Animal decision making and its ecological consequences: the future of aquatic ecology and behaviour

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Received May 21, 1986

DILL, L. M. 1987. Animal decision making and its ecological consequences: the future of aquatic ecology and behaviour. Can. J. Zool. **65**: 803–811.

It is virtually impossible to predict the next 25 years of research in aquatic ecology and behaviour with any accuracy. However, by identifying those areas that are the current frontiers of the discipline it is possible to guess at the most likely research developments over the next decade. From my own biased perspective, the research programme most likely to be productive in the near future is that of behavioural ecology, which studies, among other things, animal decision making in an ecological context. I focus on situations in which animals must make decisions under conflicting objectives, e.g., to simultaneously maximize net energy intake while minimizing risk of predation. New data on guppies (*Poecilia reticulata*) are presented and the recent literature is reviewed to support the notion that animals in such situations behave so as to maximize fitness. Habitat choices, ontogenetic habitat shifts, and the phenomena of vertical migration and downstream drift are beginning to be considered in this general evolutionary framework, with novel results, and this trend will undoubtedly continue. Extension of the logic of trade-offs to the community level leads to a number of new insights about the processes that shape community structure, and affirms the need for aquatic ecologists of the future to have a thorough understanding of animal behaviour, and a working knowledge of such tools of evolutionary ecology as optimality reasoning and game theory.

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Il est évidemment impossible de prévoir avec exactitude ce qui se produira au cours des 25 prochaines années de recherche en écologie et en éthologie aquatiques. Cependant, en mettant la doigt sur les limites actuelles de la discipline, il est possible de tenter de reconnaître les domaines de recherche les plus susceptibles de se développer au cours des 10 prochaines années. Ma propre vision des choses me porte à penser que le programme de recherche le plus susceptible de progresser dans un avenir rapproché est celui de l'écologie du comportement qui étudie, entre autres, les décisions qu'ont à prendre les animaux dans un contexte écologique. Je m'attarde aux situations dans lesquelles les animaux doivent prendre des décisions au moment où des objectifs viennent en conflit, p.ex., maximiser l'apport énergétique net tout en minimisant les risques de prédation. On trouvera ici les résultats de nouveaux travaux sur les guppies (*Poecilia reticulata*) ainsi qu'une révision de la littérature récente qui corroborent l'hypothèse selon laquelle, dans de telles situations, les animaux se comportent de façon à maximiser leur adaptation (« fitness »). Le choix d'un habitat, les déplacements vers d'autres habitats au cours de développement et les phénomènes de migration verticale et de dérive commencent à être envisagés dans la perspective évolutive générale, ce qui modifie les concepts, et cette tendance va sans doute persister. L'application de la logique des échanges à l'échelle de la communauté jette une lumière nouvelle sur les processus qui façonnent la structure de la communauté; les écologistes aquatiques de l'avenir devront posséder une connaissance profonde du comportement animal et pouvoir manipuler des outils utilisés en écologie évolutive tels que l'analyse des décisions et la théorie des jeux.

[Traduit par la revue]

Introduction

Among all forms of mistake, prophecy is the most gratuitous.
George Eliot, Middlemarch

Anyone attempting to predict in 1961 the significant developments in ecology and behaviour in the next 25 years, in any environment, would probably have been well off the mark. Many of the questions we ask today could hardly have been imagined 25 years ago, since the theory and analytical tools we use now were either then in their infancy or had not yet been applied to ecological problems. Given this evidence from our recent past it is hard to imagine predicting the next 25 years with any greater degree of accuracy, since it is likely that future progress in our discipline will be at least as great, given the acceleration which characterises scientific progress in general. I will therefore treat the number 25 as simply a metaphor for "the future," and sketch what I believe to be the major developing areas of research in aquatic behavioural ecology, the so-called frontiers of the field, where the exciting discoveries will be made and the unifying concepts developed. I would guess that this map of the future might be accurate for about 7–10 years.

My opinions are unashamedly biased and coloured by my own experience. You will notice, for example, that I have taken "aquatic ecology and behaviour" to be equivalent to "aquatic behavioural ecology." Rather than considering these two rather large and independent fields separately, I will therefore focus only on their points of contact. Furthermore, I will specifically avoid consideration of marine systems, taking "aquatic" to mean "freshwater" only, and will largely ignore plants. Other biases will become apparent as we go along, more by what I exclude from discussion than by what I actually consider.

Decision making and trade-offs

Any time an animal chooses one particular behaviour from a set of possible alternatives, it can be said to have made a "decision," and animals, including aquatic ones, make ecologically important decisions constantly: when to feed, where to feed, which prey types to eat, how much to eat, how to apportion ingested energy between maintenance, growth, and reproduction, when to reproduce, how many offspring to have, of which sex, etc. The study of such decision making is at the core of the discipline of behavioural ecology. One of the important concepts of this new discipline is the notion of "trade-offs." There are costs and benefits to any behavioural alternative and well-adapted animals ought to behave as if they

compared these to one another, and traded them off, in reaching their decisions. Some decisions are hard-wired into an animal, i.e., the alternatives have been evaluated by natural selection over evolutionary time. Others are made by individual animals during their own lifetime, and in response to current conditions. In either case animals should choose the behavioural alternative that maximizes their fitness (lifetime production of offspring); this is the optimal behaviour.

First-generation models of optimal behaviour considered only relatively simple problems, e.g., prey size choice when the sole objective is maximizing net energy intake rate (Werner and Hall 1974). Although reasonably successful at predicting individual and some population and community level characteristics (e.g., Werner 1977), these models were limited in their range of application. The next generation of models, now about 5 years old, extended the methodology to situations in which animals have to make more complex decisions under conflicting demands, when trade-offs are especially important.

I believe that increasingly sophisticated models of this type will continue to be developed, and will prove to have a high degree of predictive power in aquatic systems, explaining phenomena as diverse as vertical migration in the zooplankton, drift in stream invertebrates, and habitat selection by a variety of organisms. Furthermore, the developing theory will unify the presently largely unconnected theories of foraging, life history, and community structure. I believe we will see the development of a theory of community organization based upon a thorough knowledge of the behavioural characteristics of its constituent species. Such a research programme is already underway and will dominate aquatic ecology in the next decade. In the remainder of this paper I will consider some of these points in more detail. The trade-off that I will emphasize is that between foraging and the avoidance of predators or, more precisely, between energy intake and risk of mortality due to predation. This particular trade-off is an important one in aquatic systems, and the general conclusions drawn should apply equally well to other types of trade-off situations.

Trade-offs between foraging and predator avoidance

Animals frequently find themselves in situations in which an increase in energy intake, say by entering a particular habitat or performing a particular foraging behaviour, can only be obtained with a concomitant increase in the risk of being captured by predators of their own. This is likely to be true, for example, if predators disproportionately frequent sites where their prey's food is abundant. Thus, in deciding where to forage or how to behave, the animal must trade off these costs and benefits.

Fishes have been shown in several studies (reviewed by Milinski 1986) to make such trade-offs, and they seem to do so in an adaptive manner. Juvenile coho salmon (*Oncorhynchus kisutch*), for example, reduce their prey attack distance after exposure to a predator model, and the extent of this reduction depends upon both the salmon's hunger level and the probability that a competitor will intercept the drifting prey item (Dill and Fraser 1984). Shortening the attack distance likely decreases the risk of detection by piscivorous birds and fishes, but it also decreases the coho's encounter rate with prey (Dunbrack and Dill 1983); thus the trade-off.

Although there is now a great deal of evidence that such trade-offs are a fact of aquatic life, few attempts have been made to quantify these, i.e., to determine how much extra energy compensates for a given increase in predation risk. Recent

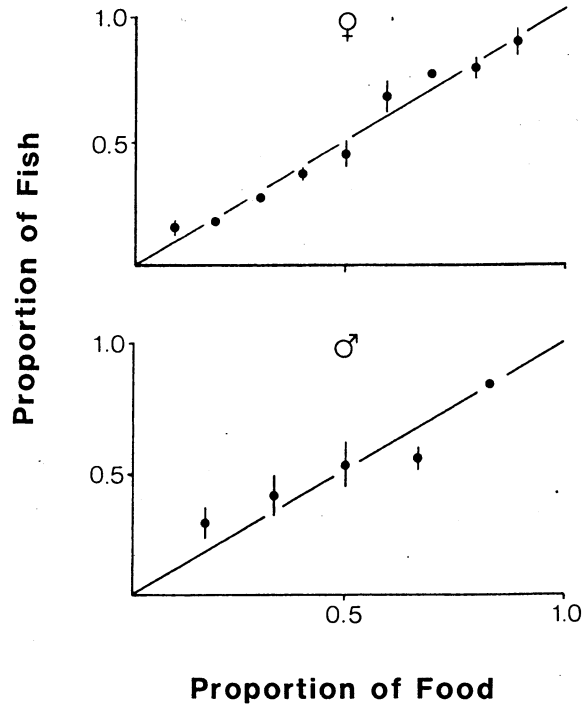

FIG. 1. The proportion of guppies (*Poecilia reticulata*) at a feeder, in relation to the proportion of the total amount of food in the system which is available there. Both sexes distribute themselves in accordance with the ideal free prediction (solid lines). Unisexual groups of 10 guppies were tested several times (six for females, five for males) at each food proportion; the total amount of food (onion fly eggs) was held constant. Bars represent standard errors.

studies in my laboratory (M. Abrahams and L. M. Dill, manuscript in preparation) have been directed at trying to answer this question. We have used guppies (*Poecilia reticulata*) to "titrate" risk against energy, taking advantage of "ideal free distribution" (IFD) theory (Fretwell and Lucas 1970). If individuals have complete (thus "ideal") knowledge of the habitat structure and are "free" to enter any patch, then they ought to distribute themselves in such a way that every individual does equally well. Only then will it not pay some individual to move to another part of the environment. Usually this prediction is tested by offering animals a choice of two feeders (patches), with food more available at one than at the other; the animals are predicted to assort themselves such that they are feeding at the same rate at each patch (for a recent example see Godin and Keenleyside 1984). But "doing equally well" involves more than just having equal feeding rates; in theory, the animals at the two patches ought to have equal fitness, and this is determined not only by their feeding rate but by their mortality rate as well. Consequently, if a risk of predation is associated with the patch providing the higher feeding rate, then deviation from a simple, food-related IFD can be used to measure the energy equivalence of risk, or at least of risk reduction.

We first showed that groups of guppies distribute themselves between two patches in accordance with the food distribution when there is no risk of predation (Fig. 1). A risk of predation was then associated with one of these otherwise identical patches by making the guppies enter a compartment containing a potential predator (a larger fish) in order to get to the feeder. The other patch was risk free, since the patches were separated by netting through which only the guppies could pass. Usually

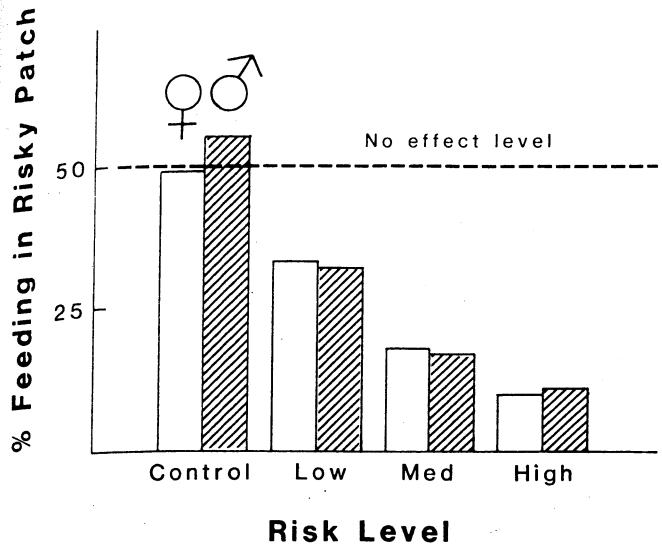

FIG. 2. When food is equally available at each of two feeders (patches), both sexes of guppies avoid the feeder at which there is a risk of predation. The extent of avoidance depends on how far the fish must swim into the predator-containing compartment to reach the feeder (increasing distances correspond to the increasing risk levels indicated on the abscissa). $n = 9$ for each sex at each feeder position; $p < 0.001$ for the effect of risk. The control data ($n = 27$ for each sex) are from trials in which no predator was actually present in the "risky" patch, but the feeder position was varied as in the experiment.

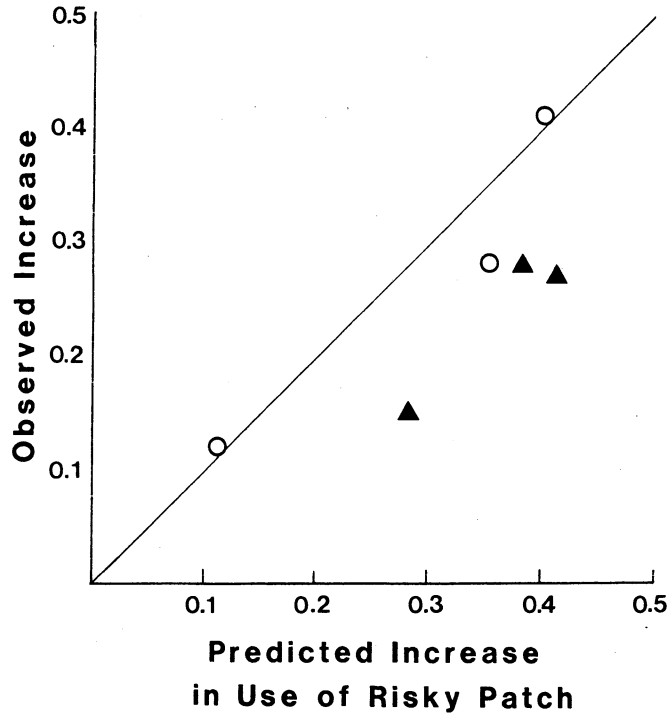

FIG. 3. When sufficient extra food is made available there, both sexes of guppies increase their use of the risky feeder, returning to near the control distribution (50:50). This is predicted (solid line) by a fitness function in which food and risk are additive. Females (circles) fit the prediction considerably better than males (triangles), which tend to undershoot. Fish distributions before the addition of extra food are those shown in Fig. 2.

some guppies accepted the risk and thereby obtained more food than their fellows at the safe patch, where competition was more intense (Fig. 2). Notice that the amount of food obtained by each of n guppies at a patch is $1/n$ times the delivery rate of the food. When the risk level was increased by placing the risky feeder further into the predator compartment, fewer guppies accepted the risk but they obtained relatively more food for doing so. Assuming that risk and energy are linearly additive in the fishes' fitness function, it is possible to predict from these data how much additional food must be added to the risky patch to make it of equal value to the safe patch from the guppies' point of view. When we made this addition of food, the fish returned to nearly a 50:50 distribution, although the males tended to undershoot somewhat (Fig. 3). This sex difference is probably related to the relative value of an increment of energy to the reproductive strategies of the two sexes (M. Abrahams, manuscript in preparation). Since the amount of food obtained by any individual depends on the behaviour of the other guppies present (i.e., the fitness of a behaviour is frequency dependent), the guppies are involved in a "game" with one another, and the IFD is actually a spatial ESS, or evolutionarily stable strategy (Maynard Smith 1982).

The above example has been presented in such detail to illustrate an experimental approach to the study of trade-offs, and to suggest how quantitative predictions about the precise form of a trade-off can be derived and tested. Doing this for any real system will be a major task, but I am optimistic that the near future will see it achieved.

In aquatic systems most behavioural trade-off studies have been done with fish, and most of these have involved patch choice problems. However, risk of predation trade-offs may be involved in a wide variety of other foraging decisions made by all types of aquatic organisms. For example, larval midges (*Chaoborus flavicans* and *C. trivittatus*) have been shown to be at greater risk of predation by visual planktivores just after the larvae have eaten, since the food bolus is highly visible through the transparent body wall (Giguère and Northcote[1]). Similarly, Zaret (1972) reported that the presence of dark (ink) particles in the guts of *Ceriodaphnia cornuta* made them more vulnerable to planktivorous fish. Thus we might expect the meal timing and prey choice decisions of *Chaoborus* and *Ceriodaphnia* to be influenced by their estimate of the prevailing risk of fish predation. Although this prediction has not been tested, it is not unreasonable, given several recent demonstrations that aquatic invertebrates are highly sensitive to the odours of potential predators (see Behavioural resource depression, below).

Trade-offs in action: the dynamics of habitat use in aquatic systems

Habitat choice

By considering both the costs and benefits associated with the various habitats available to an animal (as well as the costs of moving between them), we are very close to being able to model arrays of animals in space; nowhere is this more true than in aquatic systems. Aquatic animals have frequently been observed to avoid patches or microhabitats where predation risk is high, either because predators are especially abundant there or because protective cover such as vegetation is scarce (Table 1). In several of these cases trade-offs are apparent, in that choosing the safe habitat reduces feeding opportunities. This has been reported for crayfish (Stein and Magnuson 1976), notonectids (Sih 1980, 1982), small sunfish (Mittelbach 1981; Werner et al.

[1]L. A. Giguère and T. G. Northcote. The cost of transparency in zooplankton. Unpublished manuscript.

TABLE 1. Habitat use of aquatic organisms is affected by predation risk (in each of these cases, the prey species' choice of a foraging habitat is altered by the presence of potential predators or the absence of protective cover)

Prey species	Predator species	References
Crayfish (*Oronectes propinquus*)	Smallmouth bass (*Micropterus dolomieui*)	Stein and Magnuson 1976 Stein 1977
Notonecta hoffmanni juveniles	Cannibalistic adults	Sih 1980, 1982
Bluegill sunfish (*Lepomis macrochirus*)	Largemouth bass (*Micropterus salmoides*)	Werner et al. 1983 Mittelbach 1981, 1984
Blacknose dace (*Rhinichthys atratulus*)	Creek chub (*Semotilus atromaculatus*)	Cerri and Fraser 1983 Fraser and Emmons 1984
Minnows (*Campostoma anomalum*)	Bass (*Micropterus* spp.)	Power and Matthews 1983 Power et al. 1985 Power 1987
Various tropical freshwater fishes	Green heron (*Butorides striatus*)	Kramer et al. 1983
Armored catfishes (Loricariidae)	Piscivorous birds	Power 1984, 1987
Water striders (*Gerris remigis*)	Rainbow trout (*Salmo gairdneri*)	Cooper 1984
Mosquito larvae (*Culex pipiens* and *Aedes aegypti*)	*Notonecta undulata*	Sih 1984, 1986

1983), blacknose dace (Cerri and Fraser 1983, but see Milinski 1985; Fraser and Emmons 1984), minnows (Power and Matthews 1983; Power et al. 1985; Power 1987), and loricariid catfishes (Power 1984, 1987). In crayfish (Stein and Magnuson 1976; Stein 1977; Collins et al. 1983), notonectids (Sih 1980, 1982), sunfish (Werner et al. 1983), and catfish (Power 1984), the degree of avoidance response by a size or sex class is directly related to the degree of vulnerability of that class to predation, providing further evidence for the existence of trade-offs in these species. Negative impacts on other parameters of fitness, such as growth and fecundity, will be a necessary consequence of choosing the safer habitat; these will be discussed below.

Habitat shifts

Aquatic organisms frequently shift from one habitat (or microhabitat) to another. Ontogenetic shifts occur only when the animal reaches a particular size or age. For example, bluegill sunfish hatch in the vegetation but the larvae begin feeding in the limnetic zone. The fry later move to vegetated nearshore habitats to feed, and then shift back to open-water habitats at a still larger size, which is dependent on predation risk (Werner et al. 1983; Mittelbach 1984). Loricariid catfishes in streams shift from shallow to deep water as they increase in size (Power 1984, 1987), and many stream-dwelling salmonids move into stronger currents as they grow (e.g., Wankowski and Thorpe 1979). Predicting the occurrence and timing of such shifts will be a major goal of aquatic behavioral ecology in the years ahead, but considerable progress has already been made.

The existence of an ontogenetic habitat shift implies that the relative benefits and costs associated with the available habitats change with the size of the animal, such that the animal's optimal habitat also changes. This certainly appears to be the case for bluegill sunfish (Werner et al. 1983). Using dynamic optimization techniques and a life-history approach, Gilliam (1982; see also Werner and Gilliam 1984) has shown that animals (at least prereproductive ones in equilibrial populations) should choose at every size that habitat characterized by the minimum ratio of mortality rate to growth rate. By doing so they maximize the probability of reaching reproductive size, since slow-growing animals remain vulnerable to size-limited predators for a longer period of time. Animals need not estimate the actual growth and mortality rates associated with alternative habitats, only their relative values (Gilliam 1982). This theory will be a powerful tool for understanding habitat choices and shifts. Including frequency dependence in the theory, extending it to reproductive size classes and seasonal environments, and testing its predictions will form a major thrust of aquatic behavioural ecology in the near future. The theory is particularly relevant (and testable) in aquatic systems, where so many species are indeterminate growers and both survival and fecundity are size related.

The complex life histories of many aquatic organisms involve habitat shifts, and can be understood as evolutionary responses to the relative growth and mortality rates characteristic of alternate habitats, as these vary with size or age. The life histories of amphibians, for example, are characterized by shifts from aquatic to terrestrial habitats and Werner (1986) has recently had some success at predicting their characteristics from the above theoretical arguments. Gross (1987) has applied similar logic to the evolution of diadromy in fishes. Many aquatic insect life histories might profitably be viewed in the same light.

Vertical migration: diel habitat shifts

Some habitat shifts occur, and are subsequently reversed, with a regular temporal pattern, i.e., animals alternate between habitats, sometimes on a daily basis. Vertical migration, typically from deep water strata in the daytime to shallow strata at night, is a widespread and well-known example, characteristic of many lake-dwelling (and marine) organisms from plankton to fish. Despite this we are only now beginning to understand its true functional significance. A variety of hypotheses have been proposed to explain vertical migration, but most of these have been single-factor explanations and none seems to have sufficient generality to explain all the variant patterns observed (Levy 1986). Vertical migration will best be understood as a die

habitat shift resulting from changes in the costs (predation risk) and benefits (food availability) characteristic of the various depth strata in the lake or pond (Baker 1978; Stein 1979). Food availability will generally be greatest near the surface, but so too will be predation risk during the day, if the predators use vision to locate and capture their prey. At night, risk will be independent of depth, and the surface strata should be the preferred feeding areas. The timing and extent of daytime migration to greater depths should depend upon the overall levels of food availability and predation risk, the gradients of both factors with depth, and the energetic costs of migration itself (Baker 1978).

Some evidence already exists for this point of view. For example, Zaret and Suffern (1973) have reported that the size classes of zooplankton most vulnerable to fish predation show the most pronounced pattern of vertical migration. This is true of both *Diaptomus gatunensis* in Gatun Lake, Panama, and *Daphnia galeata* in Fuller Pond, Connecticut. A similar pattern has been reported in *Daphnia parvula* by Wright et al. (1980). Juvenile Lake Washington sockeye salmon (*Oncorhynchus nerka*) migrate over a narrower depth range when their squawfish (*Ptychocheilus oregonensis*) predators are breeding in shallow water (and therefore not attacking them in the pelagic zone), and migrate more extensively when the water is more transparent and risk of mortality is consequently increased (Eggers 1978). Such behavioural changes are consistent with the idea that vertical migration patterns result from dynamic trade-offs between predation risk and foraging opportunities. The daily horizontal migrations seen in species like the golden shiner (*Notemigonus crysoleucas*), which migrate offshore to feed at dusk and return to the protective weed beds at dawn, may be explained in the same way (Hall et al. 1979).

Since the feeding opportunities for predators depend upon the migration pattern of their prey, they might be expected to track the prey as closely as possible, yet the migration pattern of the prey depends in part upon the spatial distribution of the predators (it also depends on habitat characteristics such as visibility). Thus the predator and prey may be considered to be locked in a game with each other, in the sense that the behaviour of one player determines the optimal behaviour of the other. Iwasa (1982) has recently looked at vertical migration of zooplankton in this framework, with novel results. Because any individual's risk of predation depends in part on the behaviour of the other members of its population, we may also think of prey individuals as playing games against each other. Game theory, which has proven extremely powerful in other areas of evolutionary and behavioural eology (Maynard Smith 1982), will play an increasingly important role in aquatic behaviour and ecology. Its central concepts of frequency dependence and the evolutionarily stable strategy have already been applied to such problems as the distribution of foragers among food patches (the IFD, discussed above), and the evolution of alternative reproductive strategies in male fishes (e.g., Gross 1982, 1984).

Downstream drift of aquatic invertebrates

It is becoming apparent that the downstream drift so prevalent in stream invertebrates is best thought of as a patch search behaviour, individuals leaving patches of the stream bottom with poor feeding opportunities (or high predation levels) and actively searching for better patches (Kohler 1984, 1985). Drift therefore appears to be an active process resulting from the decisions made by individuals, rather than the passive dispersal process it has long been thought to be. This interpretation is supported by direct observations of foraging activity (e.g., Kohler 1985), which does not peak at times corresponding to maximal drifting rates (at night); accidental dislodgement of foragers by the current had been postulated as the reason for animals entering the drift.

It now seems far more likely that nocturnal peaks in drift abundance result from the invertebrates minimizing the cost of migration by drifting when risk from visual predators (mainly fish) is relatively low. This is strongly supported by Allan's (1978) finding that larger individuals and taxa, which are the most vulnerable to trout predation, are more likely to drift at night than are smaller ones; Newman and Waters (1984) and Andersson et al. (1986) have reported similar findings for *Gammarus*. Invertebrate drift shows no diel periodicity in a small, historically fishless stream in the Ecuadorian Andes (Turcotte and Harper 1982), and moonlight has been shown to suppress drift (Anderson 1966). Thus both the tendency to drift and the timing of its occurrence are probably determined by the interplay of local food availability and of predation risk, either *in situ* (e.g., Corkum and Clifford 1980) or in transit. We are certain to see an increasing number of papers on this theme in the next decade.

Behavioural resource depression: trade-offs within habitats

Animals may choose (or change) habitats to reduce predation risk, or they may alter their behaviour to reduce predation risk in the habitat they are in. Charnov et al. (1976) were the first to point out explicitly that one common consequence of the foraging activity of a predator is a lowering of capture rates with potential prey in its immediate vicinity, and that some cases of such depression are behaviourally based. They coined the term "behavioural resource depression" for this phenomenon, in which prey become more difficult to capture because of changes in aggregation behaviour, greater alertness, or reduction in risky activities. The phenomenon is very common in aquatic organisms, and a number of examples are summarized in Table 2. Interestingly, a great many of these are mediated by chemical cues. Although this may simply reflect what has been studied, it suggests that more attention be devoted to the importance of olfaction in aquatic interactions.

The very behavioural responses that reduce predation risk also reduce foraging opportunities. Obviously, an animal in hiding cannot forage actively for its own prey, but even such antipredator tactics as schooling may reduce searching rates of individual fish (e.g., Eggers 1976). Thus, behavioural resource depression is simply another manifestation of the trade-off between foraging and predator avoidance.

Ecological consequences of predation risk trade-offs

Adverse effects on other components of fitness: population consequences

If a reduced risk of mortality from predation is achieved at the cost of other components of fitness, then one ought to see evidence of adverse effects on these components whenever trade-offs have occurred. These negative effects, on growth and reproduction for example, are direct results of the animal's decision to reduce predation risk. Several such effects have been reported in the literature (e.g., Stein 1979; Werner et al. 1983; Power 1984). An early example is provided by the work of Strong (1973) who found the length of amplexus in the amphipod *Hyalella azteca* to be inversely correlated with predation intensity in a series of lakes; where predation pressure was high, average amplexus period was short, presumably since

TABLE 2. Examples of behavioural resource depression in aquatic animals

Species	Behaviour affected	Reference
Crayfish (*Oronectes propinquus*)	Reduced walking, climbing, and feeding in the presence of smallmouth bass	Stein and Magnuson 1976
Amphipod (*Gammarus pseudolimnaeus*)	Reduced drift activity in the presence of fish or their mucous	Williams and Moore 1982, 1985
Various tropical freshwater fishes	Reduced activity (including respiration) near water surface	Kramer et al. 1983
Copepod (*Cyclops vicinus*)	Reduced activity in the presence of beam	Winfield and Townsend 1983
Mosquito larvae (*Culex pipiens* and *Aedes aegypti*)	Less movement in the presence of notonectids	Sih 1984, 1986, 1987
Dragonfly larvae (*Ischnura elegans*)	Less movement in the presence of either notonectids or sticklebacks	Heads 1985
Salamander larvae (*Ambystoma texanum*)	Hiding in the presence of fish	Sih 1987
Amphipod (*gammarus pulex*)	Reduced activity (lab) and drift (field) in the presence of sculpins	Andersson et al. 1986
Mayfly and caddisfly nymphs and *Hyla regilla* tadpoles	Hiding in the substrate to avoid passing fish (kokanee)	K. Hyatt, personal communication

an amplexed pair presents a large target to a predator and moves rather awkwardly. Thus, predation risk may be traded off against reproductive payoffs (in this case, paternal certainty).

The trade-off with reproduction is not always so direct, however; often it is mediated through effects on energy intake. If foraging activity increases predation risk then trade-offs will be expressed in reduced food consumption, as reported in crayfish (Stein 1979); this can affect both growth and fecundity of the prey species. Vertical migration to avoid predators also incurs costs, both in terms of expenditure (the energy requirements of upward swimming) and opportunity (reduced food availability in the deeper, cooler waters during the day). Thus, migratory *Daphnia hyalina* have fewer eggs per adult and a longer developmental time than do nonmigratory *D. galeata* with which they coexist. Although the former species consequently has the lower instantaneous birth rate it remains more abundant than its congener throughout the summer, presumably because of reduced fish predation near the surface (Stich and Lampert 1981). Similarly, such zooplankton morphological antipredator defences as helmets, strong spines, and thick carapaces have been shown to have significant costs in terms of reduced reproduction (Kerfoot 1977; Dodson 1984). Although one generally thinks of such trade-offs as being made over evolutionary time, the several recent demonstrations of inducible morphological defences (e.g., the induction of crests and spines in *Daphnia* by chemicals produced by *Chaoborus* larvae; Krueger and Dodson 1981; Hebert and Grewe 1985), suggest that these defences and their associated costs might also profitably be viewed as trade-offs resulting from decisions made by individual organisms during their lifetime.

These sorts of trade-offs and their consequences were clearly appreciated by the late Tom Zaret in his book *"Predation and freshwater communities"* (1980), in which he stated (p. 148): "the costs of genetic, morphological, or behavioral 'predator insurance'—the indirect effects of predation—may put constraints on population distributions, densities and reproductive abilities that are more significant than the small percentage of individuals actually removed by the predators." This theme has been echoed by many authors (most recently and comprehensively by Sih (1987) in his discussion of the influence of antipredator strategies on prey lifestyles), but the population consequences have not been measured in detail in any case, nor compared in magnitude with the direct predation mortality. That remains another task for the future.

Indirect predation effects at the community level

It has only recently been realized that both habitat shifts and behavioural resource depression can have very large community level effects. Trade-offs by individuals to maximize their own fitness can have a number of unexpected consequences, causing the appearance of competition where none actually exists, enhancing or reducing competition between species or size classes, and resulting in strong interaction terms between species on nonadjacent trophic levels. Increased appreciation of the importance of such indirect effects will surely alter our views about community structuring processes in the next few years, but since the subject will be covered extensively in a forthcoming book (Kerfoot and Sih 1987) I will discuss it only briefly.

"Apparent competition" refers to the situation in which two or more species interact via a shared enemy (Holt 1977). An increase in the density of one prey species can cause a decrease in that of the second, particularly if both rely on the same sort of defence against their common enemy (Schall and Pianka 1980; Jeffries and Lawton 1984). Thus there can be competition for enemy-free space, "ways of living that reduce or eliminate a species' vulnerability to one or more species of natural enemies" (Jeffries and Lawton 1984). Among the axes of this enemy-free space are the habitat shifts and flexible responses to predator activity discussed earlier.

A major conclusion that follows from this line of reasoning is that many of the aspects of the ecology of animal species that are traditionally viewed as components of their niche have been influenced not by competitors but by natural enemies (Jeffries

and Lawton 1984). As Sih et al. (1985) put it, niche theory will have to incorporate both competition and antipredator needs of a species to predict community structure. Many community parameters might be explainable in terms of indirect antipredator effects (Sih 1987), and Jeffries and Lawton (1985) have already had some success at explaining predator–prey ratios in freshwater invertebrate communities in this context. A variety of other types of indirect effects besides apparent competition are also possible, at least in theory (Abrams 1987).

Predation and competition may also interact, and thus be difficult to separate either theoretically or empirically, if responses to predators enhance or reduce competition between species or size classes. Examples of both effects are known from aquatic systems. In sunfish, for example, predation risk concentrates the young of several species in the vegetation zone, creating competitive bottlenecks for these species at this point in their life histories (Werner et al. 1983; Mittelbach 1984; Mittelbach and Chesson 1987). At the same time, this habitat shift by young bluegills reduces competition with conspecific adults. Consequently, bluegills reach larger sizes in lakes with predators and are "stunted" in lakes without; a similar situation appears to exist in European and yellow perch (see Mittelbach and Chesson (1987) for a consideration of all these examples).

Conversely, interspecific competition can influence vulnerability to predation if competition is for refuges. The rusty crayfish (*Oronectes rusticus*) aggressively displaces other crayfish species from burrows, putting them at greater risk of predation. This is one of the major reasons that this introduced species has displaced other crayfish from a number of lakes (Lodge et al. 1985).

"Trophically-mediated interactions" (Abrams 1984), or "leapfrog effects" (Sih 1987), occur when two species on non-adjacent trophic levels have effects on one another via their effects on the behaviour of a species on an intermediate trophic level. For example, a predator may influence the foraging activity (or habitat choice) of its prey, and therefore affect the feeding rate of this species on its own food types. Alternatively, an increase in abundance of the latter may lead to increased foraging activity of the middle species, with a consequent increase in its vulnerability to the top predator. The extent of the interaction will depend upon the nature of the energy–risk trade-offs made by the species in the middle, but in theory it can be larger than the direct interaction terms between the species on adjacent trophic levels (Abrams 1984). An excellent example is provided by Power et al. (1985). Minnows emigrate from stream pools containing bass, and concentrate in bass-free pools where they graze down the attached algae. Experimental addition of bass reduces minnow grazing in their immediate vicinity (Power and Matthews 1983) and eventually leads to an increase in algal cover (Power et al. 1985). Therefore bass indirectly influence algal populations by changing the behaviour of minnows, and the removal of algae eliminates habitat for small fishes and invertebrates, further increasing the range of community level effects. Similarly, behavioural response of bluegill sunfish to predators indirectly results in increased mortality of cladocerans in the vegetated zone and higher survival of limnetic zooplankton (Mittelbach and Chesson 1987).

In summary, the behavioural decisions made by individual prey concerning habitat use and activity levels, and the ways that these decisions are influenced by energy needs and predation risk, may have unexpected but profound effects at the level of the community. Certainly such unexpected effects have been frequently observed when predator abundance has been experimentally manipulated in the field, especially in freshwater systems (Sih et al. 1985). The competing ideas that community structure is influenced more by competition or by predation are obviously overly simplistic; we will need to focus more on the interactions between these processes.

Concluding remarks

> But someone may argue that not all prophecies come true. Not all sick persons get well either, but that doesn't disqualify the practice of medicine.
>
> Cicero, De Natura Deorum

I believe that the future of aquatic eology will be characterized by a number of trends, and have given one set of examples dealing specifically with foraging – predation risk trade-offs and their ecological consequences. However, the logic of this approach can be applied to a variety of other situations in which aquatic organisms must be sensitive to two (or more) habitat characteristics, for example food and temperature conditions (Crowder and Magnuson 1983) or food and oxygen availability (Kramer 1987). The approach can therefore be useful in predicting organism responses to anthropogenic changes in their environment.

Increasingly, aquatic ecologists will become aware of the need to understand animal behaviour to understand fully phenomena at the population and community levels of organization. This will parallel an increased awareness of the importance of behaviour in ecology generally, which is already becoming apparent (Smith and Sibly 1985; Schoener 1986).

The flexibility of behaviour (Dill 1983) will be seen to be of great importance, since it allows animals to adjust their behaviours to changing conditions, minimizing the negative effects these might otherwise have on individual fitness and thus the consequences for population demography. Indirectly, this flexibility is therefore a part of the homeostatic mechanism of natural systems. The flexibility of behaviour is important for another reason as well: it allows behavioural ecologists to test their hypotheses directly, by experimental manipulation, rather than having to rely on the comparative approach with its inherent problems. Of course, not all behaviours, even antipredator ones, are flexible, but this can also be explained in a cost–benefit framework. To respond to changing predation risk, an animal must have information about the risk, but if such information is prohibitively costly to obtain (e.g., entailing a high probability of being eaten), then evolution will favour fixed behaviours (Sih 1987). There is thus a compromise to be expected between flexibility and rigidity, just as in other contexts (Grandage 1972).

Aquatic population and community ecology will become increasingly evolutionarily based, as the power of such tools of evolutionary biology as optimality reasoning and game theory become apparent at these levels of organization. Simply describing community patterns and then postulating models to explain them is not nearly so satisfying as understanding their mechanistic and functional bases (Real 1983; Mittelbach 1984). There is also a danger in drawing inferences from descriptive studies of community pattern, owing to the rich variety of indirect effects possible (Werner 1984).

Associated with the continued development of an evolutionary–functional approach, theory will become increasingly important in aquatic ecology. Experimental studies will become numerically dominant, observational studies will more often be designed to test theoretical predictions, and single factor models

of causation will be replaced by more realistic multiple causation models (Hilborn and Stearns 1982). In summary, the next few years will see the maturation of aquatic ecology as a scientific discipline.

Acknowledgements

I am grateful (?) to Ron Ydenberg and Mart Gross for convincing me to write this paper, against my better judgement. Dave Levy shared with me his thoughts on vertical migration and did much to clarify my own ideas; Peter Abrams, Dave Allan, Louis Giguère, Mart Gross, Don Kramer, Dave Levy, Gary Mittelbach, Mary Power, and Andy Sih kindly provided me with copies of their unpublished manuscripts. An early version of this paper was reviewed by Mark Abrahams, Dave Allan, Ralph Cartar, Louis Giguère, Mart Gross, Lee Kats, Don Kramer, Dave Levy, Steve Lima, Gary Mittelbach, Earl Werner, and Ron Ydenberg, and I thank them all most sincerely for their criticisms and suggestions. The research on guppies forms part of Mark Abrahams' Ph.D. thesis, and was supported by Natural Sciences and Engineering Research Council of Canada grant A6869.

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