

The group size – flight distance relationship in water striders (*Gerris remigis*)

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When food availability is constant, the distance from which first instar water striders (*Gerris remigis* Say) initiate escape from approaching (potentially cannibalistic) adults initially rises and then falls with increases in group size. This result cannot be explained by the currently accepted many-eyes hypothesis, which predicts a monotonically increasing relationship between flight initiation distance and group size, resulting from the increased probability of predator detection by larger groups. The results are consistent with an alternative hypothesis, according to which the preferred flight distance results from a trade-off between the costs and benefits of flight and declines with increasing group size due to risk dilution. The gerrids are constrained from achieving their preferred flight distance when tested as individuals, and the adult is able to approach more closely before being detected.

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Lorsque la disponibilité de la nourriture est constante, la distance à laquelle les larves de premier stade du Patineur matelot (*Gerris remigis* Say) commencent à se sauver des adultes (parfois cannibales) augmente au départ, puis diminue à mesure qu'augmente le nombre de larves dans le groupe. Ces résultats ne corroborent pas l'hypothèse généralement acceptée des «yeux multiples» qui prédit une relation d'augmentation monotone entre la distance propre à déclencher la fuite et le nombre dans le groupe, résultat de la probabilité plus grande de détection des prédateurs chez les groupes plus nombreux. Les résultats peuvent cependant s'expliquer par une autre hypothèse selon laquelle la distance de fuite est établie d'après un système de compensation entre les coûts et les bénéfices de la fuite et diminue à mesure qu'augmente le nombre dans le groupe par dilution des risques. Individuellement, les larves de Gerridae ne peuvent respecter leur distance préférée de fuite et les adultes peuvent s'en approcher plus avant d'être repérés.

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Introduction

According to the many-eyes hypothesis (Bertram 1978) prey animals gain an advantage from aggregating by receiving early warning of the approach of a predator. If prey flee as soon as they detect a predator (an implicit assumption in most studies), and if the ability to detect an approaching predator increases with group size, then flight initiation distance (or more simply, flight distance) should increase monotonically as group size increases. Such increasing relationships have been reported for the brent goose, *Branta bernicla* (Owens 1977), the woodpigeon, *Columba palumbus* (Kenward 1978), two species of macaques (van Schaik *et al.* 1982), and the marine water strider, *Halobates robustus* (Treherne and Foster 1980). In other cases, however, the relationship is approximately flat or shows a pronounced concavity, with maximum or minimum flight distance at intermediate group size (e.g., Godin and Morgan 1985; Siegfried and Underhill 1975; Greig-Smith 1981; other studies are reviewed in Table II of Ydenberg and Dill 1986). Such extreme variability in the form of the relationship between flight distance and group size is inconsistent with the many-eyes hypothesis.

We have recently proposed a more general economic model of flight distance (Ydenberg and Dill 1986) that can accommodate such variation. According to our hypothesis, an animal approached by a predator weighs the fitness costs of fleeing (e.g., lost foraging opportunity) against those of remaining (i.e., risk of capture) and flees when these are equal, since at further distances it is always advantageous to delay the response. The fitness-maximizing flight distance will be displayed so long as the approaching predator can be detected at or beyond this distance. In order to predict the relationship between group size and flight distance we need to be able to assess both the goal (the fitness-maximizing flight distance) and

the constraint (the distance beyond which predators cannot be detected) lines as a function of group size. We consider the actual forms of these relationships below, but for now simply consider three general possibilities as to how they can interact to determine flight distance. If the constraint line lies everywhere below the goal line, then the observed flight distance will be described by the former (Fig. 1A). Conversely, if the goal line lies everywhere below the constraint line, the observed flight distance will be described by the goal line (Fig. 1C). If the two functions intersect, the observed flight distance will be described by the constraint line on one side of the intersection point and by the goal line on the other side (Fig. 1B). We presume that small groups are more constrained than large ones so that the flight distances of small groups will usually be the ones described by the constraint line.

In this paper we examine the relationship between flight distance from an approaching predator and group size in the water strider *Gerris remigis* in the laboratory. First instar water striders acted as prey, while predators were adult water striders, dangerous because they are cannibalistic (Jamieson and Scudder 1979). The first instar water striders fed on a large fly and fled as the adult approached. As the size of the feeding group increases the chance that any individual will become the victim of an approaching adult diminishes, and hence flight distance should decrease. This should be true so long as the small water striders are not constrained by their inability to detect (by water surface vibration or sight) the adult's approach.

Methods

The prey were first instar water striders (gerrids) raised in the laboratory. All first instars (mean body length, 1.8 mm; range, 1.4–2.2 mm; $n = 20$) were removed from their natal aquaria at 1700 each day, held in groups, and starved for 17 to 24 h before testing; they

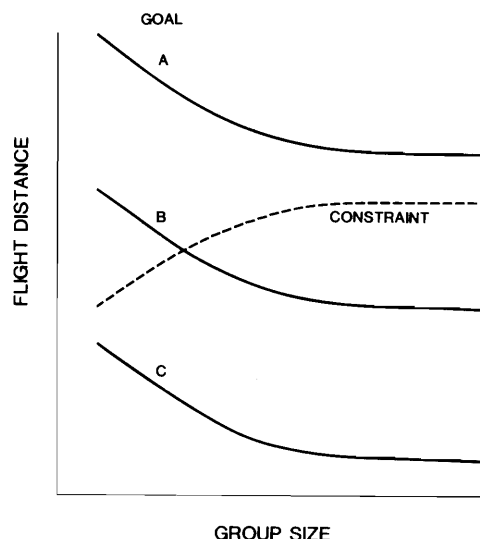


FIG. 1. Three possible positions of the goal line (—) relative to the constraint line (---). The constraint line lies everywhere below goal line A, and everywhere above goal line C, but intersects goal line B. See text for explanation.

thus ranged from 17 to no more than 48 h of age at that time. Gerrids were removed from their holding tank in small groups for the tests, and each individual was used only once.

The first instars to be tested were released into a clear plastic enclosure (8.9 cm diameter) placed in a large (1.23 × 0.81 m) shallow aquarium. A dead house fly (*Musca domestica*) was pinned upside down in the small enclosure with its dorsal surface just touching the water. The gerrids were allowed 5 min to begin feeding, after which any nonfeeders were taken out and the enclosure was removed. Resultant feeding groups ranged in size from 1 to 5. There were no obvious agonistic interactions among individuals in these groups.

Conspecific adults (mean body length, 13.2 mm; range, 12.3–14.5 mm; $n = 10$ males and 10 females) were used as predators. Cannibalism is common in this and other gerrid species (e.g., Jamieson and Scudder 1979) and adults occasionally captured first instars in our experiments. Adults were selected at random from holding tanks and starved for 48 h before use. An adult that performed well might be used in several consecutive trials on a given day. The adult was held in an enclosure of its own at the opposite end of the aquarium, about 0.9 m from the feeding first instars, and released 3 min after the prey enclosure had been removed. In successful trials the adult made a smooth approach directly towards the fly and the first instars (sometimes a little prodding was required). The adult gerrid's approach speed, measured from videotapes (see below), averaged $7.92 \text{ cm} \cdot \text{s}^{-1}$, and did not vary with first instar group size (ANOVA, $F_{[4,41]} = 0.40$, $p = 0.68$). Attack had to be made within 160 s of release or the trial was terminated; thus, the maximum possible feeding time for the first instars was 640 s.

All interactions were videotaped from above, and gerrids were very conspicuous over the white bottom of the aquarium. The flight distance of the first gerrid to flee was subsequently measured to the nearest 0.25 mm, from the tip of the approaching adult's head. Such precision was possible because of enlargement of the image.

Since the first instars had all been without food for 17–24 h and were allowed access to the house flies for no more than 640 s, individuals in groups of all sizes should have been in similar hunger states. First instar gerrids deprived of food for this length of time require about 1 h of feeding to become satiated and can consume only about $80 \mu\text{g}$ dry weight in that period (Jamieson and Scudder 1977). Consequently, even five gerrids could not have consumed more than a small percentage of the food available in the house flies used (mean dry weight \pm SD, $5.66 \pm 0.8 \text{ mg}$; $n = 20$), and food availability therefore

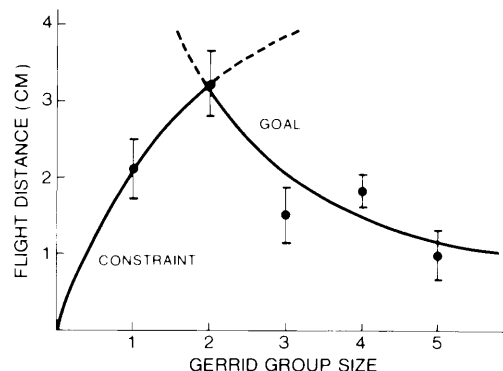


FIG. 2. The relationship between group size and flight initiation distance (mean \pm SE) in first instar water striders (*Gerris remigis*). The "constraint" line is fitted to the data for group sizes 1 and 2, and assumes that maximum flight distance is proportional to the probability of detecting the approaching adult predator. The "goal" line is fitted through the data for group sizes 2 through 5, and assumes that the preferred flight distance is proportional to individual risk of capture. Sample sizes for group sizes 1 to 5 were 15, 20, 13, 14 and 10, respectively. See text for further explanation.

should have been so uniformly high as to be effectively independent of group size.

We performed ANOVA on the data using formulae appropriate for the case in which there are many values of y for each x (Sokal and Rohlf 1981). We could therefore distinguish lack of fit from pure error.

Results

The measured relationship between flight distance and group size is shown in Fig. 2 for those trials in which the first instars reacted at a distance to the approaching adult. The group size effect is significant (ANOVA, $F_{[4,67]} = 5.30$, $p < 0.001$), and an inspection of Fig. 2 suggests the existence of a maximum flight distance at a group size of 2. However, the form of the relationship is not a simple one. Neither a linear nor a quadratic regression (both purely descriptive models) adequately fits these data; in both cases there is significant lack of fit. Nor are the data adequately explained by supposing that individuals behave differently when alone than when in groups; the decline in flight distance from group size 2 to 5 is very marked, and is significant (Student–Newman–Keuls test, $p < 0.05$).

The data apparently conform to the intersection of two functions, one describing a decline in risk with group size (goal) and a second describing how the attainment of this goal is constrained by the gerrid's ability to detect the predator (Fig. 1B).

We estimated the position of the constraint line by fitting the equation

$$[1] \quad \text{FD} = k(1 - e^{-\lambda \text{GS}})$$

over the increasing portion of the response curve (FD is the flight distance; GS is the group size), estimating the parameters k (a constant) and λ (the "looking" or vigilance rate) from the data by iteration. This equation follows from Pulliam's (1973) model of the relationship between probability of detection and GS, assuming that flight distance is directly proportional to probability of detection. Treherne and Foster (1980) found the FD–GS relationship in marine water striders to be adequately described by a relationship of this form. The values of λ and k that minimized the sum of squares of deviation around this model were found to be 0.68 and 4.34, respectively. Predicted

TABLE 1. Observed flight distances (FD) in water strider groups of various size, and those predicted by the constraint and goal models

Group size	Observed FD (cm)	Predicted FD		% reactions
		Constraint	Goal	
1	2.13	<u>2.14</u>	—	20
2	3.23	3.06	<u>3.06</u>	29
3	1.51	—	<u>2.04</u>	24
4	1.85	—	<u>1.53</u>	30
5	1.00	—	<u>1.22</u>	30

NOTE: Underlined values were used in the ANOVA (Table 2).

TABLE 2. ANOVA table for the compound constraint–goal model of flight distance

Source	df	SS	MS	F	P
Model	3	642.74	214.25	4.03	<0.025
Deviation	2	106.29	53.15	1.51	NS
Error	67	2366.05	35.31		

NOTE: The model has three fitted parameters (k , λ , and a) and thus 3 df. The total df equals the number of observations (72), since none were used fitting a grand mean. Consequently the deviation SS has 2 df, rather than 1 as in the usual polynomial regression.

and observed FD values are compared in Table 1 (constraint).

For the declining portion of the response curve (GS 2 through 5) we fitted an equation that assumes that flight distance is proportional to the risk to an individual,

$$FD = a/GS$$

The sum of squares of deviations is minimized when $a = 6.12$. Predicted values of FD are also shown in Table 1 for this model (goal).

The complete model combines these constraint and goal equations; the gerrids are assumed to flee at their preferred distance, predicted by eq. 2, unless constrained by their vigilance capabilities, in which case eq. 1 is used. Thus, at GS = 2, we used the goal equation because it predicts an achievable flight distance (i.e., one less than the allowable maximum predicted by the constraint equation). We then carried out ANOVA on this compound model (Table 2). The deviation term is nonsignificant ($p > 0.10$) and the compound constraint–goal model produces an adequate fit to the observed flight distance values (see Fig. 2). The adequacy of the fit is not a necessary consequence of the fact that the parameters were estimated from the data, since this is done in any regression analysis.

If lone waterstriders, or those in pairs, are constrained by a random detection process, their behaviour should be more variable than that of individuals in larger groups. This prediction is confirmed (F -test, $p < 0.005$). Also consistent with our model is the observation that flight responses were less common when individuals were tested alone (20% response rate) than in groups of any size (average of 28%; Table 1). This difference is significant (for angularly transformed data, $t = 6.75$, two tailed $p < 0.01$). We cannot explain the low overall response rate, but it has been previously noted in hungry gerrids (Jamieson 1973) and in those that, as in this experiment, were feeding on large prey items (Ydenberg and Dill 1986). It is also possible that the

first instars had become partially habituated to the presence of adults in their natal aquaria. All individuals (regardless of the group size in which they were ultimately tested) were exposed to approximately the same number of adults on their first day of life, so differential habituation cannot account for the effect of group size on flight distance.

Discussion

Our data show that the flight distance of first instar water striders from an approaching, potentially cannibalistic adult rises and then falls as group size increases. Of the hypotheses we considered, only the model proposing the interaction of a goal and a constraint adequately fitted the data. We explain this pattern by hypothesizing that, owing to risk dilution, the optimal flight distance falls as group size increases, but lone animals are constrained in their ability to detect the adult. The observed FD–GS relationship therefore results from the intersection of the goal and constraint functions. Relationships very similar to that observed here have been reported for banded killifish (*Fundulus diaphanus*) responding to model predators (J.-G. Godin and A. R. Hanson, unpublished data); in this case groups of three prey fled at the greatest distance. The data of Siegfried and Underhill (1975) suggest that laughing doves (*Streptopelia senegalensis*) are also maximally reactive in groups of intermediate size, and reanalysis of their data (Krebs and Barnard 1980) confirms this. Recently, Magurran *et al.* (1985) have shown that minnows (*Phoxinus phoxinus*) progressively delay their response to an approaching model pike as their shoal size increases.

The goal and constraint model we propose is capable of producing other FD–GS relationships than the one reported here. The optimal flight distance will depend on a number of habitat, social, and internal factors, the most important of which are group size and food availability. The effect of risk dilution can be counteracted by higher levels of competition in larger groups. If competition for food intensifies with group size, animals will have less to gain by delaying flight, and flight distance could increase with group size for economic reasons completely unrelated to those proposed by the many-eyes hypothesis. Most studies of the flight distance – group size relationship neither measure nor control food availability, making it impossible to reject either hypothesis.

Although our data are consistent with our compound hypothesis, a more convincing demonstration would involve experimental manipulation of either the goal or constraint lines and a predictable directional shift in the group size showing the maximal response. For example, if the opportunity cost of flight were increased through an increase of food quality, the goal line ought to move down. The intersection of the constraint and goal lines should then move towards the left, and maximal flight distance should occur in smaller groups. Alternatively, a more dangerous predator should increase the benefit of flight, raising the goal line and shifting the intersection point to the right (maximal flight distance in larger groups). To our knowledge no one has carried out such experiments, although the data of J.-G. Godin and A. R. Hanson (unpublished), who varied predator size, are suggestive.

While our “goal” line results from a trade-off between the costs and benefits of flight, and we treat the “constraint” line as something outside the animal’s control, this distinction is not strictly true. The so-called constraint may itself be the result of a trade-off in two ways. First, any individual prey could increase

its probability of detecting a predator by increasing its scanning rate (λ), but this would be at the expense of feeding time. Second, the design features of the sensory system that determine the maximum possible flight distance have probably resulted from trade-offs in evolutionary time. For both these reasons, we expect flight distance to be determined in an economic fashion and frequently to be less than the maximum distance "possible."

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