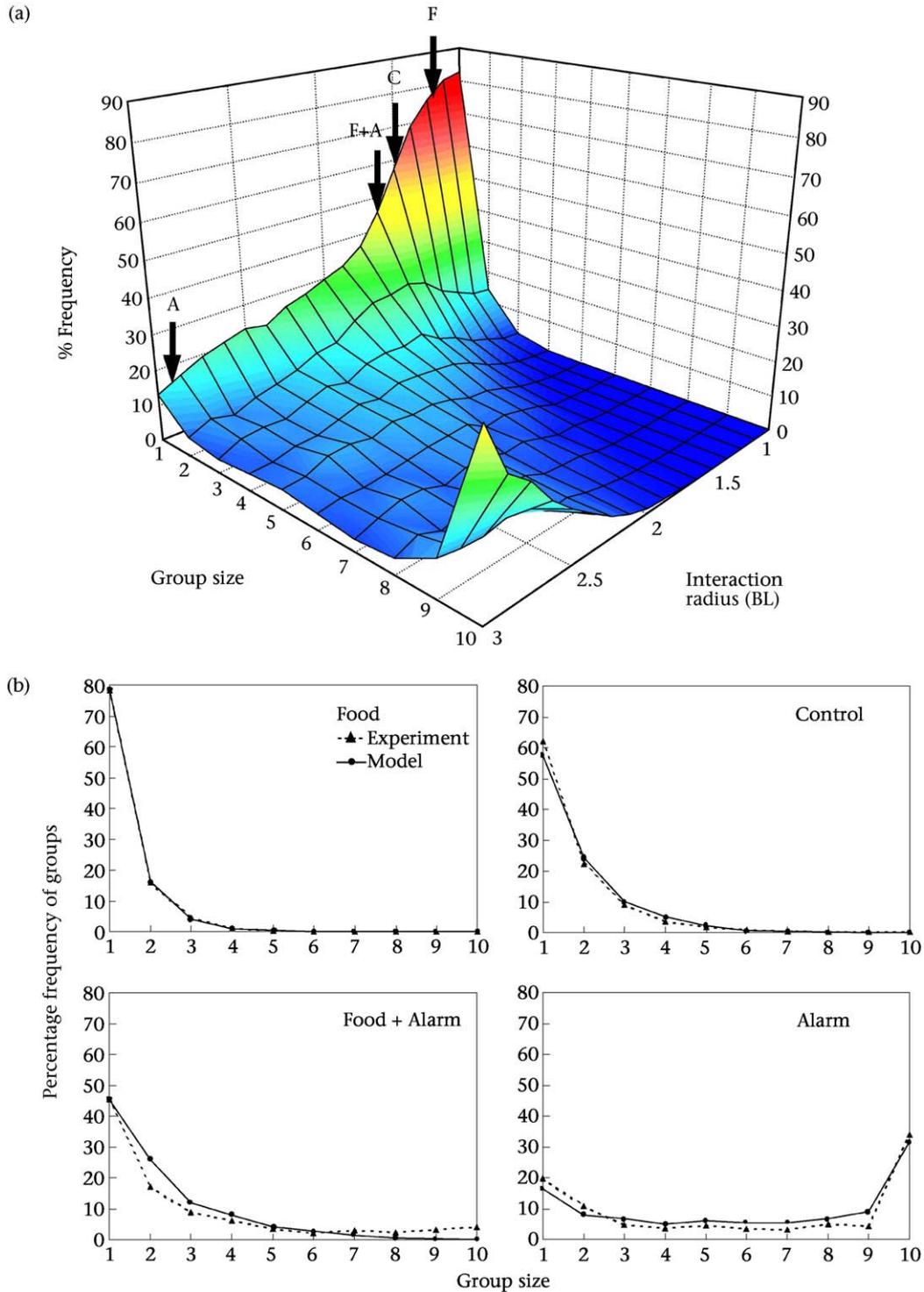
Fish are able to turn through an angle of at most  $\theta \Delta t$  degrees, where  $\theta$  is the maximum turning rate. If the angle between  $\mathbf{v}_i(t)$  and  $\mathbf{d}_i(t + \Delta t)$  is less than  $\theta \Delta t$ , then fish  $i$  achieves alignment with its desired vector,  $\mathbf{v}_i(t + \Delta t) = \mathbf{d}_i(t + \Delta t)$ ; otherwise it turns  $\theta \Delta t$  towards it. All turning is assumed to be subject to slight error. This is simulated by rotating  $\mathbf{v}_i(t + \Delta t)$  by angle  $\sigma$  (a Gaussian-distributed random deviate centred on 0 with standard deviation  $\sigma = 0.1$  radians).

This completes the calculation of the new direction vectors. The new position vector of fish  $i$  is then given by  $\mathbf{c}_i(t + \Delta t) = \mathbf{c}_i(t) + \mathbf{v}_i(t + \Delta t) \Delta t s$ , where  $s$  is the speed of movement of the fish. Simulated fish have a body length of 4 cm (= 1 BL) as in our experimental trials, and other parameters are set accordingly;  $N = 10$ ,  $s = 1.25$  BL/s (J. Krause, unpublished data),  $\delta = 1$  BL (Partridge 1982),  $\theta = 100^\circ/\text{s}$  (Krause & Tegeder 1994). We investigated the influence of interaction radius  $\rho$  over the range 1–3 BL.

## Results

Five hundred replicate simulations of the model were run for each value of the interaction radius  $\rho$ . For each replicate, data on group size were collected at the 5000th timestep, by which time group behaviour in the model had reached a dynamically stable state. To assess the spatial distribution of individuals in the model, we used the same criterion (of grouping together fish within four body lengths of a neighbour) that was applied to live fish in our test tank. The minimum distance 'personal space'  $\delta$  remained constant, as this is expected to be a function of the need to avoid collisions (Partridge 1981, 1982). However, we explicitly changed the interaction radius  $\rho$  within which individuals are attracted to others in the model to explore how this affected group size. Theory predicts that increases in food availability may increase this interaction radius (Morgan 1988) and that increases in predation risk may decrease it (Krause 1993a), making the model a useful point of comparison with our experimental data, although we did not explicitly make  $\rho$  a function of any particular biological factor.

Modifying the continuous interaction radius  $\rho$  produced a broad range of group size distributions (Fig. 3a). As the interaction radius  $\rho$  in the model is increased, the resultant group size frequency distribution shows a transition from left-skewed distributions, in which small groups are very common, to a right-skewed distribution where the most frequent group sizes are large (Fig. 3a). At intermediate values of  $\rho$ , the distribution is relatively flat,



**Figure 3.** Percentage frequency distributions of median group sizes in the model, using the 5000th timestep from 500 replicates. (a) Group size as a function of interaction radius  $\rho$  (measured in body lengths, BL). (b) Vertical slices through the model output. F:  $\rho = 1.2$  BL; Food treatment; C:  $\rho = 1.5$  BL; Control; F + A:  $\rho = 1.6$  BL; Food + Alarm treatment; A:  $\rho = 2.9$  BL; Alarm treatment.

as all group sizes are observed, although individuals and pairs are still the most frequent. This transition is in the same direction as predicted, and corresponds closely to distributions derived from the experimental treatments (Fig. 3b). Note that values of the interaction radius highlighted in the model are not necessarily quantitative

predictions of those used by fish in the experimental trials. Instead, the model is intended to demonstrate the logical consistency of the type of underlying mechanism we propose and to reveal qualitatively how changing the interaction radius results in changes in group size distribution.

## DISCUSSION

Animal group sizes are the result of membership decisions made by all group members. We have shown that freely formed group sizes in banded killifish are highly context dependent, with fish forming shoals of very different sizes in response to nondirectional food or alarm cues. This is consistent with the group size choices made by individual fish in laboratory binary choice tests (e.g. Krause & Godin 1994a), and with theoretical predictions based on the costs and benefits of grouping.

Although median group size was generally small in the control treatment, as predicted it was significantly reduced by the presence of a simulated food source. In the food treatment, group size decreased to the extent that 60% of individual fish were found alone at any one time compared with 36% alone in the control trials. Our fish were allowed to acclimatize to the tank conditions overnight, such that the results of the control treatment probably reflected relatively low anxiety levels in the absence of external disturbance or predator stimuli. This does not necessarily reflect a 'normal' level of grouping behaviour in the wild (where cues from both food and predators are probably ubiquitous), but provides a reference point of killifish behaviour under laboratory conditions for comparison with experimental treatments. We predicted that fish would prefer to forage alone or in small groups to reduce potential food competition. Although there can be foraging benefits associated with grouping (Magurran & Pitcher 1983; Morgan 1988; Ranta & Kaitala 1991), competition appears to be the major cost of shoal membership (Pitcher & Parrish 1993). Fish may respond to this by changing foraging strategies, for example by reducing food handling time in larger groups (Street et al. 1984). In binary choice tests, food-deprived fish show reduced preferences for larger shoals, again suggesting that competition leads fish to avoid large groups when foraging is a priority (Krause 1993b; Reeb & Saulnier 1997). Our results confirm that free-ranging fish choose to form small groups or forage singly in a feeding context. Indeed, among small shoaling species, solitary fish and small groups are commonly seen in the wild (e.g. banded killifish: Godin & Morgan 1985; spottail shiner, *Notropis hudsonicus*: Seghers 1981; guppy, *Poecilia reticulata*: Dugatkin & Godin 1992; rainbowfish spp.: Brown 2000), despite a wealth of evidence that individuals are safer in groups.

Most strikingly, killifish in our study commonly formed the largest groups possible when conspecific skin extract was added to simulate a successful predatory attack. To our knowledge, ours is the first report of chemical cues eliciting an antipredator response in the banded killifish, although Reed (1969) reported alarm responses in the congener *Fundulus olivaceus*. In our experiment, as predicted, individuals responded to a perceived increase in predation risk by forming larger groups: while some pairs and singletons persisted, more than 60% of individuals observed were in shoals of 10. Similarly, Magurran & Pitcher (1987) reported increased shoal size and cohesion for free-swimming minnows, *Phoxinus phoxinus*, on detection of a pike predator. In the present study, however, we were able to confirm that large groups formed as a

result of group choice and not simply because fish cluster in a particular area away from an attacking predator. This is consistent with binary choice experiments in which individual fish show increased preferences for larger shoals in the presence of a predatory threat (Hager & Helfman 1991; Ashley et al. 1993; Krause & Godin 1994a; Tegeder & Krause 1995). Such a response is unsurprising, given that fish in large groups have a reduced per capita risk of predation as a result of several mechanisms, including earlier predator detection, numerical dilution of risk and predator confusion during attacks (e.g. Neill & Cullen 1974; Magurran et al. 1985; Morgan & Godin 1985; Godin 1986; Pitcher & Parrish 1993; Krause & Godin 1995).

Individual fish are expected to trade-off foraging gains and safety from predation in their group membership decisions and, when provided with both food and predation risk cues in the food + alarm treatment, median group sizes were intermediate between those of the single-cue treatments. In this treatment, fish formed larger groups than in either control or food treatments, but smaller groups than those seen with the alarm treatment alone. Thus, it appears that fish took greater risks by forming smaller groups when food odour was present, even in the presence of an alarm stimulus. Fish can integrate multiple cues regarding predatory threats (Smith & Belk 2001) and it seems likely that killifish in our study displayed a graded, threat-sensitive response (sensu Helfman 1989) to our nondirectional alarm cue, allowing them to retain some of the safety benefits of group membership without incurring excessive competition for food.

It is important to note that the observed frequency distributions of groups and individuals were not identical. Although intuitive, this is not a trivial matter: as natural selection typically operates at the level of the individual, it may be more relevant to our understanding of the evolution of group living to ask what the majority of individuals do rather than what the commonest group size is. Several authors examining shoal size in fish have discussed their results primarily in terms of the frequency distribution of group sizes observed (field data: Seghers 1981; Godin & Morgan 1985; Dugatkin & Godin 1992; Bonabeau & Dagorn 1995; laboratory data: Pitcher et al. 1983; Magurran & Pitcher 1987). Here we stress the importance of considering the distribution of individuals within groups: even when large shoals are comparatively rare, they can contain a sizeable proportion of the population and thus reflect the group choice of many individuals.

Mechanistically, group level properties such as shoal size are a result of the movement decisions of individuals (Parrish & Turchin 1997), and understanding such mechanisms is an important step towards understanding how grouping behaviour evolved (Camazine et al. 2001). We have presented a model of a possible mechanism which may underlie shoaling in fish, in which individuals used simple rules-of-thumb to regulate their local interactions. By varying the degree to which simulated individual fish respond to neighbours (modelled here by modifying the range over which interactions take place), we showed that such local movement rules are sufficient to generate realistic patterns of group sizes. The shift in

group size distributions from small to large groups in our model was in the same direction as that seen in live killifish in our experimental treatments.

Changes in a number of individual variables, such as swimming speed or turning rate, may affect the interactions between fish and thus also shoal level properties such as group size. We chose to model a modification of individual interaction distances as a plausible local mechanism regulating group behaviour because it facilitates manipulation of group size, yet maintains the schooling ability of fish, even when group sizes are small. Experimental evidence shows that fish schools can vary in size (Hoare et al. 2000), yet individuals within a school will tend to maintain coordinated behaviour, maintaining close proximity with one another (this may have important antipredator benefits, even when group size is small, Krause & Ruxton 2002). Thus, in our model, as the interaction range is decreased, individuals will form smaller, but still coordinated, groups. This is in contrast to a hypothetical alternative model in which individuals would modify the minimum distance between themselves and others at all times (in our model formulation this would be expressed as keeping  $\rho$  constant while modifying  $\delta$ ).

In our model, reducing a fish's local interaction radius (effectively reducing the number of neighbours which an individual approaches) produces a frequency distribution dominated by small groups and solitary individuals that is very similar to that seen in our experimental food treatment. Laboratory studies have shown that individual fish increase their distance to shoalmates when hungry (Keenleyside 1955; Robinson & Pitcher 1989a), illustrating that local interactions between individuals are modified by changes in motivational states.

Fish may increase the range over which they interact with neighbours to increase group cohesion under predation risk (fish decrease their distance to groupmates following predatory threat: Magurran & Pitcher 1987; Krause & Tegeder 1994). Increases in the interaction radius (increasing the number of attractive neighbours) in the model resulted in the formation of large groups, in line with the results of our experimental alarm treatment.

Individuals in our model do not make explicit decisions about membership of particular groups; instead group sizes result from the set of local interactions made simultaneously by all fish. Group size is an emergent property of the system, and the model uses a self-organizing approach in which individuals use local decision rules that do not require access to global information (Camazine et al. 2001). It is unlikely that fish are able to assess potential shoalmates accurately or rapidly over anything other than a limited area once shoals grow large (Hager & Helfman 1991; Tegeder & Krause 1995). Our model suggests that individuals may be able to alter their group membership by changing their position relative to others based only on local information. Thus, an individual fish does not need to know the range of possible group sizes available to it, but rather fish create groups of a particular size by behaving in a particular manner with respect to their neighbours.

However, while simple individual rules may generate behaviour patterns similar to those seen in real life, it remains to be shown to what extent living systems actually

follow such rules (Parrish & Edelstein-Keshet 1999). Technical advances in video equipment and automated tracking software should make it possible to confirm the functional and mechanistic assumptions of such models, for example by measuring how interindividual distances change under controlled conditions and examining correlations in speed and orientation among neighbours.

Simple individual behavioural rules might allow fish to respond rapidly to changes in environmental conditions (for example predator cues: Smith & Belk 2001) or internal state (such as hunger or parasitism: Morgan 1988; Krause 1993b; Krause & Godin 1994b), and make shoaling behaviour a flexible strategy for balancing individual trade-offs in the face of limited local information.

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