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DISRUPTIVE SELECTION ON PREY GROUP SIZE: A CASE FOR PARASITOIDS?

The prevalence of group living in animals has generated several hypotheses about the potential benefits of gregariousness. Although some of these hypotheses involve specific behavioral interactions among group members (Bertram 1978; Pulliam and Caraco 1984), others concern the purely statistical effects of gregariousness in decreasing predation risk (Treisman 1975; Turner and Pitcher 1986). Sillén-Tullberg and Leimar (1988) modeled the costs and benefits of gregariousness in unpalatable and aposematically colored insects. Their analysis primarily concerned group formation in insect eggs, larvae, and adults, whose predators are often larger and more mobile than their prey. In such cases, predators can consume a large proportion of the prey group (no dilution), and gregariousness would not be expected to evolve. Nevertheless, in the case of unpalatable and aposematic prey, Sillén-Tullberg and Leimar showed that disruptive selection on prey group size may arise, because of the predator-satiating effect of unpalatability and aposematism.

In this study, we demonstrate that disruptive selection on prey group size generally arises if a predator consumes a certain number of individuals (exceeding one) in a group rather than a fixed proportion of a group. This occurs whenever some type of predator-satiating mechanism is acting—for example, when parasitoids infest insect eggs, larvae, or pupae. In such situations, unpalatability and aposematism need not be invoked to explain bimodal distributions of prey group sizes.

THE MODEL

Two statistical effects may reduce the risk of predation for group members compared with solitary individuals (Turner and Pitcher 1986). The *avoidance effect* arises whenever a group's risk of being encountered by a predator increases less than in direct proportion to the number of group members. The *dilution effect* favors gregariousness by decreasing each specific individual's risk of being taken as prey once the predator has detected the group. The model below considers prey individuals' risk of predation in relation to group size. The model is based on the number of predators that a group of prey individuals are expected to encounter during a certain time period. This approach is advantageous in making long-term predictions of predation risks, since the number of expected encounters may increase linearly with group size (i.e., may exceed one), as opposed to the

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probability of detection (cf. Turner and Pitcher 1986, p. 231; Inman and Krebs 1987, p. 32).

We define the probability that a solitary prey individual survives an encounter with a predator as α_1, and the average number of expected predator encounters for a solitary individual as ϕ. Predation pressure is assumed to be constant. If there is no avoidance effect (a group of n individuals is encountered n times as often as a solitary individual) and no dilution effect (all individuals have the same probability of surviving an encounter irrespective of group size), we obtain

$$p(n) = 1 - \alpha_1^{\phi n}, \tag{1}$$

where $p(n)$ is the predation risk for a prey individual in a group consisting of n individuals. In this case, grouping increases predation risk.

The avoidance effect arises whenever the expected number of encounters increases asymptotically, rather than linearly, with group size (Treisman 1975; Turner and Pitcher 1986; Sillén-Tullberg and Leimar 1988). However, the exact nature of this relationship is affected by factors such as prey-group geometry and the sensory physiology and behavior of the predator (for a discussion, see Treisman 1975). Any relationship could be fitted into the current model, but in the interest of simplicity, we assume that this relationship is asymptotic according to

$$p(n) = 1 - \alpha_1^{\phi n^k} \qquad \text{and} \qquad 0 < k < 1. \tag{2}$$

In this case, the avoidance effect is operating alone (the risk of being taken in each encounter is unrelated to group size; i.e., the predator takes a certain proportion of the prey group).

The dilution effect occurs when a specific individual's probability of surviving a predator encounter (α_n) increases with group size. If the predator takes an average of x prey in encounters with solitary prey individuals ($x \leq 1$), α_n may relate to group size according to

$$\alpha_n = (n - x)/n, \tag{3}$$

which is the highest possible manifestation of the dilution effect. Hence, the overall predation risk is

$$p(n) = 1 - [(n - x)/n]^{\phi n} \tag{4}$$

when dilution is acting alone. Hence, dilution and avoidance effects acting in concert are described by the equation

$$p(n) = 1 - [(n - x)/n]^{\phi n^k}. \tag{5}$$

Maximal dilution occurs if the predator has a fixed probability, irrespective of group size, of catching one prey (imagine a lion attacking a herd of zebras). No dilution effect occurs if the predator catches a certain proportion of the prey group, irrespective of group size (as could be the case with a whale feeding on pelagic fish). What predictions can be made if the predator preys on a fixed number of prey individuals (>1) at each encounter? This is the case whenever

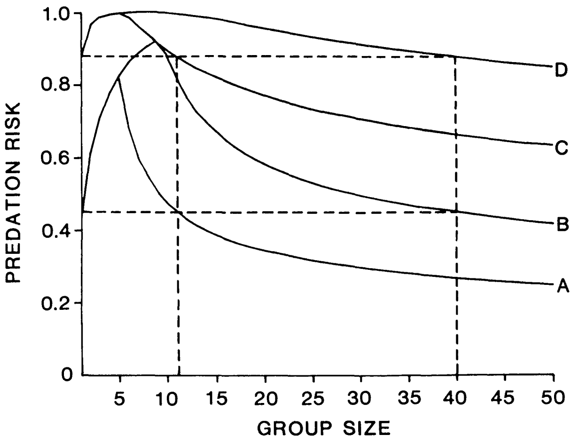

FIG. 1.—Predation risk for prey-group individuals when the predator preys on an average number (>1) of prey individuals at each encounter. *Dashed lines,* Critical group sizes (α_n = 0.05 and $k = 2/3$ in all cases: curve A, $\phi = 0.2$, $x = 5$; B, $\phi = 0.2$, $x = 9$; C, $\phi = 0.7$, $x = 5$; D, $\phi = 0.7$, $x = 9$; see the text for an explanation of the symbols).

some type of predator-satiating mechanism occurs. Such situations are likely to be common in many insect species. One case would be when parasitoids prey on insect eggs, larvae, or pupae, since each parasitoid female has a satiation level caused by limitations in the number of mature eggs available at each encounter. Given that the avoidance effect is acting and that the predator has an average consumption capacity (satiation level) of x ($x > 1$) prey individuals in each encounter, we obtain

$$p(n) = 1 - [(n - x)/n]^{\phi n^k} \quad \text{if} \quad n > x. \tag{6}$$

If the group size is smaller than or equal to the predator's average capacity ($1 \leq n \leq x$) and if the prey have a low chance of escaping the predator, no dilution effects occur (α_n low and constant). Hence, the predation risk may be expressed as

$$p(n) = 1 - \alpha_n^{\phi n^k} \quad \text{if} \quad 1 \leq n \leq x. \tag{7}$$

Combining these two equations produces a pattern (fig. 1) in which the properties of the predator as well as the prey yield a critical group size, above which it is beneficial to be gregarious but below which it is more profitable to be solitary. This critical group size is sensitive to the predator's satiation level (fig. 1, curves A and C vs. B and D): the lower the satiation level of the predator, the lower the critical group size. Thus, prey unpalatability is only one of several mechanisms giving rise to disruptive selection acting on group size. A bimodal distribution of egg-cluster sizes may be expected in palatable insects under certain forms of predation, for example, when the eggs are subjected to predation by parasitoids. The situation resembles that described by Sillén-Tullberg and Leimar (1988) in that there is some form of predator satiation in both situations. A general conclusion would be that predator-satiating mechanisms seem to generate multiple adaptive peaks with respect to the spatial distribution of prey individuals.

A CASE STUDY: WATER STRIDERS AND THEIR EGG PARASITOIDS

Water striders (Heteroptera: Gerridae) are predatory insects living on water surfaces. Females of most species lay their eggs on objects at the water surface, such as floating leaves (Andersen 1982). Water strider eggs are parasitized by a scelionid wasp, *Tiphodytes gerriphagus* (Marchal), a widely distributed Holarctic parasitoid. Eggs of most water strider species have been found to be parasitized in the field, and eggs of all species exposed to the parasitoid in the laboratory have been parasitized (Spence 1986; Nummelin et al. 1988). Predation by this parasitoid on water strider eggs may be very intensive (Spence 1986; Nummelin et al. 1988).

Spence (1986) identified the spatial placement of eggs and the presence of jelly coats on eggs as two potential mechanisms for reducing the predation rate on water strider eggs by parasitoids. Since females of some water strider species lay their eggs in groups (e.g., *Limnoporus dissortis, L. notabilis, Gerris pingreensis* [Spence 1986]; *L. rufoscutellatus, G. lacustris, G. paludum* [Nummelin et al. 1988]), whereas other species tend to spread out single eggs (e.g., *G. buenoi* [Spence 1986]; *G. odontogaster* [Nummelin et al. 1988]), we conducted an experiment to test whether the number of eggs in each egg cluster may also be an important component in determining the predation risk for water strider eggs.

Water strider females of three species (*G. odontogaster, G. lacustris,* and *L. rufoscutellatus*) were allowed to oviposit on artificial plastic leaves in the laboratory. Leaves with egg clusters of different sizes (one egg cluster per leaf) were introduced during mid-June 1988 into a natural habitat (the Gimonäs pond) known to harbor *T. gerriphagus* (for details, see Arnqvist 1989). Cluster sizes ranged from 1 to 65, and sample sizes for different cluster sizes ranged from 11 to 29. After 6 d of exposure to parasitoids in the field, the leaves were brought back into the laboratory. Eggs older than approximately 6 d are not successfully parasitized by *T. gerriphagus* (Spence 1986). The leaves were kept individually in plastic containers until all water strider larvae had hatched. The number of parasitized eggs in each egg cluster was then recorded (for methods, see Nummelin et al. 1988).

The predation risk for individual eggs varied significantly with group size (Kruskal-Wallis ANOVA adjusted for ties, $H = 19.43$, df = 8, $P < .02$). The predation risk was highest in intermediate cluster sizes, whereas solitary eggs and eggs in larger clusters suffered lower risks (see fig. 2). Spence (1986) reported a daily fecundity limit for *T. gerriphagus* females of 8–11 eggs, which corresponds well with the satiation level of the wasp in this experiment ($x \approx 10$; fig. 2). Highest predation risk for intermediate group sizes was also found for infestations by a chironomid parasitoid of aggregations of caddisfly pupae (Otto and Svensson 1981). In conclusion, predator-satiating mechanisms in host-parasitoid systems can favor either very small or very large prey group sizes in host insects, as predicted by theory.

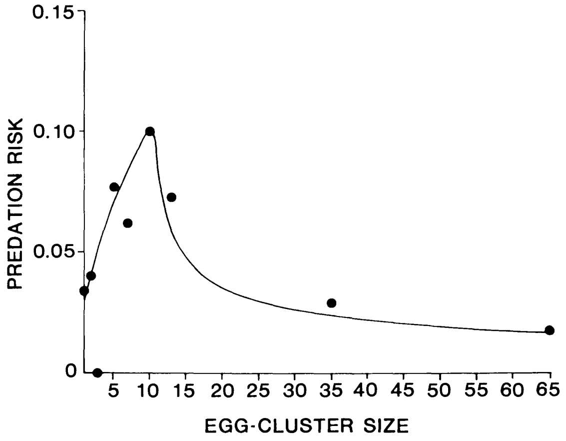

FIG. 2.—Individual risk of infestation by a parasitoid wasp for water strider eggs in egg clusters of different sizes. Eggs in intermediate group sizes suffered highest infestation risks. The curve fitted to data represents the predation risks predicted by the model ($\alpha_n = 0.05$, $k = 0.55$, $\phi = 0.01$, $x = 10$).

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