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FORUM

Initial evolution of warning coloration: comments on the novel world method

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Our previous study (Alatalo & Mappes 1996) has motivated the recent paper by Tullberg et al. (2000), which includes a critique of our results and two new experiments. The goal of our work was to study the prevailing selection pressures that would have affected the initial evolution of aposematic signals. We compared an initial situation where predators had limited knowledge of the conspicuous warning signals with the more common secondary situation where some other prey species had already acquired similar types of signals. While these experiments can never tell us what really happened in the past, they give an indication of the selection pressures acting along the possible routes of initial evolution. Two major results emerged from our study.

(1) In the initial stage, when predators faced the signalling unpalatable prey for the first time, the prey would have survived much better if they were aggregated. Thus, in aggregations the prey with warning signals would not have suffered as high costs as solitary prey, when facing evolutionarily naïve predators.

(2) In the secondary stage, when predators had already learnt to avoid the signal in the 'initial stage' experiment, they avoided the mimicking prey in first encounters irrespective of prey distribution. Thus, the benefit of aggregation disappeared when the predators generalized their learned avoidance to another prey that looked different but had the same signal. Thus, it seemed that much of the previous controversy about the role of aggregations in facilitating aposematism might be due to differences in the conditions, in terms of initial versus secondary situations, in each experimental or comparative study. To us this was the main result of our study.

Tullberg et al. (2000) 'reanalysed' our initial stage experiment by excluding all the palatable items. However, if cryptic palatable items are excluded, trials I, II and III in the solitary situation cannot be compared directly with the respective trials in the aggregated situation, since in the solitary presentation unpalatable items were used much more in each trial than in aggregated presentations. During all three trials with aggregated prey, only 11 unpalatable items were used, while among solitary prey the same number of unpalatable items were used in two trials. Therefore, to compare unpalatable items with respect to the signal, it is necessary to have the total number of unpalatable items used as the appropriate reference line. We analysed this (Fig. 1), and there is no difference in the relative mortalities of aposematic unpalatable items in aggregations and in the solitary setup within the first two unpalatable items used.

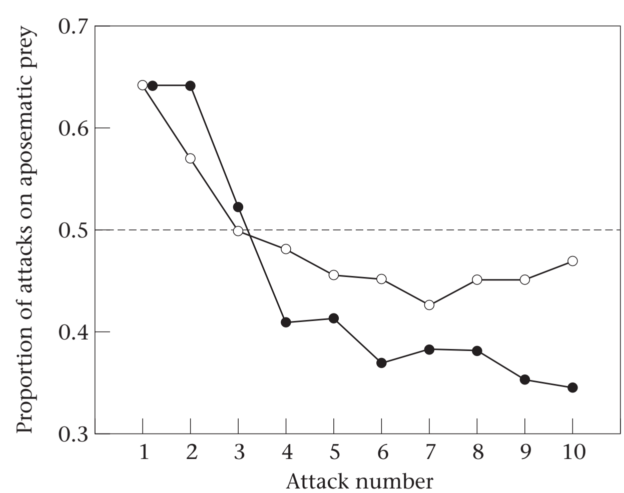

Figure 1. Proportion of attacks on aposematic prey during the first 10 attacks in the experiment by Alatalo & Mappes (1996), when only the unpalatable items are considered. Following Tullberg et al. (2000), the proportion was computed from all attacks up to and including the given attack number. ○: 14 birds presented with solitary prey; ●: 14 birds with aggregated prey.

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However, there is a clear difference soon after (pooling unpalatable items 3–10, *t* test after arcsine square-root transformation of proportions, t_{26}=2.34, P=0.028). Thus, aggregated aposematic items benefited in our experiment compared with solitary items even when palatable items were excluded.

Our experiment included palatable cryptic prey (50% of all items) together with unpalatable cryptic and aposematic items (25% each), since we mimicked the selection pressures on aposematic signals when only a part of the population has acquired unpalatability. Alternatively, the results can be applied for the very likely cases when predators have alternative cryptic palatable prey species as their staple food but, without any signals, they cannot completely distinguish the palatable cryptic species from the unpalatable species. We argue that both of these situations should be considered.

Tullberg et al.'s (2000) design emphasizes the crucial comparison of aposematic versus cryptic unpalatable items. However, the problem is that predators faced these two alternatives alone, without any palatable items present. If two types of unpalatable prey are presented simultaneously, it is to be expected that predators, baffled by the two nasty prey types, will eventually use them equally irrespective of prey dispersal. Another difference in the experiments is that Tullberg et al. (2000) trained birds to eat the cryptic items as palatable. In conclusion, we suggest that the differences in the set-ups may explain why they failed to find any aggregation benefit, which, indeed, was present in our study, and which has also been found in many other studies (e.g. Gagliardo & Guilford 1993; Mappes & Alatalo 1997; Gamberale & Tullberg 1998).

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