APPENDIX Defining and measuring group sizes and responses

A.1 ABSTRACT

Animals form groups for a variety of reasons. Some groups form through mutual attraction while others may come about due to aggregation around a limiting resource. There are multiple benefits associated with group living, but foraging and predator avoidance appear to be of primary importance. There has been substantial debate over how we define groups of animals. The definition most widely accepted today is that of Pitcher (1983). Even still, a number of authors use variations on Pitcher's theme especially with respect to the maximum distance between individual group members. In this chapter I examine the definition of group size and apply multiple measures of group size to rainbowfish shoaling data. I then develop my own index for recording changes in group size. Measuring changes in group responses enable us to gain a greater understanding of the forces acting on individuals to form groups. The behaviour of animals within a group is highly influenced by other group members. The tendency to from groups is therefore a function of the compromise between intrinsic and extrinsic factors. However, the indices used to record these changes must be carefully selected.

A.2 DEFINING GROUPS

Predators and foraging are the keys to understanding why many animals live in groups (Pitcher and Parish 1993). There are, however, many other factors to consider (not all of them positive) but a full analysis of the costs and benefits of group living is beyond the scope of this chapter (see Hamner and Parrish 1997 and Ritz 1997 for reviews). Animals may avoid predators using any number of methods, but a large number of animals rely on safety in numbers (e.g. a herd or flock) or some form of group response towards predation (e.g. mobbing). There are three common explanations for the maintenance of groups. The first is that members of groups show increased foraging efficiency in a patchy environment (Pitcher *et al.* 1982), although this is offset by increased foraging competition once a patch has been located (Eggers 1976). The second is the hydrodynamic or aerodynamic benefits of moving in groups (Abrahams and Colgan 1985, Lissaman and Shollenberger 1970). The vast majority of work conducted in this area, however, relates to the third explanation, namely increased individual protection from predators (Abrahams and Dill 1989).

The selfish herd theory (Hamilton 1971) suggests that animals come together because it benefits them individually rather than benefiting the group itself (ca. group selectionist paradigm; Shaw 1978). For the most part this seems to be true, especially for groups of fish. Aggregations of fish are generally made up of unrelated individuals (e.g. stickelbacks; Peuhkuri and Seppa 1998) whose primary concern is their own well being. Within the group, individuals compete against one another for the most beneficial position to gain access to recourses or avoid predators (Hamner and Parish 1997). Within these aggregations information transfer appears to occur passively (Magurran and Higham 1988). This passive transfer of information ensures that the group acts as one, enabling mesmerising, synchronous group responses to occur such as flash expansions (Pitcher and Parrish 1993). It is in the interests of all individuals to act as one, which is why the apparent individual versus group selection paradox exists.

There are multitudes of anti-predator benefits associated with being a group member. The simplest benefit of joining a group is attack dilution. Theory suggests that if a predator attacks, there is a smaller chance that the attack will be directed at a particular individual, as group size increases. This hypothesis relies on the assumption that groups of prey items do not attract more attention from predators than the sum of the individuals. Another relatively simple benefit of group formation is the confusion effect. This hypothesis explains the phenomenon whereby the sheer number of moving targets bamboozles a predator as it attempts to lock on to a single prey item. This pressure also explains the oddity effect and explains why individuals prefer to shoal with like individuals. The list goes on (see Chapter 1).

If we accept that the formation of a group is a successful anti-predator response, then we may be able to measure an index of the propensity to join groups to gauge anti-predator responses (although group formation may not always be an appropriate response, see Brown and Warburton 1997). How then, do we decide what a group is, and can we differentiate between different types of groups?

Groups of animals may form for a number of reasons. Passive aggregations may form as a result of localised physical sorting. In contrast to this, many groups of animals form around a limiting resource or attracting stimuli where the members are actively recruited to a specific location at a specific time. Such groups may be referred to as active aggregations (Parish *et al.* 1997). Many animal groups form through mutual attraction, that is the stimulus for grouping is the group itself. This behaviour is called congregation (Turchin 1997). Romey (1997) suggests that groups that show mutual gregariousness, unrestricted group entry and exit, and limited individual recognition should be referred to as FSH (Flocks, swarms/schools, and herds), although the descriptive term "passive congregation" (Parrish 1997) seems a little more reasonable. However, when individual recognition occurs, as well as some degree of cooperation between members the group, and entry and exit is restricted, the group may be referred to as a social congregation (Romey 1997). Romey classifies most fish shoals into the earlier category, however, it is becoming increasingly clear that fish are quite capable of identifying individuals and preferentially cooperate with them (see Chapter 1 and Chapter 8).

A.3 DEFINING FISH SCHOOLS AND SHOALS

There have been innumerable studies considering the anti-predator responses of fish, a group of organisms that rely heavily on safety in numbers, yet we still find huge variation in our definition of groups even by the same authors. After great debate Breder (1967) applied the term "school" to a group of fish exhibiting characteristic spatial orientation. However, it was widely believed that the definition was too rigid and should be applied to any aggregation of fish since common orientation is too short-lived to be of any use. The trouble with eliminating orientation from the definition is that there may be any number of environmental factors (e.g. a food source) that may cause fish to come together independently (Shaw 1978). By 1970 some agreement had been reached; a school should be considered as a group composed of fish that are mutually attracted to one another (Shaw 1970). Once the group has come together then the spatial orientation of all members becomes a useful index to describe the “state” of the school at any point in time. When fish are orientated randomly, they may be referred to as being non-polarised. Alternatively when the spatial array is highly structured, the school may be said to be polarised (Shaw 1978). By 1981 Seghers had added further to the definition by acknowledging that the space between individuals is important; a school is comprised of two or more fish swimming together in a co-ordinated (usually polarised) fashion. Adjacent individuals within a school are typically one-six body lengths apart (Seghers 1981). Partridge (1982) recommended that groups should be characterised by a measure of time spent schooling and the degree of organisation, but did not define exactly what a school was.

Pitcher (1983) pointed out that confusion still reigned over the use of the term “school". He noted that a number of teleost species exhibit highly co-ordinated group swimming behaviours. Many more, however, spend most of their lives in cohesive social groups (ca. FSH; Romey 1997). For this reason the term “shoal” was introduced to describe the more generalised social group of fish (Pitcher 1979). The term ‘schooling’ is therefore reserved for synchronised and polarised swimming groups and is one of the behaviours that may be performed by a shoal of fish. To explain the terms more clearly, Pitcher (1983) developed a Venn diagram accommodating most of the behaviours displayed by fish. The diagram provides us with an excellent framework within which to decide on definitions (Figure A.1).

The definitions defined by Pitcher (1983) have been adopted in this thesis. The anti-predator behaviours pictured in this diagram occur both within the group and individual behaviour ‘spaces’. Recording the change from individual to group tactics (or vice-versa) provides us with some insight as to what cues fish perceive as threatening.

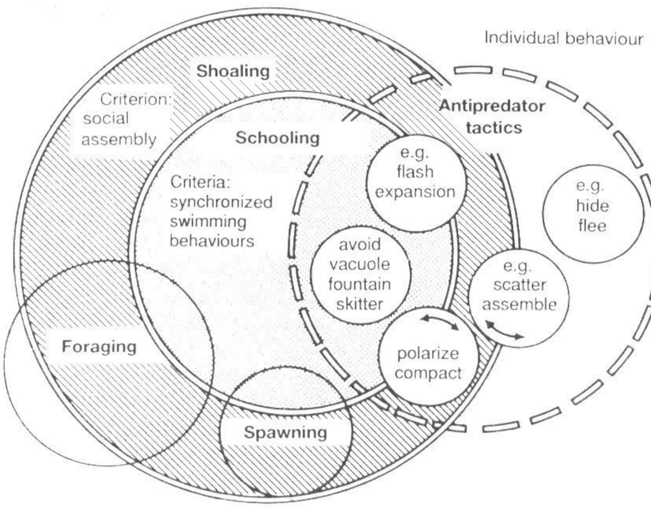

Figure A.1. Venn diagram developed by Pitcher (1983) accommodating most of the behaviours displayed by fish. The work encompassed by this thesis is dedicated to the dotted circle entitled “Anti-predator tactics”.

A.4 MEASURING SHOALING BEHAVIOURS

There appear to be at least three important characteristics of schools that we may be interested in measuring. 1) the level of polarisation (i.e. how individuals are orientated relative to one another), 2) the distance between individuals, or the density (i.e. how fish they spaced relative to one another) and 3) the degree of synchrony between members. The majority of studies have concentrated on the first two measures while the degree of synchrony has largely been ignored, although it may be incorporated into certain measures by default (e.g. elective group size; Pitcher and Parish 1993).

In order to measure schooling tendency researchers have used two broad methods. Some have considered a sample individual, while others looked at all of the fish in a shoal. Measurements on the movements and position of individual fish are generally lost in pooled data, making the analysis of school structure difficult to interpret at the fundamental level of the individual. However, for the same reasons, choosing a sample fish is treacherous owing the level of individual variation that is often apparent when one studies behaviour. By studying the entire group we see general trends in conformity, produced by processes of mutual feedback and behavioural averaging. In this way we can test the way in which changes in food availability or the level of predation affect the observed group size, shape or density. If, on the other hand, we are interested in studying how the internal state of a fish may shape the decision to join a shoal (i.e. individual variation), then choosing a focal individual is a good alternative.

A.4.1 Nearest neighbour distance

The most commonly used index of changing shoal parameters is nearest neighbour distance (NND). NND has been recorded in several different ways. In a few studies the researchers have chosen an individual at random and recorded the distance to its nearest neighbours at various points in time throughout an experiment (focal sampling) (Hunter and Nicholl 1985, Aoki *et al.*1986, Magurran 1986). Others have recorded all the nearest neighbour distance (including reciprocal pairs) within a shoal and provided a mean NND for every shoal (Hunter 1968, Godin and Morgan 1985, Pitcher *et al.* 1985).

The inclusion of reciprocal pairs to produce group mean NND, however, provides us with the statistical dilemma of pseudoreplication. Van Olst and Hunter (1970) acknowledged the inclusion of reciprocal pairs in their data set but did not mention them any further. Koltes (1984), on the other hand, acknowledged the statistical problem presented by including reciprocal pairs and chose to ignore it. Partridge and Pitcher (1980) pointed out that by ignoring the problem of independence, estimates of NND is biased downwards, but exclusion of one of the pairs biases estimates of NND upwards. Koltes (1984) cites Dill *et al*. (1981), who explained that the difference in mean NND estimation calculated by including and excluding reciprocal pairs in their data set was around 6%. To get around this problem Partridge and Pitcher (1980) used a "hemisphere" method. Unfortunately this method involves complex calculations in three-dimensional space.

A.4.2 Elective group size

The next most commonly used index is elective group size (EGS) (Pitcher 1983). EGS is very similar to the scores developed by John (1964) and later used by Andorfer (1980) and Cerri (1983). EGS is a measure of the number of individuals in a school and uses a much stricter criterion for a group; the number of fish considered to be behaving together within four body lengths of one another (Pitcher 1983). The important term in this measure is "elective". This distinguishes an EGS from an artificial group size deliberately set by the experimenter. EGS can be measured for individuals or for shoals and is a sensitive measure of a fish's perception of the relative costs and benefits of shoaling (Pitcher and Parrish 1993). The scores are robust and are readily repeatable by different observers (Magurran and Seghers 1990a). A number of investigators have used EGS successfully (McNicol and Noakes

1984, Allan and Pitcher 1986, Magurran and Pitcher 1987, Magurran and Seghers 1990a). The trouble with EGS is the problem of deciding exactly when an individual is part of a school. Pitcher (1983) stipulates quite clearly in his definition that the distance of four body lengths (BLs) is critical in determining which fish are members of a group. Data from predator inspection studies suggest that members of a school should be within two body lengths (Milinski et al 1997, Murphy and Pitcher 1991) if both members of the inspecting group are to share the risk of inspection.

A review of the literature suggests that the number of BLs used to describe a group has been somewhat arbitrary (Table A.1). Magurran, for example, has used three, four and five body lengths to define schools of guppies. In some papers a definition of the use of school is not even provided (e.g. Butler 1988). Magurran (1990b) defines schooling as “swimming in a polarised, cohesive group” with no mention of the minimum distance between individuals required to consider them as a group. None of the authors listed in Table A.1 explain why a specific number of body lengths was chosen to qualify schooling behaviour.

Table A.1. A list of authors who have used EGS as an indication of schooling response and the number of body lengths they used to define a group. Species listed; Atlantic salmon (*Salmo salar*), Guppies (*Poecillia reticulata*), spottail shiner (*Notropis hudsonius*), European minnow (*Phoxinus phoxinus*), and the banded killifish (*Fundulus diaphanus*).

Author	**Species**	**Min. distance to neighbour (body lengths)**
Jarvi and Uglem (1993)	Atlantic salmon	< 2
Giffiths and Magurran (1997)	Guppies	< 3
Allan and Pitcher (1986)	Cyprinids	< 3
Seghers (1981)	Spottail shiner	< 3.5
Magurran (1986)	European minnows	< 4
Magurran and Pitcher (1987)	European minnows	< 4
Magurran and Seghers (1991)	Guppies	< 4
John (1964)	*Astyanax mexicanus*	< 4
Andorfer (1980)	*Leucaspius delineatus*	< 4
Cerri (1983)	*Rhinichthys aratulus*	< 4
Griffiths and Magurran 1998	Guppies	< 4-5
Godin and Morgan (1985),	Banded killifish	< 5
Magurran and Seghers (1990a)	Guppies	< 5
Magurran and Seghers (1990b)	European minnow	< 5
Magurran and Seghers (1994)	Guppies	< 5

A.4.3 Inter-individual distance and others.

Inter-individual distance (IID) is also fairly widely used to define the distance between all individuals in a group (Warburton and Lazarus 1991). Unlike NND, IID is not plagued by statistical problems and is relatively sensitive to changes in schooling behaviour. There are some other, more unusual methods of recording shoal cohesion based primarily on calculating shoal density (Williams 1964, Abrahams and Colgan 1985, Hunter and Nicholl 1985, Eklov and Persson 1995) or shoal shape and width (Warburton and Lazarus 1991). These methods, however, will not be discussed here.

A.5. CHOOSING AN INDEX OF SCHOOLING

Choosing an index of schooling behaviour is fraught with difficulties. Recording EGS data for example sounds simple (having decided on the number of body lengths to use), but, there are a number of statistical options to consider once the data have been collected. If a researcher is interested in the size of a group that the fish most commonly form, then the mode of the observed EGS's is probably the best index to calculate. Mean EGS, by contrast, is simply a measure of the average group size formed. If at one time there is a group of four and a singleton, the average group size is 2.5. Similarly, a group of two and three has a mean EGS equal to 2.5. If all the calculations are conducted on the permutations of a group of five fish one finds that mean EGS is a measure of the number of fish in the tank divided by the number of groups formed. However, neither of these two indices indicate how many groups were formed, or how the groups were spaced with regard to one another and the experimental arena.

If there is a large number of fish in every replicate observation, EGS can be a useful index for comparing anti-predator responses. In many experiments, however, we can seldom afford the luxury of using 10 fish per replicate and so smaller group sizes are commonly used. Fish that are strong schoolers seldom break away from their group members particularly when there are only five fish in the entire experimental arena. In these circumstances there is rarely enough variation in EGS to differentiate between responses. In this situation it is far better to consider the exact location of all individuals with reference to one another. Fish that may be considered part of a single group according to a given definition of EGS, may still differ in terms of the distances between individuals. In this situation inter-individual distances or nearest neighbour distance may also be a more useful measure.

Having read most of the literature on the definitions of animal groups, I became aware of the need to ensure that definitions meaningfully reflect behavioural processes. As a result, I have adopted the practice of determining school membership by sight from pre-recorded video footage. Any fish acting on its own outside a reasonable distance or time frame is considered to be a singleton. However, having collected group size data by sight, I wondered what my definition of EGS would be in terms of the number of body lengths within which an individual was considered to be part of a group. The exact location (x, y co-ordinates) of every fish was noted every time I determined EGS from video. From the x-y coordinate data it was possible to estimate my definition of EGS. As it turns out the mean distance for an individual to be considered part of a group corresponded to 15 cm or three body lengths. This distance is on the lower side of Pitchers' definition of EGS (four body lengths), however it is probably on the safer side (according to the predator inspection literature), and represents a more conservative estimate of group membership.

A.5.2 Shoal dispersal index

Unfortunately EGS data were not sensitive enough given the small number of fish used throughout most of my experiments. In order to get over this problem I developed an independent index of shoal spread (Shoal Dispersal Index; SDI). At each point in time the mean x and mean y co-ordinates and the variance around that location were calculated for a shoal of fish. The standard deviation of the two dimensions was then used to calculate (by Pythagorus Theorem) a circular radius defining the spread of the fish around the mean location.

Table A.2 shows an analysis of data collected for the active and passive predator experiment in chapter 3 (Brown and Warburton 1998b). Statistical analysis revealed no treatment effects, but the high level of variation in *P*-values strongly suggests the need for care in selecting techniques for the collection and analysis of data. Clearly IID and SDI are the most sensitive indices when the number of fish used in the experiment is relatively small. Interestingly the analysis of nearest neighbour distances (NND) was not affected by the inclusion of reciprocal pairs in the data set. This is primarily due to the fact that the inclusion of reciprocal pairs, although biasing the data downwards, acts evenly across the data set. The effects ranged from 6% difference to 13% difference with an average downsizing of NND estimates of 10.5 %. This is somewhat larger than, although obviously within range of, the 6% stated by Dill *et al*. (1981).

Table A.2. An analysis of the data presented in Chapter 3 using a number of different group descriptors. The first 4 columns represent means (mode in one case) and the last column the ANOVA result.

Measure	Naïve (act)	Naïve (pas)	Exper. (act)	Exper. (pas)	ANOVA *P* value
Mean EGS	4.714	4.382	3.820	4.375	0.4795
Mode EGS	5.000	5.000	5.000	5.000	1.0000
SDI	7.732	8.284	15.920	13.345	0.1041
NND	4.740	4.322	5.958	4.154	0.9097
NND reciprocal	4.112	4.043	5.179	3.732	0.9097
IID	7.554	6.853	17.097	14.004	0.1212

A.6 FORCES ACTING ON SCHOOL SIZE

It is interesting to note that throughout the experiments conducted by most investigators, fish constantly move between schooling and shoaling (as defined by Pitcher 1983). For the most part therefore, it becomes difficult to distinguish between the two since the behaviour of groups of fish is highly dynamic. The definition becomes irrelevant once we invoke an index of group size. We might presume that when groups break up into many smaller groups or singletons this is indicative of shoaling or individual behaviour, whereas when the fish come together and travel as a single group it might represent schooling. As we make comparisons between different conditions (e.g. before and after the inclusion of some stimuli or between test and control), we are essentially looking for a stimulus that may cause fish to move from one state to the other (i.e. from schooling to shoaling or vice-versa). This transition may not necessarily be abrupt. As I pointed out in the opening statement of this chapter, the key to understanding the shift in grouping behaviour is foraging and predation. The internal hunger state of every individual and its perception of danger are delicately weighed in the decision to join or leave a shoal. However, this is not the only truth. Fish within a group are often influenced by what other members of the shoal are doing. Shoaling enforces uniformity in the behaviour of school members (Helfman 1984). Add into the equation, then, the additional influence of social monitoring. The grouping behaviour observed in fish is therefore a function of the compromise between intrinsic and extrinsic factors.

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