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### Countershading in caterpillars

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*Document Version*

Publisher's PDF, also known as Version of record

*Publication date:*

1955

[Link to publication in University of Groningen/UMCG research database](#)

*Citation for published version (APA):*

de Ruiter, L. (1955). *Countershading in caterpillars*. s.n.

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A predator will have a chance to detect a given prey only when within a certain distance of this prey. This distance will depend on the properties of both predator and prey. Therefore, for a given predator a prey may be said to be surrounded by a definite danger zone. Of course, in our experiments the danger zones of all preys should lie well within the space accessible to the predators. If part of the danger zone of a prey would be inaccessible, the risk run by this prey would be reduced accordingly. The radius of the danger zone can be estimated by observations on the behaviour of the predator. For a special case, a method to determine this radius was worked out by LAING (1938). In most of the published investigations, too little attention has been paid to this point. As the larger danger zones of the more conspicuous preys are more likely to lie partly outside the experimental space, this may at times have resulted in too low relative values for the risk run by these preys.

Further, in order to get consistent results, we must guard against the effects of adaptation (PRECHTL, 1953), and learning processes. For instance, all preys should consist of the same material and differ only in appearance, so as to exclude conditioned preferences. The test preys should not be made the staple diet of the predator, because monotony of diet might make them gradually less attractive.

It will be clear that many obstacles must be surmounted in work of this sort. In addition, because of the wide accidental fluctuations in frequencies of captures, conclusions can only be based on a large material. The choice of predators and preys is therefore very important. For instance, it would take a prohibitive amount of time to collect data on countershading suitable for the present purpose with the predators and preys used by us.

Nevertheless, in favourable circumstances, results of considerable value, from both the ethological and the ecological points of view, might be obtained in cage experiments on the value of camouflage. The prospects for further work in this field seem promising.

## VI. SUMMARY

In this paper, evidence is put forward to show that countershading (for an explanation of the term, see p. 2) in caterpillars is an adaptation protecting the larvae from visual predators.

Our first argument in support of this conclusion is the fact that in their natural environment countershaded larvae always turn the dark side of their body towards the light, although there is wide variation among species in the anatomical substrates of the patterns and in the orienting mechanisms (chapter II).

equation (2) derived here will prove applicable without modification in a single concrete case. It is based on too many simplifying assumptions. However, each of these assumptions is open to verification. Perhaps, the result of this verification may sometimes be such that the formula can be modified accordingly. Even when, in a given case, the real situation proves too complicated for such mathematical treatment, the effort spent on the falsification of the assumptions will not be wasted, as each of them is a hypothesis of some ecological interest. In any case, from the ecological point of view the best way to express the results of experiments on the survival value of camouflage is to give data on the frequencies of captures and on the population density of the preys in the cage.

From the ethological point of view, camouflage in a prey is an adaptation to the releasing mechanism of feeding behaviour in its enemies: the prey cannot control the predators' hunger, but it can try to avoid eliciting their feeding activities. Consequently, data on the frequency of the feeding responses evoked by preys with varying degrees of camouflage may provide useful information on the properties of this releasing mechanism.

These data might shed some light, for instance, on such problems as the quantitative rules governing the co-operation of stimuli ("heterogeneous summation"; TINBERGEN, 1951), the supposed influence (PRECHTL, 1953) of internal factors on the selectivity of the releasing mechanism, and several others.

Feeding responses seem to be a particularly suitable subject for work in this field because they can be evoked with great frequency in all seasons by a very wide range of stimuli. Of course, the frequency of the captures of preys of a given type will depend not only on the releasing value of that type, but also on the number of preys per unit of space, and on the hunger of the predator. We can standardise the population density of our preys, but the effect of the predator's hunger can only be eliminated from our data by comparing the frequency of captures of the prey studied with that of the captures of simultaneously present preys of a standard type.

Therefore, we must always work with at least two types of prey in our experiments. This necessitates a special precaution. If two preys of different type are seen simultaneously, they may well influence each other's releasing values. Hence, the density of the preys should be kept so low that never more than one is seen at a time. It was shown by POPHAM (1943) that the density of the preys does indeed influence their relative releasing values. His data suggest that at sufficiently low densities this influence will no longer exist.