Inside or outside? Testing evolutionary predictions of positional effects

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The schooling phenomenon presents the student of animal behavior with a paradox. On the one hand, schooling is superficially a simple phenomenon and would seem to lend itself readily to quantification and casual analysis. On the other hand, there has been a notable lack of success in relating schooling to general biological principles, and there are no really convincing ethological, ecological, or evolutionary explanations. There is no vital function to which it seems to make an efficient contribution, and it can not be immediately assigned to reproductive, defensive, or any other category of adaptive behavior.

(Williams 1964: 331)

12.1 Introduction

During the three decades since the above statement was made a great deal of theoretical and empirical work has established a number of plausible functions for animal grouping. These functions typically relate to feeding efficiency or predator avoidance. Such generalizations may allow us to see overall patterns and generate hypotheses which can be tested experimentally. However, by considering the selection pressures on groups in general, there is the danger of missing some of the details. Instead, the relative advantages and disadvantages of group membership may vary in different parts of the group (Bertram 1978). For example, although individuals at the edge of a group may be more likely to be preyed upon than those at the center, they may also be more likely to obtain food. The costs and benefits to an organism as a function of location within the group has rarely been assessed. I hope to convince the reader that groups are not homogeneous units, and that different selective pressures operating in different locations within a group lead to position preferences by its members. Furthermore, by focusing on individuals and differences between group members (see Magurran 1993), we may study the function of grouping more effectively.

Because researchers have traditionally had difficulty generalizing and structuring their observations on grouping, many definitions of social groups have been created to fit each particular case. I wish to define and discuss a subset of the more general term congregation as defined by the editors of this book. I shall hereafter call this subset an FSH (for flocks, swarms/schools, and herds). In the continuum of grouping types, FSH are more structured than active aggregations, in which each member's movement is independent, and below social congregations, which may be structured by age and sex and within which cooperation may be displayed (Fig. 12.1). Thus, FSH is a type of passive congregation (see Parrish, Hamner, & Prewitt Ch. 1). I shall also refer to a single member of such a group as a "flocker" whether it is a bird or not.

Behavioral ecologists might break the study of FSH into three major questions: (1) Does grouping serve a function? (2) What are the constraints on grouping? and (3) Are there differences between individuals? Several chapters in this

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Figure 12.1. The grouping continuum from less to more complex, from left to right. This figure serves as a guide to the terminology used in this chapter. Although individuals spend most of their time in one type of grouping, a number of factors, such as mating, may lead individuals into higher or lower grouping classifications. For example, butterflies which are normally solitary will form complex age and sex structured mating groups during the mating season.
book deal with the adaptive value of schooling (Hamner & Parrish Ch. 11) or possible constraints such as the sensory modality of flockers (Grünbaum Ch. 17; Edelstein-Keshet Ch. 18). This chapter focuses primarily on the third question. How do differences between individuals and differences in selection pressure influence positional preferences within a group?

Magurran (1993) summarized five areas where individual differences in behavior are well documented: mating, habitat use, dominance hierarchies, foraging, and predator avoidance. Yet almost no attention has been paid to adaptive individual differences between flockers. There is a common misconception that each focker in a group shares the same background and needs (Kearey, 1979; Magurran, 1993). Magurran (1993) suggests that as schooling tendency increases, the degree of individual differences is expected to decrease. However, as individuals are packed closer to one another, there may be a greater need to structure FSH according to individual motivations such as hunger. A primary limit to the study of FSH is that it is often difficult to identify individuals in a group. Therefore, the first hurdle to overcome is a methodological one. Recent advances in three-dimensional tracking (Jaffe Ch. 2; Osborn Ch. 3; Parrish & Turchin Ch. 9) should aid the task of studying individual differences between group members.

12.2 Where should a focker be in a group?

12.2.1 Evolutionary predictions based on external selection pressures

The adaptionist stance, that an organism and its behavior are a reflection of its current environment (given some developmental limitations) is often the best starting place for biological studies such as these because this view provides testable hypotheses (Krebs & Davies 1981). Most of the evolutionary predictions elaborated in this chapter arise from adaptionist thinking, which assumes that most behaviors and other phenotypes are adaptive, having been fine-tuned over evolutionary time to maximize fitness (evolutionary fitness = the contribution to future generations) (Maynard-Smith 1978). However, it must be noted that other starting points in explaining causation may also be taken and that the nonadaptive hypotheses must be falsified if we are to rigorously accept adaptionist hypotheses (Gould & Lewontin 1979).

There are a number of commonly cited, and debated, explanations for why animals congregate (e.g. Pulliam & Caraco 1984; Bertram 1978; Hobson 1978; Pitcher & Parrish 1993). Many of these hypotheses carry implicit predictions about the location within the group where an individual can best accrue the associated benefit. I will briefly describe those hypotheses in which there appears to be some inequality as a function of location, and then rank the different locations in the group based on each hypothesis (Fig. 12.2). Pitcher and Parrish (1993) give a more complete review of the overall explanations for many of these hypotheses, with regard to fish.

12.2.2 Homeostasis

In most instances the center of the FSH would be most advantageous for maintaining homeostasis. In many homeothermic species such as birds and bison, there is a thermoregulatory advantage to grouping in cold weather. This advantage is probably less important for poikilotherms but may still be important to some insects who have warmed up during the day and want to maintain their heat into the night (e.g. bees). Insects may also group in order to reduce water loss (Friedlander 1965; Lockwood & Story 1986), especially in ladybug beetles which overwinter together (Greenslade 1963; Thiele 1977; Lee 1980; Copp 1983). It has also been shown that intertidal invertebrates reduce water loss by grouping. In these situations, maximal benefit is achieved by centrally located members at the expense of those individuals on the edge (Fig. 12.2).
12.2.3 Locomotion

Flockers moving in the same direction (i.e. polarized flocks and schools) have long been thought to benefit from the reduced drag incurred by "drafting" - i.e. flockers in the middle or back of the group would expend less energy than those on the vanguard (fish - Welna 1973; 1975; bird flock structure - Heppner Ch. 5). This belief may stem from the group-level observation that there appears to be a distinct and regular architecture to moving fish. In other words, all individuals are precisely located with respect to their immediate neighbors. To date, empirical studies have not found that flockers are able to take advantage of this effect (Gould & Heppner 1974; Partridge & Pitcher 1979). Both the theoretical and empirical treatment of position-related energetic benefits need have been explored. For instance, it has not been shown whether there is truly no difference in energetic expenditure by flockers in the front versus the back. This could perhaps be addressed by remotely monitoring the metabolic rate of different individuals within the group as a function of their position.

12.2.4 Foraging

It should not be forgotten that one of the most important disadvantages of grouping is increased competition for food. This is because grouping increases the number of organisms eating the same patch of food, which decreases the probability that the average individual will either find food or acquire a given ratio (see Ritz Ch. 13). However, feeding efficiency is also one of the most commonly cited advantages of forming FSH. Some hypotheses predict that organisms should group in order to efficiently utilize dispersed resources (e.g. Cody 1971). Other hypotheses predict that organisms should group in order to take advantage of clumped resources that are difficult to find (Brown 1986). In either situation, it is important to ask what is the best location within an FSH. Hypotheses related to foraging vary more in their predictions of optimal location in the group than any of the other postulated FSH functions. Some of these theories suggest that group cooperation may play a role in the development of truly social congregations, as opposed to FSH.

Some species seemingly gather for the purpose of displacing territory holders from a feeding ground ("Gang Theory" - Barlow 1974; Altman 1956). The preferred location for an individual may be at the rear of the group so that flockers can avoid injury if the territory holder defends its position. The whole group gains equally from gaining access to the resource, while only the lead individuals incur the potential cost of being attacked by the territory holder.

If food is distributed in patches and is difficult to find, then staying in an FSH will increase the probability of detecting and profiting from the food discoveries of others (Brown 1986). This applies equally to FSH that are moving forward and to those that are static. Pitcher and Magurran (1983) found that fish in groups find food more quickly than loners. They hypothesized that changes in the behavior of the discoverers transmitted information (either overtly - active information transfer, or inadvertently - passive information transfer) to other nearby flockers. There may be some minor advantages for flockers at the leading edge of such groups because individuals can enjoy some amount of uninterrupted feeding time before the rest of the group discovers the food source.

When resources are randomly distributed and relatively nonrenewable, or renewal time is slow, it pays organisms to reduce the probability of returning to the same location. This "clear-cutting" technique involves extracting as much as possible from a particular area and not returning to that area until much later. The group trajectories and return times of some foraging flocks have been found to closely mimic the path predicted by optimality models employing clear-cutting strategies and reduced return times (e.g. Cody 1971). In this case, the best location within a group would be the leading edge and sides.

Occasionally, especially in heterogeneous environments, food resources may be concealed or cryptic such that flockers on the leading edge pass into a patch without discovering the prey. This effect has been noted for insectivorous bird flocks (Morse 1970). Here, the combined effect is greater than the sum of the individual effects with regard to disturbing, and thus discovering, the prey. The best location for individuals to take advantage of this effect is toward the trailing edge of an FSH.

12.2.5 Antipredation

Many researchers consider predator avoidance to be the primary function explaining the initial formation of FSH (Barnard & Thompson 1985; Vullers 1990). Certainly the greatest percentage of adaptive hypotheses for grouping have centered around defensive strategies. Defense against predation, whether group-oriented or not, can happen at several time points along the predator-prey interaction. There are a number of behavioral steps that many predators go through before consuming prey. For example, Neill and Cullen (1974) described the following sequence of steps for a predatory pike attacking schooling prey: contact-orient-stalk-attack-capture. Although some species have developed adaptations for interrupting one of these steps, grouping often provides advantages at more than one stage.
Increased conspicuousness

Grouping in many species of insects has been explained as a "secondary" defense system which reinforces a primary morphological or chemical defense (Sillen-Tullberg 1988; Valinec 1990). Aposematism usually occurs as warning coloration (e.g., distasteful insects often develop bright colors so that predators will learn to avoid them). However, instead of evolving bright coloration, selection may have favored gregariousness. Grouping may be considered an aposematic characteristic which warns predators. In fact, many aposematically colored insects also group to form a supernormal stimulus. It has been suggested that whirligig beetles congregate in order to warn predators about their primary defense: gyritidal, a nasty-tasting exudate (Heinrich & Vogt 1980). Riffle bugs also seem to group to advertise their unpalatability (Brönmark et al. 1984). A bad-tasting organism without aposematic coloration might use grouping as a type of "facultative aposematism" so that it could be alone at other times (e.g., during mating territoriality). For a group whose main function is to warn predators of distastefulness, the best location would be anywhere but the very edge, where naive predators might occasionally attack.

Vigilance

Lack (1954) first suggested the "many-eyes" hypothesis as an advantage for individuals joining a group. This hypothesis assumes that the predator relies on surprise and that once a predator is detected, flockers will have a better chance of evading it. There are actually two advantages to the "many-eyes" hypothesis. First, by becoming alerted early to an approaching predator, there is more time for evasive action. Earlier action is the part of the most vulnerable prey may also warn other flockers in time for them to escape an attack. Indeed, the reaction wave passing through a tightly packed group of prey is transmitted much more quickly than the speed of the approaching predator (Foster & Treherne 1980). Whether flockers respond, once the predator has been detected, is another question (see Seghers 1974; Caro 1989).

The second advantage applies only to species where vigilance and feeding are mutually exclusive. Birds, for example, maintain a higher feeding rate while in groups because the vigilance time of any individual decreases as a function of increasing group size (for review see Elgar 1989). Vigilance time may vary as a function of distance in from the edge. This is because edge flockers are more vulnerable and also have an unimpeded view. If food is clumped, there would initially be a disproportionate advantage to being in the center because the flocker would spend relatively less time looking for predators and could feasibly get more food. However, food may quickly become depleted, especially if the FSH is static, leading to increased competitive interactions (Caraco 1979). Therefore, if the food is dispersed, there may be an advantage to being on the periphery, where competition is lower and the chance of intercepting new patches is high, even though predator exposure may also be high.

The confusion effect

This hypothesis predicts that incoming predators will be unable to select a single individual within the confines of a homogeneous group of interweaving individuals, forcing the predator to hesitate or even abort an attack. Therefore, a flocker should not have a preferred location within a group as much as it has a preferred pattern of movement. As soon as the flocker’s behavior becomes predictable, the predator has a greater chance of catching it. The related Oddity Effect (Landeau & Terborgh 1986) predicts that the minority phenotype in a mixed-species FSH should stay with like flockers. Here, oddity can refer to morphology/coloration (e.g. Hobson 1978; Landeau & Terborgh 1986) as well as movement/behavior (e.g. Major 1978). In the former, it might be more important to facilitate the confusion effect rather than to follow the dictates which other adaptive positioning hypotheses might argue. However, Wolf (1985) demonstrated that odd individuals may stay at the edge of groups in order to escape more easily, once a predator has detected the group.

Predator swamping

Assuming a predator will eat grouped prey until satiated, if the FSH is large enough the majority will be left alone. This is essentially the same as the "Dilution Effect" (Bertram 1978). Traditionally, the center of the group is thought of as the best location because predators attack flockers on the edge first. On the other hand, if the predators are attacking the region of highest density, such as a turtle nest site or a swarm of Daphnia (Milińska 1977a), then the center of the group may be the worst location. In short, we need to consider the prospect that different predators prefer to attack groups in different locations. The best place for an anchovy to avoid an attacking tuna may differ from the best location to avoid an attacking pelican. If there is time to assess what type of predator is attacking, then an anchovy’s behavioral response should be flexible: i.e. it will depend on the type of predator. However, if there is little time for the anchovy to respond, then natural selection may have favored a fixed response in anchovies to take the position which is safest overall.
Hamilton (1971) predicted that an organism will minimize the "domain of danger" around itself by ducking between neighbors whenever possible. An assumption which underlies this theory is that an organism responds to local density optima rather than an absolute knowledge of where the center or edge of the group exists. The best position, therefore, is not necessarily the geometric center of a group, but the localized center of density. Flockers with exposed flanks, either because they are on the edge or in an interior gap or vacuole, sustain the highest risk. This may lead to an uneven distribution of flockers within the FSH, and at the extreme, the formation of several separate FSHs (see Hamilton 1971). Vine (1971) finds similar theoretical results even when the predator attacks only from the edge of a group (vs. the predator being allowed to appear anywhere such as in Hamilton's model).

12.3 Individual differences in location

Several early studies concluded that flockers were randomly dispersed throughout FSH. For example, Radakov (1973) found that all fish have an equal probability of being on the periphery or within a group when a predator approaches. However, several recent studies have found evidence for position preferences within FSH. Jakobsen and Johnsen (1988a) present indirect evidence that the largest individuals in a swarm of water fleas, Bosmina, are the first to get to the center of the group when threatened (because they are faster swimmers). Several recent studies of schooling fish have also demonstrated individual differences in position preference. Healey and Prieston (1973) demonstrated individual preferences in position among 12 schooling sockeye salmon. Each fish was marked and photographed many times over several days, and the rank order of each fish from front to back was determined. Using Principle Component Analysis, they determined that different fish maintained different positions within the group. Partridge (1978) found individual position preferences in one small school of five saithe. And Pitcher et al. (1982b) also concluded, on the basis of Principal Component Analysis, that individual preferences existed in their study of ten mackerel. Interestingly, these differences seemed to disappear when the school was under attack, perhaps because individuals were exhibiting protact displays (Humphries & Driver 1967) which lead to random positions within the group.

Unfortunately, none of the above studies adequately addressed the question of why there were nonrandom distributions within groups.

12.4 Differences in selection

Krebs and Davies (1981) describe three causes for individual differences in behavior: (1) a variable environment, (2) phenotypic differences, and (3) the behavior of others. It is important to examine all three of these causes when evaluating selective forces relevant to grouping. Differences in the environment within groups (e.g., temperature or the probability of food acquisition or predation) can be important selective forces which may lead to heritable behaviors within a group. McFarland and Moss (1967) found that there was a decrease in oxygen at the center of large schools of striped mullet, Mugil cephalus (see also McFarland & Okubo Ch. 19). Differences in size, sex, and color of individuals may also account for different optimum positions within a group. Lastly, the best behavior to pursue at a particular time depends on the behavior of others. This is especially true when considering groups, in which all behaviors are dependent and thus measured in relation to the position/behavior of others.

Although most adaptionist models assume that predators preferentially attack prey located alone or on the outside of FSH, few studies have actually tested this (except see: Milinski 1977a,b; Jakobsen & Johnsen 1988a). In some cases, fish at the center of the group may be at greater risk because they become the stragglers as the group breaks up (Parrish 1989). Ideally, it should be possible to obtain enough data to determine "danger isopleths" within a group so that we could test where choosy flockers (those most likely to exercise their preference) position themselves based on past predation pressure.

To determine which areas of the group are generally more advantageous for foraging, individual rates of food intake must be measured as a function of food distribution. It is also important to estimate the total amount of food eaten, as opposed to simple foraging attempts, which may not give a good indication of food consumed (Keys & Dugatkin 1990). Major and Dill (1978) found that the front of the school is the best place to be to get the most food in predatory groups. Krause et al. (1992) also reported that fish in the front of a school obtained more food than those in the rear. Similarly, Keys and Dugatkin (1990) reported that starlings at the edge of a feeding flock obtained more food than those at the center.

12.5 Differences in motivation

"Causation does not indicate adaptiveness and functional analysis does not reveal causation" (Colgan 1986). In showing adaptation, as when proving a case in court of law, it is not enough to establish that the individual was at the scene of
the crime and had the means, it is important to establish the motive. When applied to positional benefits within an FSH this caveat might be summarized as: even if difference in position and selective pressures within a group have been demonstrated, one has not conclusively demonstrated a function. Positional differences within a group may be due to lack of mobility within the group, or non-adaptive reasons, such as activity levels. Romey (1996) showed that individuals who moved faster than others, but otherwise followed the same movement rules, might, in a simulation model, end up at the edge of a group, much as a faster electron ends up in the outer orbital of an atom. So the rule of thumb for a hungry individual may not actually be to move to the edge per se, but to simply raise its activity level. Hunger, fear, aggression, and sex account for most of the immediate motivations of an organism (Colgan 1986). Although the level and specific response to each of these factors is either learned or "programmed" by natural selection, the current state is dependent on immediate history.

12.5.1 Differences in hunger

Differences in hunger may be the single greatest force promoting individual differences in position within a group. There are two primary methods for testing how hunger affects positional preference: (1) short-term satiation levels can be manipulated by experimental feeding, or measured indirectly (e.g. crop-distention in birds, or fullness of the gut in fish), and (2) long-term satiation levels (e.g. lipid storage or overall measures of body condition) can be assessed. There is already some evidence that hunger-level affects the overall spacing of some groups. Hunter (1966) found that schools of juvenile jack mackerel grouped more tightly after feeding. Morgan (1988) also found a relationship between hunger (as well as shoal size and predator presence) and group spacing in bluntnose minnows. Robinson and Pitcher (1989a, b) also found such a relationship in schools of herring. Romey (1993) and Krause et al. (1992) are some of the first to explicitly address the effect of hunger on location within groups. When half of the whirling beetles in a group of 20 were kept hungry, they maintained positions significantly farther from the center of the group than the well-fed beetles (Romey 1995). These differences in position disappeared within 24 hours of feeding both groups equally. It was also confirmed that beetles at the outside of the group consistently discovered floating food before individuals near the center of the group. Krause et al. (1992) showed that hungry roach, Rutilus rutilus, are at the front of schools more often than satiated individuals.

12.5.2 Differences in fear

Predation is arguably the major cause for the initial formation of many types of FSH, but may be less responsible for the individual differences which then develop. If flocks mostly stay within a FSH then there will be little difference in the average exposure time to the predator. However, there are certainly different risks associated with different positions within the group. It is this perception of risk of attack that I define as "fear." Differences in phenotype may lead to differences in fear, which may lead to different optimum positions within a group. Alternatively, differences in exposure to predators, or experience, may also result in positional preference as flocks learn to associate location, predator type, and risk. Naive individuals might be expected to be less "choosy" or even risk prone (e.g. Magurran & Seghers 1991). Krause (1993) found that the minnows alerted to danger by Schreckstoff relocated to positions nearer to schoolmates. Schreckstoff is a pheromone released by fish in the minnow order (Ostariophysi) when specific epidermal cells are broken. Other fish in the school are sensitive to its smell and take evasive measures when they sense it. In some cases the minnows group more tightly or leave the group altogether and take shelter elsewhere.

12.5.3 Differences in aggressiveness

Aggression can structure groups through dominance hierarchies or through the defense of a particularly advantageous location within a group. In regard to my original definition of FSH, species with a high degree of intragroup aggressiveness would not be considered true FSH congregations, but would instead fall under the rubric of social congregations. Dominant individuals may obtain positions with the best food, least risk, and most access to mates. Satiated whirling beetles are more aggressive within the group than are hungry beetles (Romey & Rossman 1995). In those groups where there is no clear hierarchy, those individuals that have the highest motivation level at a particular moment may obtain the desired position. Some individuals may not be able to occupy optimal positions, or even enter a group, due to weakness or other inability. Kenward (1978) found that the wood pigeons were more likely to be successfully attacked than those in groups, and that the loners were by themselves because they were in poor physical condition. Flockers in poor physical condition may be in the least beneficial location within an FSH. If the center of the group is the best location to avoid predators, then one would expect the strongest individuals to push their way to the center of the group when the group was under attack (e.g. Jakobsen &
12.5.4 Experimental manipulation of motives in whirligig beetles

Whirligig beetles, *Diineutes*, are a useful study organism to test some of the predictions that have been raised in this chapter. They are useful because they: (1) exist in two-dimensional groups at the surface of the water, (2) can be easily marked and video-taped from above (Fig. 12.3), and (3) are amenable to experimental manipulation in the laboratory. Individual beetles are not distributed randomly within groups; their position has to do with individual motivations, as well as size and sex (Romey 1993). The relevant selection pressures as a function of location seem to be: (1) a variety of potential predators with different attack preferences, and (2) unequal probability of finding food because beetles on the edge will encounter insect prey, trapped at the surface of the water, first.

The effect of hunger, fear, aggression, and sex on positional preference within groups was studied in a series of controlled laboratory and field experiments (Romey 1993). The positions of marked individuals within the group were measured following manipulation of fear and hunger levels. To avoid being consumed by fish, whirligig beetles release gyristal, a noxious defensive chemical (Bentfield 1972). Individuals that have recently released gyristal must perceive a higher probability of predation (i.e., have more fear) because they are left with a lesser supply of chemical defenses against future predators. Therefore, tracking the movements of “fearful” individuals should indicate which positions within the group represent “safety.” Fear levels were manipulated by experimentally changing the level of gyristal. This involved “squeezing” the whirligigs with tweezers and then comparing them to a control group which was also handled, but not squeezed. Both groups, the squeezed and the control, were marked with different colors and then observed. Subsequent observations showed that there were no significant differences in group position based on differences in the level of defensive chemical, corroborating the observation that fish predators were equally as likely to attack the center of the group as the edge (Romey 1993). Direct studies are underway by the author to determine if fish attacks are equally likely at the edge and center. It would be interesting to note the effect of age on position within the group, since the gyristal-producing gland of younger individuals is less well developed (Romey 1993). Sib (1980) has found that some smaller/younger water striders have a greater risk of predation and will choose the location which is safest.

Figure 12.3. Upper panel: Marking whirligigs allow individuals to be tracked. Lower panel: Whirligigs are videotaped and transferred to computer screen to obtain coordinates.
As predicted, individual differences in hunger-levels were significantly correlated with positional preference. However, rather than all hungry individuals moving to the edge, there was a complicating sex by hunger interaction, even though experiments were carried out in the nonmating season. Experimentally fed females were more likely to be at the center of the group than experimentally fed males (Fig. 12.4). The trend for males was confirmed for measures of long-term satiation (i.e., relative lipid levels per beetle). Males on the periphery had significantly more lipids than those at the center (Romey 1993).

It appeared that while female beetles were following the motivation-based predictions, male behavior may have been modified by aggressive encounters. One of the main motivational underpinnings of positional differences within whirling beetle congregations appears to be aggression. Central males were the smallest; larger beetles remained on the outside of the group. There was a significant correlation between the size of the beetle, measured as length of elytra, and distance from the center of the group. Large males were able to dominate smaller conspecifics and maintain favorable locations.

### 12.6 Balancing motivations

Both the proximate and ultimate fitness of an organism depends on simultaneously balancing a number of factors such as feeding, predator avoidance, and mate selection (Shib 1989; Godin 1986; Dill & Ydenberg 1987; Gilliam & Fraser 1981). The optimal position to avoid predation may be in the center of a group (assuming most predators attack the edge), although the edge might be the optimal location in which to find food. Theoretically, a flocks position within an FSH should reflect the best balance of these sometimes contradictory motivations. Individuals trying to optimize their fitness would have to strike a dynamic balance between center and edge (Fig. 12.5).

The relative importance of each of the adaptive hypotheses mapped out at the beginning of this chapter will vary with the environment (both biotic and abiotic), genes, and motivational level of a flocker. Individuals may also make temporal rather than spatial compromises when balancing selection forces. For example, FSH may tighten during the day when predation is most likely, and then break into looser feeding groups during the night when predation pressure is reduced. The limits of optimality theory should also be remembered, and one should consider the following points when trying to understand why individuals are in different parts of the group: (1) the cognitive requirements of ideal strategies, (2) the relative efficiency of alternative approximations (rules of thumb), and (3) the importance of stochastic factors relative to deterministic movements by individuals.
It should be possible to rank each of the above factors in terms of their relative importance to fitness: a "weighted average" of the costs and benefits that could be used to predict the optimal location in a group for an individual of a particular species in a given environment (Fig. 12.5). For example, the energy gained in adopting a position to take advantage of drafting might not be as important as keeping a position that enables you to detect and evade predators. In theory, individual fitness is determined by the average of many minute-by-minute fitness consequences over a lifetime of choices. However, this reductionist level of detail should not be necessary (and possibly not relevant to the individual flocks) for an assessment of the adaptive value of individual positions.

12.6.1 Environmental fluctuations

There are many important physical factors structuring FSH (e.g., time of day, season, and temperature). However, most of these abiotic factors affect all of the flocks in a group similarly and do not greatly affect our predictions of how individuals should balance conflicting positional preferences within a group except through their interaction with other motivations such as hunger and fear. One of the most important biotic factors influencing an individual's decisions is the distribution of food. When food is clumped and abundant, the center of the group is the best place for feeding and avoiding predators, whereas when food is distributed evenly, there is a tension between optimal foraging location and the optimum location for avoiding predators. If an individual is on the brink of starvation, it may favor a position which maximizes feeding, even if it also maximizes the chance of predator encounters (e.g., Sih 1980; Gilliam & Fraser 1987). If there is a single optimum location, this should select for increasing competition leading to smaller group sizes, increased aggression, and perhaps even the development of dominance hierarchies. On the other hand, in an environment with dispersed food or small patches relative to FSH size, there may be a natural sorting of individuals between the outside and inside of a group due to differences in food obtained during the previous foraging period. This would lead to larger group sizes, lowered aggression, and a decreased occurrence of dominance hierarchies. As mentioned before, resource renewability is also an important factor in structuring the degree of group sociality.

12.6.2 Genes and chance

Differences in phenotype arising from discrete genotypes may have a strong impact on motivation and how flocks balance conflicting demands. Most of these phenotypic differences relate to the relative ability to compete within groups. But differences in ability to utilize a food source are also important (Fig. 12.6). A larger flocks, whether due to genes or previous luck at finding food, has several advantages. For one, it may be less susceptible to predation because of its size. It may also be the winner in aggressive interactions with other members of the group and therefore get priority access to its preferred locations within the FSH.

Although flocker behavior usually lends itself to FSH cohesion and thus may be constrained, even canalized to some degree, there is no reason to assume a
12.7 Conclusions

During the last 20 years a great number of hypotheses have arisen for why animals congregate. A number of theoretical studies for the function of grouping (i.e. Hamilton [1971; Eshel 1978; Rubenstein 1978]) spurred the field studies of the 1980s (Bertram 1980; Partridge 1980; Elgar & Catterall 1981; Thompson & Barnard 1983). In this chapter I have made a number of predictions for how a constantly changing environment might interact with individual differences between group members to influence the evolution of preferred locations within groups. I have then described a few of the studies which have tested these predictions, and have suggested some future directions for studying the internal structuring of groups. Hopefully the understanding of dynamics within groups can benefit from the incorporation of the following key questions: (1) What are the differences in selection pressures in different parts of the group? (2) How does an individual's past history and genetic makeup alter how it balances the costs and benefits of conflicting selection pressures in choosing, or being relegated, to a particular location within a group?

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