

# Prey approaching predators: a cost-benefit perspective

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When faced with the presence of a predator, many species of prey initially approach rather than retreat from such a potential threat. Although seemingly paradoxical, this type of approach behaviour has been noted in a wide variety of taxa. We adopt a cost-benefit perspective on the question of why prey approach potential predators, and aim to outline what is known about the putative costs and benefits of such behaviour. We identify five major types of costs associated with approach behaviour: (i) increased risk of mortality to the approacher, (ii) increased risk of mortality to relatives of the approacher, (iii) lost opportunity costs associated with approaching a predator, (iv) energetic costs of approach, and (v) potential costs of the approacher being 'exploited' by other group members. Benefits of approach behaviour are categorized as (i) acquiring information about the nature of the potential threat, (ii) informing others of the potential threat, (iii) deterring predator attack, and (iv) advertising one's quality to mates. After reviewing putative costs and benefits, we present a game theory model of prey approaching potential predators. Based on the costs and benefits of approach behaviour and group size, the model predicts the equilibrium frequency of 'approachers' and 'non-approachers' and the (relative) mean approach distance (as a function of group size). To date, much of the work on prey approaching predators is either anecdotal or non-experimental. We hope that the review of the costs and benefits of approaching predators presented here, in conjunction with our game theory model, will help provide direction for future studies of this interesting, but understudied, behavioural phenomenon.

## 1. Introduction

Natural selection will favour animals which minimize their individual risk of mortality due to predation by avoiding being detected and captured by their predators (Endler 1986, 1991, Sih 1987, Lima & Dill 1990). This can be achieved by prey using a variety of structural and behavioural defences, such as cryptic colouration and a flight response, respectively (Edmunds 1974, Endler 1986, 1991, Sih 1987). However, individual animals commonly approach their predators, or the predators of their offspring, when they are initially encountered. Such behaviour has been extensively documented for vertebrates, particularly in fishes (e.g., Dominey 1983, Pitcher et al. 1986, Helfman 1989, Foster & Ploch 1990, Dugatkin & Godin 1992), birds (e.g., Altmann 1956, Kruuk 1976, Curio 1978, Shields 1984) and mammals (e.g., Walther 1969, Kruuk 1972, Owings & Coss 1977, Loughry 1987, Cheney & Seyfarth 1990), but less so for invertebrates (Seeley et al. 1982). Prey approaching predators has been referred to as boldness (Huntingford 1976a), investigative behaviour (Loughry 1987), predator inspection behaviour (Pitcher 1986, Pitcher et al. 1986), predator harassment (Hennessy & Owings 1978, Curio & Regelman 1986) and mobbing (Altmann 1956, Owings & Coss 1977, Curio 1978), depending mainly on its outcome and putative function(s).

Among vertebrates, there exists remarkable convergence in the dynamics of approaches towards predators. Prey typically approach a potential predator or an unknown putative threat (e.g. mobbing chorus) from a distance in a tentative, saltatory manner. The approach is characterized by a series of moves towards the predator interrupted by stationary pauses and sometimes alternating with moves away from the predator (e.g., Curio et al. 1983, Regelman & Curio 1986a, Owings & Coss 1977, Pitcher et al. 1986, Milinski 1987, Dugatkin 1988). In birds and mammals in particular, the prey may emit alarm signals (Owings & Owings 1979, Curio & Regelman 1985, Cheney & Seyfarth 1990) and/or exhibit distraction or threat displays (Owings & Coss 1977, Dominey 1983, Donaldson 1984, Brunton 1990) during an approach towards the potential threat. The approach may culminate

in a number of possible outcomes along a continuum, ranging from the prey simply retreating, perhaps to rejoin a social group of conspecifics nearby (Pitcher et al. 1986, Magurran & Pitcher 1987, Dugatkin & Godin 1992) to an escalation of prey attacking the predator (Owings & Coss 1977, Curio 1978, Dominey 1983). Approaches with the latter outcome are generally referred to as predator harassment or mobbing. Prey commonly approach predators alone or in pairs, and less often in larger groups (Owings & Owings 1979, Bildstein 1982, Regelman & Curio 1986a, Shields 1984, Pitcher et al. 1986, Magurran & Pitcher 1987, Magurran & Seghers 1990a, Dugatkin & Godin 1992), which sometimes include heterospecifics (Altmann 1956, Ishihara 1987).

Prey approaching predators appears paradoxical, since such behaviour presumably renders the prey more conspicuous to the predator and increases its risk of mortality by closing the distance between itself and the predator (Curio & Regelman 1986, Dugatkin 1992). For any behaviour to evolve and to be maintained in a population, the average fitness benefits accrued must equal or exceed its associated average fitness costs (Crawford et al. 1987, Alcock 1989). Therefore, a resolution of the apparent paradox of prey approaching their predators should be based on a consideration of this behaviour's fitness-associated benefits and costs to individual prey. Functional models/hypotheses of avian mobbing (Curio 1978) and of parental defence of offspring against predators (e.g., Andersson et al. 1980, Curio et al. 1983, 1984, Curio 1987, Montgomerie & Weatherhead 1988, Redondo 1989), which includes the parent(s) approaching and perhaps attacking a potential predator, have been proposed. However, to our knowledge, there has been no functional analysis of prey approaching predators in general, similar to that of Ydenberg & Dill (1986) for prey fleeing from predators.

In this paper, we initially review the possible costs and benefits to individual prey animals when approaching predators. This literature review is not intended to be exhaustive for any taxonomic group. We attempt rather to identify costs and benefits common to species which approach their predators, identify gaps in current knowledge

and propose new research directions. Since animals are expected to trade-off the costs and benefits of alternative behaviours in making behavioural decisions (Ydenberg & Dill 1986, Godin 1990, Lima & Dill 1990), we assume that individual prey are sensitive to the benefits and costs associated with approaching predators and should therefore 'choose' an approach distance which maximizes their fitness. In this context, we develop a general game-theoretical, cost-benefit model of prey approaching predators, which predicts the optimal relative distance of approach for individual (and groups of) prey. It is hoped that the general predictions of this model will help direct future research. We finally compare the simulation results of the model with data which we (Dugatkin & Godin 1992) collected in a field study of predator inspection behaviour in the Trinidadian guppy (*Poecilia reticulata*).

## 2. Costs of approach behaviour

There are several potential fitness costs to individual prey associated with their approaching predators. These costs may be incurred through either reduced probability of survival of the approacher, its offspring or other relatives nearby. In the context of life history theory, any loss in residual reproductive value as a result of approaching a predator is a fitness cost (Curio et al. 1984, Montgomerie & Weatherhead 1988, Redondo 1989).

### 2.1. Increased risk of mortality to the approacher

An individual prey presumably incurs an increased risk of mortality by approaching a potential predator at a distance, and particularly by rendering itself more conspicuous during its approach by alarm signaling or threat/distraction displaying. A systematic investigation of this potential direct fitness cost has been difficult, mainly because predator attacks on approaching prey are infrequently observed in nature. Nevertheless, numerous anecdotal field observations strongly indicate that this cost is real (but see Hennessy 1986). There exists many accounts of

predators attacking and killing individual prey which had approached them too closely (e.g., Huntingford 1976a, Kruuk 1972, Buitron 1983, Brunton 1986, Curio & Regelman 1986, Poiani & Yorke 1989, Sordahl 1990). The attack success of certain predators is also known to be greater the closer their prey at the instant of attack (e.g., Dill 1973, Webb & Skadsen 1980). Recently, Dugatkin (1992) examined the relationship between the risk of mortality and predator inspection in male guppies. When guppies with known predator inspection tendencies were placed in a pool containing a fish predator, a negative correlation was found between the distance an individual approached a predator (determined independently in a prior trial) and its probability of survival over a specific time period. Dugatkin's (1992) results indicate that predator inspection, or some correlated behaviour, is risky.

Despite the aforementioned evidence for an increased risk of mortality associated with approaching predators, the particular form of the relationship between the probability of death and distance to the predator during an approach is unknown, and should be investigated experimentally with species suitable for staged encounters (e.g., fishes). This relationship may be non-linear, and more specifically concave downward, as assumed by parental investment theory models of avian predator mobbing behaviour (Montgomerie & Weatherhead 1988, Redondo 1989). It appears that the only data available in support of this particular form of relationship are those of Webb & Skadsen (1980), who demonstrated an exponentially increasing probability of a successful attack by muskellunge (*Esox* sp.) as the distance to their prey, fathead minnows (*Pimephales promelas*), decreased. However, it is unclear whether the minnow was aware of the predator on every attack in this latter study. Consequently, the aforementioned risk — distance relationship obtained by Webb & Skadsen (1980) may not accurately reflect that of prey approaching predators whilst being aware of the latter's presence.

Additional, but more indirect, evidence for an increased risk of mortality associated with approaching predators is revealed in the graded, threat-sensitive (*sensu* Helfman 1989) manner in which prey commonly respond to their perceived

current threat of predation. If approaching a predator entails no risk, then an individual's approach behaviour should not be expected to change in response to variation in the level of predation threat, regardless of its putative benefit(s) (Curio & Regelman 1986). However, several lines of evidence outlined below clearly indicate the contrary, as they demonstrate that approach behaviour varies at least geographically, with the level of threat imposed by the predator and with the prey's social organization (cf. Curio & Regelman 1986).

Prey generally do not approach potentially dangerous predators as frequently nor as closely as they do less dangerous predators or non-predatory species (Curio 1975, Kruuk 1976, Hennessy & Owings 1978, Bildstein 1982, Curio et al. 1983, Coss & Owings 1985, Pitcher et al. 1986, Magurran & Pitcher 1987, Dugatkin & Godin 1992; but see Gottfried 1979 and Robinson 1980 for exceptions). Prey are also more likely to approach potential predators, and tend to approach them more frequently and more closely, when in pairs or larger groups as compared to when they are alone (Bildstein 1982, Regelman & Curio 1983, 1986a, Curio & Regelman 1985, Curio & Regelman 1986, Pitcher et al. 1986, Magurran & Pitcher 1987, Dugatkin & Godin 1992, but see Regelman & Curio 1983 for an exception), perhaps owing to the predator confusion and dilution effects associated with social groups (Godin 1986, Pitcher 1986, Magurran 1990a). However, the risk may not be shared equally among members of a pair or larger group that approaches a predator. For example, a male great tit (*Parus major*) is more likely to initiate an approach towards a potential threat (a raptor or mobbing chorus), and approaches it more closely, than its mate when both sexes are involved in the approach (Regelman & Curio 1983, Curio et al. 1984, 1985, Regelman & Curio 1986a,b). Conversely, female guppies are more likely than males to initiate and lead joint approaches towards a potential fish predator (Magurran & Nowak 1991). In a mobbing group, the individual closest to the predator is more likely to die from a predator retaliatory attack than others in the mob (references in Curio & Regelman 1985). Dugatkin (1990) discusses some theoretical implications of such asymmetries in risk-taking.

Less vulnerable (e.g., larger, older, faster, better armoured, etc.) prey generally behave more boldly towards predators than do more vulnerable conspecifics, as revealed by their greater tendency to approach predators and to approach them more closely (Reist 1983, Loughry 1987, 1988, Curio & Regelman 1985, Helfman 1989). However, there are instances where more vulnerable and predator-naive prey, such as newly-emerged ground squirrel pups (Owings & Coss 1977, Poran & Coss 1990), approach (apparently maladaptively) a predator more closely than less vulnerable and more experienced adults. Many prey species also tend to avoid approaching the head region of predators, but instead preferentially approach them laterally or posteriorly (Curio & Regelman 1985, Ishihara 1987, Helfman 1989, Foster & Ploch 1990, Magurran & Seghers 1990b, Dugatkin & Godin 1992). In avoiding the most dangerous area around a predator (i.e., its head), prey presumably reduce their risk of mortality whilst approaching the predator. Working with fishes, George (1960) coined this phenomenon 'cone avoidance'. Altmann (1956) and Owings & Owings (1979) provide examples of prey species which approach their predators directly head on.

Approach behaviour also varies geographically in many species in a manner which suggests that such behaviour is particularly tuned to the population-specific magnitude of predation risk experienced over evolutionary time. In general, individual prey from populations which have evolved in sympatry with dangerous predators tend to behave more cautiously (e.g., approach less frequently, less closely and in larger groups, attack predator less frequently) towards potential predators compared with prey from populations which have not been exposed to the same predators or have experienced only weak predation pressure over recent evolutionary time (Curio 1975, Owings & Coss 1977, Hennessy & Owings 1978, Huntingford 1982, Giles & Huntingford 1984, Coss & Owings 1985, Magurran 1986, 1990b, Pitcher et al. 1986, Tulley & Huntingford 1988, Goldthwaite et al. 1990, Magurran & Seghers 1990a, Towers & Coss 1990; but see Owings & Owings 1979, Robinson 1980 and Loughry 1988 for exceptions). Evidence indicates that such population-specific approach behaviours towards predators are heritable (Owings &

Coss 1977, Tulley & Huntingford 1987, Magurran 1990b, Magurran & Seghers 1990b).

Lastly, other aspects of the dynamics of prey approaching predators suggest that prey assess the apparently increasing risk of mortality as they gradually get closer to the predator and modify their behaviour accordingly. For example, with increasing proximity to a potential predator, mobbing great tits increase their rate of alarm calling and shorten the length of forward moves (Curio et al. 1983, Curio & Regelman 1985), ground squirrels (*Spermophilus becheyi*) decrease their rate of tail flagging (Goldthwaite et al. 1990) and adult European minnows (*Phoxinus phoxinus*) increase their rate of predator inspection and 'skittering' (= rapid semi-circular turns associated with fright) (Pitcher et al. 1986, Magurran & Higham 1988). Therefore, these behaviours appear to be threat-sensitive and apparently reflect the prey's perceived current level of predation risk. Their putative communicative functions are discussed in Section 3.

## 2.2. Increased risk of mortality to the offspring or other relatives of the approacher

An individual may also incur a fitness cost if, as a direct result of it approaching a predator, its offspring or other kin nearby are more likely to be detected and killed by predators than if an approach had not been initiated. More specifically, the prey's approach towards a predator per se, or conspicuous signals (e. g. alarm calls, tail flagging) which it emits during such an approach, may attract this predator (or others in the vicinity) to its offspring or other kin nearby, thereby increasing their risk of predation. McLean et al. (1986) and Robertson & Norman (1977) reported that parental mobbing behaviour in birds attracted predators and brood parasites, respectively, to the nest. There exists a paucity of other direct evidence for such a fitness cost to individuals who approach predators.

In addition, limited circumstantial evidence indicates that certain species appear sensitive to the cost of their predator mobbing behaviour potentially revealing the location of their brood to predators, and accordingly adjust their behaviour to apparently minimize this risk. For exam-

ple, parental great tits did not approach a potential predatory threat (playback of mobbing chorus) as closely when it was near their nest compared to when it was further away (Zimmermann & Curio 1988). Parental American robins (*Turdus migratorius*) directed fewer mobbing attacks at a putative predator (human intruder) when their nests were well concealed compared to when they were exposed and readily visible to a visually-oriented predator (McLean et al. 1986).

Clearly, this potential (collateral) cost of approaching predators requires more experimental investigation.

## 2.3. Lost opportunity costs to the approacher

Animals must continuously make decisions (sensu Dill 1987), from a set of alternatives, about which behavioural activity to engage in at any given time (Dill 1987, Godin 1990, Lima & Dill 1990). However, because many behavioural activities are in conflict for expression in the animal's daily time budget (e.g. foraging vs. anti-predator behaviour), an individual that is currently engaged in a particular activity may be losing some fitness-related benefits by not having engaged in an alternative activity. Such a loss in gains is generally referred to as the lost opportunity cost of currently being engaged in a particular behaviour (Dill 1987, Lima & Dill 1990). A prey that is in the process of approaching a predator may incur a lost opportunity cost of foraging and mating, for example. The limited evidence for such a potential fitness cost of approach is reviewed below.

As a result of defending their brood by mobbing nearby predators, parental birds use time which otherwise could have been spent feeding their nestlings (Collias & Collias 1978, Curio et al. 1984). In doing so, they may incur a fitness cost, if reduced feeding of nestlings increases their risk of starvation or decreases their weight at fledgling and subsequent survival. Similarly, the food intake rate of parents themselves may be depressed as a direct result of frequently approaching and attacking potential brood predators, which reduces time available for foraging (Rangeley & Godin 1992). Reduced food intake may compromise a parent's future reproductive success through lowered fecundity and survivorship, for example.

Other evidence is suggestive of a lost foraging opportunity cost associated with approaching predators in animals that are not necessarily defending offspring. For example, individual European minnows which frequently approached a potential predator spent less time foraging than those which inspected the predator less often (Magurran 1986). Similarly, Loughry (1987) noted a negative relationship between time spent foraging and the magnitude of predator-directed behaviour (which includes approaches towards the predator) in individual black-tailed prairie dogs (*Cynomys ludovicianus*). The feeding rate of free-living guppies was lower in the presence of a fish predator model, which the guppies vigorously approached, than in its absence where no predator inspections occurred (Dugatkin & Godin 1992).

#### 2.4. Energetic cost of approaching predators

Of course, any behavioural activity involves expenditure of energy. Because approach behaviour comprises locomotion, movements of other body parts (e.g. tail flagging, head bobbing) and commonly vocalizations, it is undoubtedly expensive energetically. A question of interest here is how much energy an individual expends in approaching a predator compared with that expended in an equivalent time interval while not approaching. The difference between these two costs would represent the net energetic cost per unit time of approach. Equally of interest is the proportion of an individual's daily energy budget utilized in predator approach behaviour. Obtaining estimates of these energetic costs from free-living animals is understandably problematic (cf. Bennett 1986). Therefore, it is not surprising that, to our knowledge, there exists no data on the energetic costs associated specifically with approaching predators in prey animals. This is thus an area warranting further research. One approach involves obtaining a daily time budget for the various activities of focal animals, and then converting time engaged in any given activity into energy expended for that activity with (laboratory-generated) knowledge of the per unit time energetic cost of that activity (e.g. Puckett & Dill 1985). Other approaches to investigating behavioural energetics are reviewed in Bennett (1986).

#### 2.5. Costs to the approacher of being exploited by others

Whilst an individual is in the process of approaching (and visually fixating) a predator, it may incur a cost of exploitation. Exploitation could take the form of the approacher's unattended mate being cuckolded by other males nearby and other resources (e.g. food), which it may be defending, being stolen by others not engaged in the approach. Such possible exploitation costs remain largely unexplored. A notable exception is a laboratory study by Magurran & Nowak (1991), in which male guppies attempt to circumvent female mate choice by increasing their frequency of sneaky mating attempts ('gonopodial thrusts') towards females that are in the process of approaching a predator at a distance and thus less likely to avoid the males' attention. The exploitation cost to the female here is being inseminated by a male that she did not choose as a mate.

Although not specifically an exploitation cost of approaching a predator, the following phenomenon may represent an exploitation cost of antipredator behaviour in general. In some species, certain individuals in a group use false predator alarm calls (in the absence of predators) that result in other competitors nearby being distracted from their current activities and adopting appropriate predator avoidance behaviour. In doing so, the signaler increases its opportunities to exploit, uncontested, a localized resource such as food (Munn 1986, Møller 1988) or reduces the risk of its mate being copulated by other male competitors (Møller 1990). We are unaware of any similar use of alarm signals by individuals to deceive others in approaching a putative predator. This is certainly an interesting possibility which warrants further investigation.

### 3. Benefits of approach behaviour

As with the above costs, there are also many potential fitness benefits to individual prey associated with their approaching predators. In other words, such approach behaviour is likely multifunctional (cf. Curio 1978, Shields 1984, Regelman & Curio 1986b). These fitness benefits

may be gained through increased probability of survival of the approacher, its offspring, other relatives nearby or an entire group cooperating in the approach (Curio 1978, Shields 1984, Poran & Coss 1990, Towers & Coss 1991). Much of the available evidence for the benefits of approach behaviour originates from studies of predator mobbing behaviour, particularly in birds and mammals, and predator inspection behaviour in fishes. Because reproductively active vertebrates commonly defend their offspring against predators by aggressively mobbing them, mobbing behaviour has generally been viewed as brood defence and functionally interpreted in the context of parental investment theory (e.g. Andersson et al. 1980, Curio et al. 1983, 1984, Regelman & Curio 1983, Curio 1987, Montgomerie & Weatherhead 1988, Redondo 1989). We do not intend here to reiterate the known determinants and benefits of such parental defensive behaviour specifically, as these have been reviewed recently (Montgomerie & Weatherhead 1988, Redondo 1989). We attempt rather to identify the potential fitness benefits accrued to individuals which approach predators in general, regardless of their reproductive status.

### 3.1. Acquiring information about the nature of the potential threat

Because approach behaviour is costly (see sections 2.1. – 2.5.), prey need to assess the risk associated with any potential predator encountered. Therefore, one function of approach behaviour might be that it permits prey to obtain information, which otherwise would be unavailable, about the nature of a potential predator and to monitor its behaviour at a distance. Having so assessed its risk of predation, a prey could then adjust its behaviour to minimize the costs or maximize the benefits associated with approaching the putative predator. We review here the evidence for such an information-gathering benefit of approach behaviour.

Many animals are naturally curious and will approach novel, even inanimate, objects (e. g. Csányi 1985, Magurran & Girling 1986, personal observations). An individual's tendency to approach a potential predator may partly reflect

its particular level of curiosity and general activity (Huntingford & Giles 1987), among other factors. The behaviour of animals approaching potential predators is often suggestive of curiosity-based investigation. For example, prey commonly approach a potential threat in a series of discrete and tentative forward moves, interrupted by stationary pauses of varying length during which they visually (e. g., Kruuk 1972, Curio et al. 1983, Curio & Regelman 1985, Magurran & Pitcher 1987, Towers & Coss 1990), olfactorily (e. g., Owings & Coss 1977, Owings & Owings 1979, Loughry 1987) and/or mechanically (e.g., Owings & Coss 1977, Owings & Owings 1979, Loughry 1987, Magurran 1990a, Rowe & Owings 1990) investigate the threatening object. Such approach behaviour likely serves to identify the potential threat, monitor its behaviour and/or assess its likelihood of attacking (cf. Kruuk 1976, Curio et al. 1983, Curio & Regelman 1985, Magurran & Pitcher 1987, Rowe & Owings 1990).

Additional evidence strongly suggest a predator-assessment function of approach behaviour. For example, European minnows are more likely to inspect a live pike early than late in the encounter; that is, before the pike has revealed its identity and intentions by initiating a stalk (Magurran & Pitcher 1987). In fishes, potential threats which do not clearly resemble natural predators at a distance (Csányi 1985, Magurran & Girling 1986) and do not move (Magurran & Pitcher 1987, Dugatkin & Godin 1992) are inspected more frequently than those which resemble predators or are moving. Such apparent ambiguity about the identity, and perhaps attack tendency, of a potential predator promotes inspection visits. The closer the prey approaches the putative predator, the less ambiguous the potential threat presumably becomes.

A predator is less likely to be approached by other prey after it has been recently observed to kill a prey or to be in possession of a dead prey (Kruuk 1976, Csányi 1985, Magurran & Pitcher 1987), perhaps because its attack motivation is no longer in doubt. Approach behaviour may also allow prey to differentiate between hungry and satiated predators (Licht 1989), presumably through subtle differences in their behaviour.

Many prey species live in close proximity to their predators and thus encounter them frequently

in nature (e. g., Foster 1980, Pitcher 1980). However, not all large species are necessarily dangerous, and predators are not always motivated to feed. Therefore, a prey which always fled or hid immediately upon encountering a potential threat would incur some lost opportunity costs and waste energy. When a potential predator is detected at a distance, approaching it would likely provide the prey with more reliable information to confirm its identity and assess its motivation. Following this assessment, the prey should then modify its behaviour according to its perceived risk of predation (cf. Helfman 1989). If the potential threat is real, the prey may adopt one or more of a number of anti-predator tactics (e.g. Godin 1986, Pitcher 1986, Magurran 1990a) which reduce its risk of predation. Conversely, if the threat is judged innocuous, the prey may safely resume other activities, such as foraging and courting, and thereby not incur further immediate opportunity costs (e. g. Magurran & Girling 1986, Magurran & Pitcher 1987).

### 3.2. Informing others of the potential threat

An individual who has approached a potential predator presumably possesses more accurate information about the current threat of predation than other individuals who didn't approach or did not approach as closely. Hence, an information asymmetry possibly exists in favour of the initial approacher. Of particular interest here is whether the approacher shares its knowledge about the predator's presence, identity and perhaps attack motivation with other nearby and less-informed prey.

There are several lines of evidence supporting the general hypothesis that individuals which approach predators commonly transmit information to others (especially conspecifics) nearby. Such information transfer appears to function mainly in warning others of the presence of a predator in the vicinity, recruiting more individuals to collectively approach the threat, and 'teaching' others to recognize dangerous predators (cf. Curio 1978). This evidence is briefly reviewed below.

Approach behaviour by one or more individuals in a social group may provide advanced

warning of a potential predator to other conspecifics nearby who are unaware of the impending threat (cf. Curio 1978). The latter benefit from advanced warning of the presence and perhaps attack motivation of the predator if it is assessed as a real threat by the approacher(s). Alternatively, if the potential predator is innocuous, then both approacher(s) and non-approachers in the group still benefit by resuming non-defensive activities and thus not incurring further immediate opportunity costs (cf. Section 2.3). For example, after approaching (= inspecting) a potential predator, inspecting minnows typically return to the safety of their shoal and reduce their feeding whilst concurrently increasing their rate of movement and 'skittering' (Pitcher et al. 1986, Magurran & Pitcher 1987). Shortly thereafter, other individuals leave the shoal at a rate greater than that observed before the initial predator inspection visit. Presumably, some information was transmitted from inspectors to non-inspectors within the shoal. This was experimentally confirmed by Magurran & Higham (1988) who showed that 'receiver' minnows, which were unaware of the presence of a predatory pike (*Esox lucius*), decreased their feeding and increased their time spent in hiding in response to simply viewing a predator-mediated increase in the rate of inspection visits and skittering in nearby 'transmitter' minnows. It remains unknown in this case whether skittering served as a predator-alarm signal specifically directed at non-inspectors by inspectors or whether the inspection behaviour per se of a few individuals served as a general warning signal to other conspecifics to become more alert. Similarly, the predator-induced 'bobbing' behaviour of gobies (*Asterropteryx semipunctatus* and *Gnatholepis anjerensis*) appears to be a predator-warning signal directed at nearby conspecifics that have not yet seen the predator (Smith & Smith 1989).

Many terrestrial animals emit predator-specific alarm calls (e. g., Curio et al. 1983, Cheney & Seyfarth 1990, Poran & Coss 1990) and (or) non-vocal alarm signals, such as head bobbing, tail flagging, jumping and sand kicking (e. g., Owings & Owings 1979, Poran & Coss 1990, Towers & Coss 1990) during their approach towards putative predators. These signals may alert



other conspecifics of a potential threat in the vicinity (cf. Curio 1978). In addition, other aspects of approach behaviour in prey (e. g., minimal approach distance, frequency of approach), which vary in relationship to the magnitude of the current risk of predation (see Section 2.1), may provide information about the potential threat. Therefore, an individual who does not approach a potential predator could conceivably obtain information passively about the nature of the threat by observing individuals who dare approach the predator. By observing conspecifics approach (and perhaps harass) potential predators, predator-naïve individuals may also learn to recognize dangerous predators and to subsequently approach (and harass) them more vigorously, avoid them or avoid the particular area in which they were last seen. Such cultural transmission of predator recognition has been experimentally documented for predator mobbing behaviour in birds (Curio et al. 1978a, b).

An additional benefit in socially transmitting information about a potential predator is the recruitment of other nearby individuals, who in turn will join it in approaching and perhaps harassing the predator (Kruuk 1976, Curio 1978, Owings & Owings 1979, Pitcher et al. 1986, Ishihara 1987, Loughry 1987). Approaching a predator in a group dilutes one's individual risk of predation and may confuse the predator (cf. Godin 1986, Pitcher 1986, Magurran 1990a), while perhaps being more effective in deterring attack or chasing the predator away (see Section 3.3 below).

Given that approaching a predator is costly (see Section 2), why should an 'approacher' share any information about the potential threat with its group mates? At least three non-exclusive possibilities exist. First, information transfer may be 'selfish' in that the transmitter recruits others into approaching the predator, thereby diluting its own risk. Second, the information transferred may benefit the transmitter's kin. Third, information transfer promotes the survival of groups containing risk-taking transmitters (Dugatkin 1990). At this time, it is difficult to distinguish between active transfer of information from the initial approacher to receivers, which specifically manipulates the latter into approaching the predator also, and passive information transfer,

where the receivers simply respond to cues based on predator-mediated changes in the transmitter's behaviour (cf. Curio 1978, Owings & Owings 1979, Magurran 1990a). More research is clearly required on information transfer between individuals in the context of prey approaching predators.

### 3.3. Deterring predators

Although approaching predators is potentially risky (see Section 2.1.), approach behaviour could benefit prey if, on average, the probability of a predator attack on the approacher itself, its kin or members of a cooperating group is reduced as a result of the approach. There exists only limited evidence for approach behaviour inhibiting predator attack. Several mechanisms have been proposed for such predator deterrence, particularly for mobbing behaviour (Curio 1978). However, the precise effects of approach behaviour in general, and mobbing in particular, on predators remain largely unknown. We briefly review below three possible, but not mutually exclusive, mechanisms by which prey approach behaviour may deter predator attack (cf. Curio 1978).

#### *Moving on the predator*

Approach behaviour in birds and mammals (e.g., Owings & Owings 1979, Curio et al. 1983, Loughry 1988), and less commonly in fishes (e.g., Ishihara 1987, Foster & Ploch 1990, Rangeley & Godin 1992), often escalates into prey harassing and even attacking and chasing predators. Such escalated approaches are generally referred to as predator harassment or mobbing behaviour. Mobbing may function to 'move on' the predator outside the immediate vicinity of the prey (Curio 1978), thereby presumably reducing its own risk of predation and(or) that of its offspring. It may thus serve as defence of both self and offspring, as it occurs outside as well as inside the breeding season and by breeding and non-breeding individuals in many species (Altmann 1956, Shedd 1982, 1983, Shields 1984, Pettifor 1990). Mobbing by reproductively active individuals may also serve to protect their mates from predation,

thus ensuring their continued availability as fitness-enhancing resources (Regelmann & Curio 1983, 1986b, Shields 1984, Curio et al. 1985).

Evidence for approach behaviour, and particular mobbing, resulting in predators abandoning a hunting attempt and moving away from the prey is largely anecdotal. For example, predators have been observed to leave the vicinity of the prey after being mobbed by it (them) and not to return to the area in the immediate future (Bildstein 1982, Buitron 1983, Donaldson 1984, Carroll 1985, Helfman 1989, Foster & Ploch 1990). Ishihara (1987) observed that, on 62% of occasions, various fish predators would leave the immediate area after being mobbed by damselfish (*Pomacentrus coelestis*). Furthermore, inter-attack intervals of the predators on damselfish were shorter when no previous mobbing occurred compared with when mobbing had previously occurred. Mobbing thus appeared to reduce the future risk of predatory attack of individual damselfish. Similarly, Pettifor (1990) showed that kestrels (*Falco tinnunculus*) moved further between hunting positions when they were mobbed by birds compared to when they were not mobbed, as predicted by Curio's (1978) move-on hypothesis. Mobbing likely caused the kestrels to vacate their immediate foraging area, thereby reducing the prey's ambient risk of predation.

In a number of bird species, the nesting success of mated pairs is positively correlated with the intensity of their predator mobbing response, as measured independently with predator models or human intruders (Andersson et al. 1980, Blancher & Robertson 1982, Weatherhead 1989; but see McLean et al. 1986). These results provide indirect support for a predator deterrence role of mobbing behaviour, but not necessarily for the move-on mechanism, at least in birds. Montgomerie & Weatherhead (1988) have reviewed the factors which influence the intensity of nest defence (including mobbing) in birds. Similarly, reduced parental defence level in cichlid fishes may result in high offspring mortality to predation (Keenleyside 1991).

#### *Confusing the predator*

A prey approaching the predator in a saltatory manner, whilst simultaneously making noises (e.g. alarm calling) and/or various movements

(e.g. tail flagging, head bobbing, sand kicking), may confuse the predator (e.g., via 'sensory overload'), thereby perhaps inhibiting its attack or causing it to divert its attention to other prey. The potential confusion effect is likely magnified when several, similarly behaving prey approach the predator in a group (cf. Curio 1978). However, to our knowledge, there is no direct evidence that predators are confused by prey which approach them in such a manner. Although predators can be confused by groups of mobile prey (Ohguchi 1981, Godin 1986, Pitcher 1986, Magurran 1990a), there is no indication that the confusion effect is specifically generated by the movements of prey *approaching* the predator. This latter possible antipredator mechanism merits more attention experimentally.

#### *Perception and condition advertisement*

Prey benefit from information about the nature of a potential threat of predation they might be facing (see Section 3.1). Likewise, predators may benefit from information about encountered prey in making decisions about whether and when to attack (pursue). If this information is incomplete, then the predator is likely to pursue its prey when it should not. When the predator is likely to commit such an error of being too anxious to pursue (Hasson 1991) or when its hunting success is enhanced by attacking unwary prey (Webb 1982, FitzGibbon 1989), prey can benefit from signaling their alertness and/or physical condition (escape ability) to the predator (Magurran 1990a, Hasson 1991). Such signals directed at predators may result in the re-evaluation of their decision to attack (pursue), and may thus deter attack or further pursuit (Curio 1978, Baker & Parker 1979, Woodland et al. 1980, Caro 1986a, b, Magurran 1990a, Hasson 1991).

To date, the evidence for prey communicating their alertness and escape ability to predators by approaching them is scanty and largely circumstantial. The saltatory manner in which prey generally approach a predator per se, whilst visually fixating it, may signal to the predator that it has been detected and consequently that the element of surprise has been lost (Owings & Owings 1979, Curio et al. 1983, Pitcher et al. 1986,

Regelmann & Curio 1986a, Magurran 1990a, Rowe & Owings 1990). The predator may then choose to abandon its current hunting attempt and divert its attention to less vigilant prey (Curio 1978, Woodland et al. 1980, FitzGibbon 1989, Magurran 1990a). During their approach towards a predator, prey commonly emit energetically expensive signals, such as alarm calls (Curio et al. 1983, Curio & Regelmann 1985), tail flagging (Owings & Coss 1977), sand kicking (Coss & Owings 1985, Rowe & Owings 1990), jumping (Loughry 1987) and rapid turns (Pitcher et al. 1986), which may honestly advertise their alertness and ability to escape an attack. Most of these signals vary in frequency and(or) intensity with distance to the predator (see previous sections), and thereby may provide the predator with reliable information on the relative level of prey alertness and condition.

Whether the aforementioned signals associated with approach behaviour indeed deter predator attack (pursuit), like other prey signals associated with escape (cf. Hasson 1991), remains largely unexplored. A notable exception is Magurran's (1990a) experimental evidence showing that individual pike attacked European minnows less frequently when the latter inspected the predator than when they did not inspect. However, her experiment could not distinguish whether the reduction in pike attack rate resulted as a direct consequence of minnow inspection behaviour per se or as a consequence of fewer target prey being present near the predator when inspections occurred compared to when they did not occur. Recently, Magurran's (1990a) findings have been corroborated in a similar experiment (with one- and two-way mirrors) using guppies as prey, in which differential proximity to the predator of inspecting vs. non-inspecting prey could be discounted, and in an additional experiment where predator and prey could freely interact (J.-G.J. Godin & S.A. Davis, unpubl. data). The precise mechanism(s) of attack deterrence in both these studies is unknown; the observed reduction in predator attack tendency associated with inspection behaviour could be due to a predator confusion effect of prey approach behaviour (as noted in the previous sub-section), to prey informing the predator that it had been detected, and(or) to prey informing the predator

of their boldness and ability to escape if attacked.

### 3.4. Advertising one's quality to mates

In many species with biparental care, males tend to take more risk by approaching potential predators more frequently and more closely than females during the reproductive season (e.g., Buitron 1983, Loughry 1987, Curio et al. 1983, Keenleyside 1991, Rangeley & Godin 1992). This sexual difference in risk taking has been particularly well studied in parental great tits, where the male typically approaches a potential threat sooner and more closely than its mate (Curio et al. 1983, Regelmann & Curio 1983, 1986a, b, Curio & Regelmann 1985). This observation cannot be readily explained by parental investment theory models (Andersson et al. 1980, Regelmann & Curio 1986b, Montgomerie & Weatherhead 1988, Redondo 1989). Several hypotheses have been proposed to explain why male great tits take greater risks in approaching predators than females. First, males take greater risks because they gain more than females in long-term eviction of predators from their home range, whereas females disperse from the male's home range following reproduction (Curio et al. 1985, Regelmann & Curio 1986a). Second, the male may be protecting the female as a fitness-enhancing resource (Curio et al. 1985, Regelmann & Curio 1986a, b). Third, by approaching the predator more closely and more vigorously, a male may be advertising its 'prowess' or viability to its mate, so as to keep her bonded for future broods (Curio et al. 1983, Regelmann & Curio 1983, 1986b).

The possibility that males use approach behaviour towards predators to advertise their viability to females, and that females preferentially choose bold males as mates, is potentially of great interest. Since approach behaviour is costly, it may be a good candidate for an honest signal of male viability that is resistant to cheating (cf. Alcock 1989). However, the role of approach behaviour (i.e. boldness towards predators) in female mate choice and sexual selection has not been explored systematically, and therefore represents a promising area for future research.

### 4. A game theory model of approach behaviour and a qualitative test

In this section, we expand a game-theoretical model developed by Dugatkin (1990) to examine the evolution of predator inspection behaviour in fishes. Although presented in the context of predator inspection behaviour, the model is general and applies to any system in which certain individuals (e. g., inspectors) share benefits with others (e. g., non-inspectors) while bearing all the costs alone. We begin by briefly reviewing the original model (model I in Dugatkin 1990), and then proceed to modify the payoff structure of the game to allow us to predict the relative distance to a predator individuals should inspect — a prediction lacking from the original model. Lastly, we compare the results of the model with data collected from a field study of predator inspection behaviour in guppies.

#### 4.1. The model

In the original model (and the model developed below), inspectors and non-inspectors are assumed to be randomly distributed into groups of size  $N$ . If we let  $j$  = the number of inspectors in a group (thus making  $N-j$  = the number of non-inspectors) and  $f$  = the frequency of inspectors in the metapopulation, then the probability that a group of size  $N$  contains  $j$  inspectors is

$$\binom{N}{j} f^j (1-f)^{N-j} \tag{1}$$

If we denote  $Z_i(j)$  as the payoff to inspectors ( $i$ ) when in a group of  $j$  inspectors and  $Z_{ni}(j)$  as the payoff to non-inspectors ( $ni$ ) when in a group of  $j$  inspectors, the fitness increment due to inspection is:

$$\frac{\sum_{j=0}^N \binom{N}{j} f^j (1-f)^{N-j} j Z_i(j)}{\sum_{j=0}^N \binom{N}{j} f^j (1-f)^{N-j} j} \tag{2}$$

for inspectors and

$$\frac{\sum_{j=0}^N \binom{N}{j} f^j (1-f)^{N-j} (N-j) Z_{ni}(j)}{\sum_{j=0}^N \binom{N}{j} f^j (1-f)^{N-j} (N-j)} \tag{3}$$

for non-inspectors.

In Dugatkin (1990),  $Z_i(j)$  was set to  $B-C/j$ , where  $B$  = the benefit of inspection and  $C$  = the cost of inspection to a lone inspector (i.e. an inspector in a group where  $j = 1$ ). Similarly,  $Z_{ni}(j)$  was set equal to  $B$  for all  $j \neq 0$  and to 0 when  $j = 0$ . The payoff to non-inspectors assumes that inspectors share the benefit of inspection with non-inspectors, an assumption supported by Magurran & Higham's (1988) study on information transfer during predator inspection in minnows. (Refer also to Section 3.2 above).

The results of the original model can be summarized as follows (see Dugatkin 1990 for more details):

1. Inspection can only increase from mutation frequency when  $B > C$ .
2. The inspection strategy increases from mutation frequency but does not go to fixation. That is, when  $B > C$ , a stable internal equilibrium, in which both inspectors and non-inspectors coexist, arises. At the internal equilibrium, the fitness of inspectors is exactly equal to the fitness of non-inspectors.
3. Even though the inspection strategy is maintained at relatively low frequencies (i.e. between 0–10%) for large  $N$ , the proportion of groups with at least one inspector is always much greater (40–85%; see Dugatkin 1990, Fig. 3b). Thus, one expects to see inspection behaviour in a large proportion of groups in nature. It may be appropriate at this point to note the similarity between  $N$ -person game and intrademic group selection models (reviewed by Wilson 1983) in which a single  $N$ -person group is equivalent to a trait group and gene frequency is partitioned into within and between group components.
4. For any given values of  $B$  and  $C$ , increasing group size decreases the frequency of the inspection strategy at the internal equilibria. This occurs because larger groups decrease

the probability that a non-inspector finds itself in a group of  $j = 0$  (i.e. where it receives a payoff = 0).

- Increasing the difference between  $B$  and  $C$  always results in an increase in the frequency of inspectors at the equilibria.

(For an example of how conditionally cooperative strategies such as TIT FOR TAT can be modeled using the framework developed here, see Model II of Dugatkin (1990)).

It is important to note two properties of the payoffs used in the original model (Model I in Dugatkin 1990). First, costs and benefits were assumed to be invariant with respect to the distance to which prey inspected (approached) a predator. Second, letting  $Z_{ni}(j) = 0$  for  $j = 0$  implies that group size per se does not dilute costs in groups of non-inspectors. For example, in Dugatkin (1990), non-inspectors in groups of composition  $N = 2$  and  $j = 0$  have the same risk of predation as non-inspectors in groups of  $N = 20$  and  $j = 0$ . If group size itself dilutes individual risk of predation risk (Godin 1986, Pitcher 1986), then this assumption is clearly violated.

We now modify the costs and benefits of the inspection game to make them a function of inspection distance. In addition, we incorporate a 'dilution' effect for groups composed solely of non-inspectors. A dilution effect is invoked only for pure non-inspector groups because, in mixed groups, inspectors are under much greater predation pressure than non-inspectors (Dugatkin 1992). That is, non-inspectors rarely seem to be the victims of predatory attacks when in groups containing both inspectors and non-inspectors, thus rendering the magnitude of any dilution effect relatively minor in such cases.

For the purpose of this paper, we assume very simple benefit and cost functions. We assume that the benefits of inspection increase at a decelerating rate with distance inspected, such that

$$B(x) = a(1 - e^{-nx}) \quad (4)$$

where  $a$  represents the asymptotic value of the benefit function,  $n$  measures the rate at which the asymptote is reached and  $x$  represents the proportion of total potential distance inspected, such that  $x = 0$  represents no inspection and  $x = 1$  rep-

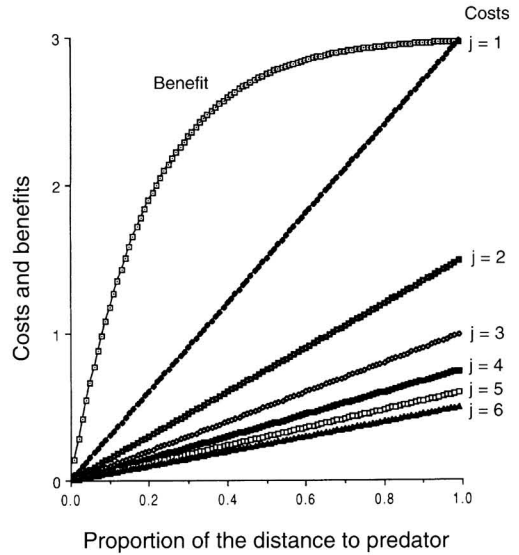


Fig. 1. The costs and benefits of approaching a predator as a function of the proportion of the total potential distance approached and the number of inspectors ( $j$ ). A relative distance to predator value of 0 indicates that predator and prey are separated by a distance great enough to preclude visual contact (this distance will vary across predator-prey systems), while a value of 1 indicates the predator and prey are close enough to each other to be in physical contact. For the case depicted above,  $B(x) = 3(1 - e^{-0.5x})$  and  $C = 0.3x/j$ .

resents inspecting the predator as close as possible. We also assume that the cost of inspection increases monotonically with distance to the predator such that

$$C(x) = (mx + b)/j \quad (5)$$

where  $m$  and  $b$  represent the slope and Y intercept of the cost function, respectively. It is critical to remember that the costs of inspection are paid only by inspectors, but the benefits are accrued by all group members.

One set of cost and benefit functions is shown in Fig. 1. We can also use the information provided in Fig. 1 to compute an optimal inspection distance for a group of  $j$  inspectors. This is done by simply taking the maximum value of  $B(x) - C(x)$  for a given value of  $j$  and noting the corresponding value of  $x$ . Ydenberg & Dill (1986) use a similar

graphical approach to determine the optimal distance to flee from an approaching predator.

The dilution effect assumes that the probability of a group being sighted by a predator is independent of group size (Godin 1986, Pitcher 1986). If this is not the case, however, the per capita benefits accrued by individuals in larger groups will be reduced by the greater probability that such groups will fall victim to predator attacks (Pitcher 1986). We incorporate a dilution effect for non-inspectors into the model by letting the net payoff to non-inspectors in homogeneous groups (i.e. groups where  $j = 0$ ) asymptotically approach (with group size) the payoff of a non-inspector in a group containing a single inspector. That is, we assume a non-inspector in a group with any inspectors always has a higher fitness than when it is in a pure group, but that these payoffs converge as group size becomes very large.

#### 4.2. Results of the model

All of the general results from Dugatkin (1990: outlined above) hold true for the simulations described below. Because of the large number of parameters used in the expanded model, we restrict our description of the results to a small fraction of the parameter space, unless otherwise noted. Although we have run simulations for  $N = 2$  to  $N = 8$ , we focus on the case of  $N = 6$ . This will enable us to compare the predictions of the model with field data on the inspection behaviour of groups of guppies of known composition in their native streams of Trinidad, West Indies.

##### *Equilibril frequency of inspectors, optimal inspection distance and the distribution of inspector group sizes*

Calculating the equilibril frequency of the inspection strategy is a two-step process. First, we must know both the payoff to non-inspectors in groups of  $j = 0$  and the value of  $\max[B(x) - C(x)]$  for all  $j > 0$  (see Fig. 1). With this, we have the net payoff for inspectors and non-inspectors in all possible group types ( $j = 0, 1, 2, \dots, N$ ). Second, these net payoffs are then plugged into equations (2) and (3) to calculate the equilibril frequency of the inspection strategy in the metapopulation.

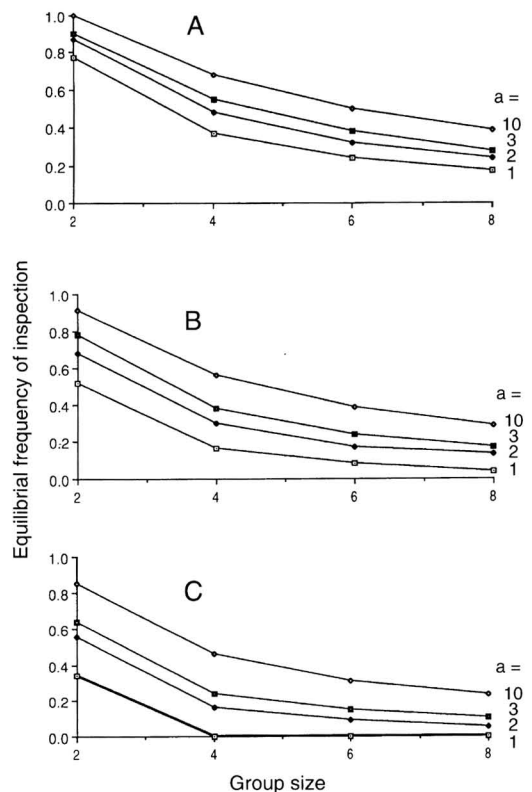


Fig. 2. Equilibril frequency of inspectors as a function of group size. A)  $C = 0.1x/j$ , B)  $C = 0.3x/j$ , C)  $C = 0.6x/j$ . For all cases,  $B(x) = a(1 - e^{-0.5x})$ .

As in Dugatkin (1990), equilibril frequencies of the inspection strategy decrease with increasing group size (Fig. 2). This occurs because increasing group size increases the probability that non-inspectors will be present in groups with numerous inspectors. Since the benefits of inspection are greater in groups with many inspectors, non-inspectors (who receive  $B(x)$  compared to  $B(x) - C(x)$  for inspectors) increase in frequency. Table 1 shows (one case of) the optimal inspection distance for different values of  $j$  and the equilibril frequency distribution of  $j$ .

##### *Mean inspection distance*

The results generated from this model also allow us to predict the (standardized) mean inspection distance for a given group size. Specifically, we wish to calculate mean inspection distances given

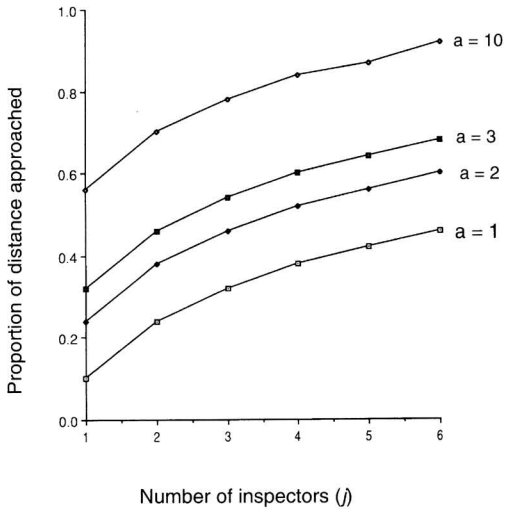


Fig. 3. Relative distance approached as a function of the number of inspectors. Here, shoal size equals 6 individuals and  $B(x) = a(1 - e^{-0.5x})$  and  $C = 0.3x/j$ .

that an inspection has taken place. To do this, we examine only the cases in which some inspection may take place; for example,  $1 < j \leq 6$  for the case of  $N = 6$ . We then standardize the proportion of inspector shoal sizes such that they sum to 1 (i.e. we reweigh the proportion of groups of size  $j$  when no  $j = 0$  are allowed; see SF in Table 1). Optimal inspection distances (see Table 1, Fig. 3), are also standardized such that the proportion of the distance inspected by solo inspectors ( $j = 1$ ) is set equal to 1 (Table 1, SA). Standardized

approach distances are then weighted by standardized frequencies of inspector group sizes and summed. Let's imagine that this procedure produces a sum of 1.27 (as in Table 1). From this we would predict that the average distance inspected would be 1.27 times the distance that solo fish (on average) inspect or about 30% ( $= 1.27 \times 0.24$ ) of the distance to the predator.

#### *A qualitative test of the model using field data*

Here we compare the expected distribution of inspector group sizes generated by the game theory model with data collected on the inspection behaviour of wild guppies (see Dugatkin & Godin 1992 for more details on the field experiments). The field data we use for the comparison were collected between 16–26 January 1990 in Ramdeen Stream, a second order tributary of the Arima River, Trinidad, West Indies. A circular enclosure (1m in diameter, 40 cm high) was constructed in a small stream pool. The enclosure naturally contained various foraging substrates for guppies. Thirty-four 5-min trials were conducted. In each trial, six female guppies (dipnetted from the stream 24 h earlier) were placed in the enclosure and a model of a cichlid fish predator was presented 30 min later. Observers noted each predator inspection visit and the size of the inspecting group. The protocol, however, did not allow us to identify individual guppies.

Because of the way the field data were collected, no inspector groups of size zero were possible. That is, since we only recorded inspector group size, it is not possible to know the number of non-inspections that occurred (nor

Table 1. Example of the method used for calculating standardized mean inspection distance (SMID).

Number of inspectors	Proportion of distance approached	Standard approach (SA)	Frequency	Standardized frequency (SF)	SA $\times$ SF
1	0.24	1.00	0.40000	0.59701	0.5970
2	0.38	1.58	0.20500	0.30597	0.4845
3	0.46	1.92	0.05600	0.08358	0.1602
4	0.52	2.17	0.00860	0.01284	0.0278
5	0.56	2.33	0.00070	0.00104	0.0024
6	0.60	2.50	0.00002	0.00004	0.0001

Standardized mean inspection distance = 1.27

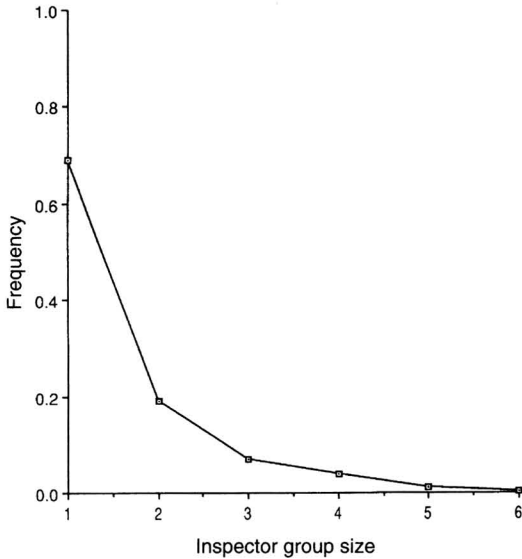


Fig. 4. Frequency distribution of inspector group size for guppies in Ramdeen Stream, Trinidad, West Indies. Thirty-four shoals of six females each were tested.

can we use our data to examine the amount of time a group had some members undertaking an inspection). As such, we examine conditional probabilities by comparing the distribution of inspector group sizes, given that an inspection has occurred. As for average inspection distances, we do this by looking at the model's predicted distribution for the case of  $N = 6$  and  $j = 1$  to 5. That is, we subtract the expected proportion of inspecting groups of size 0 from unity and then normalize the remaining frequencies such that they add to 1. We then compare these results with the field data collected in Trinidad (Fig. 4). Since the costs and benefits of inspection have not yet been quantified in the field, we have not compared expected vs. observed distributions of inspecting group sizes using statistical tests. Rather, we attempt a qualitative test and examine whether the shape of the observed distribution differs from those generated by the model.

Fig. 5 shows a number of different cost/benefit scenarios. It appears that the shape of the observed distribution (Fig. 4) is similar to that predicted by the model (Fig. 5) when both the

costs and benefits of inspection are intermediate rather than very large or small. It is interesting to note that compared to other tributaries of the Arima River, Ramdeen Stream appears to have an intermediate number of piscine predators (personal observations).

## 5. Concluding remarks

Over the past twenty years, most behavioural and evolutionary ecologists have adopted a cost-benefit approach to understanding the evolution of behaviour (Alcock 1989, Dupré 1987). Such an approach entails not only detailing the costs and benefits associated with a particular behaviour(s), but developing predictive models which incorporate such costs and benefits. Here, we have attempted to do just that with respect to the question of why prey approach their predators. The major (known and potential) costs and benefits associated with approaching predators were reviewed. Most of the fitness benefits are anti-predatory in nature, whereas the types of costs are more diverse. Although some recent work provide strong evidence for particular costs and benefits, most of the evidence reviewed is either anecdotal, non-experimental or simply non-existent.

Future work, either in the laboratory or the field, must be designed to test specific hypotheses regarding the costs and/or benefits of approaching predators. One way to do this is to develop economic models of prey approach behaviour, and then attempt to test these models using controlled experiments. We developed such a model for predator inspection behaviour in fishes. However, due to the current lack of quantitative measures of associated costs and benefits, only a qualitative, rather than quantitative, test of this model could be carried out using what some might call reverse optimality (i.e. using the model to tell us what the magnitude of the costs and benefits may be). Nonetheless, when data on costs and benefits are available a priori, such models provide a first step in using this information in a predictive manner. We would urge future researchers to adopt such an economic (cost-benefit) approach when studying why prey approach their predators.



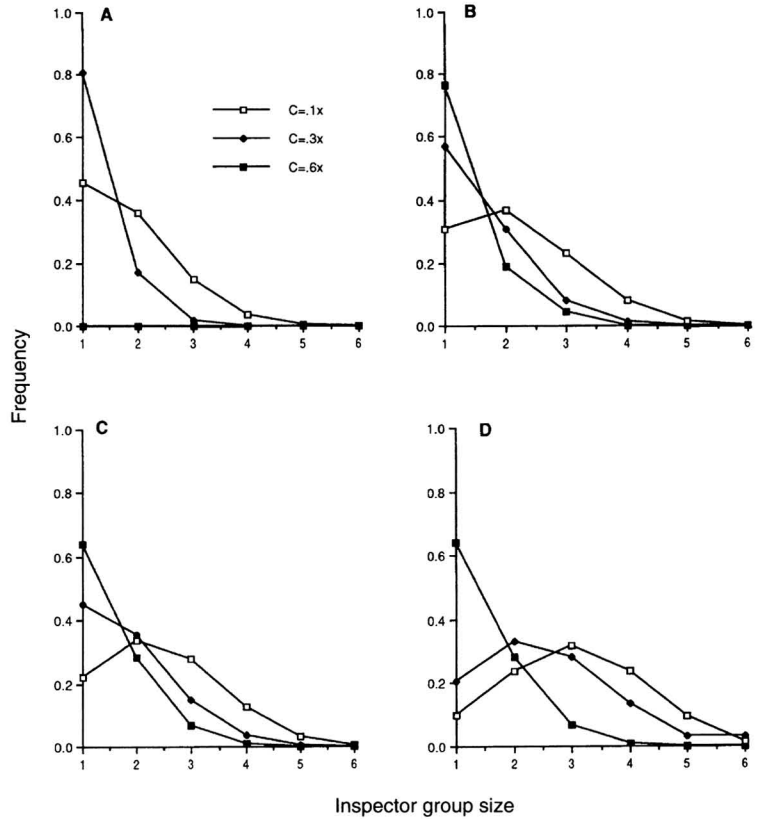


Fig. 5. Predicted frequency distribution of inspector group sizes for various  $B(x)$  and  $C(x)$ 's.  
 A)  $B(x) = 1(1 - e^{-0.5x})$ ,  
 B)  $B(x) = 2(1 - e^{-0.5x})$ ,  
 C)  $B(x) = 3(1 - e^{-0.5x})$ ,  
 D)  $B(x) = 10(1 - e^{-0.5x})$ .

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