

NEW PERSPECTIVES

Density-dependent prophylaxis: evidence from Lepidoptera–baculovirus interactions?

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Insects from a range of taxa use early larval density as a cue to the future deterioration of their current habitat (Dingle, 1996). Their response to this cue is often to redirect resources away from activities favouring immediate reproduction at the natal site (e.g. egg maturation) towards those that favour reproduction in a different location or at a different time (e.g. the development of wings and flight muscles or the deposition of lipid reserves). As well as predicting a decline in the quality or quantity of the larval food resource, early larval density may also predict the risk of exposure to pathogens, which often increases in a predictable manner with population density. Under such circumstances, natural selection will favour those individuals that use early larval density to predict the optimal level of resources to allocate to pathogen resistance later in life. Such an adaptive prophylactic response to larval density may explain the results of several recent studies of moth caterpillars and their baculoviruses.

Kunimi & Yamada (1990) reared caterpillars of the Oriental armyworm moth (*Mythimna separata*) at densities ranging between one and twenty larvae per container. They then orally inoculated newly emerged fourth-instar caterpillars with various concentrations of nuclear polyhedrosis virus (NPV) and recorded the number of deaths. They found that NPV-induced mortality declined gradually from 95% for insects reared solitarily to 37% for those reared at a density of twenty larvae per container. The LC₅₀ value for caterpillars reared at the highest density was about tenfold that for individuals reared solitarily. In a second experiment, Kunimi & Yamada (1990) allowed second-instar caterpillars to feed for 2 days on artificial diet contaminated with a granulosis virus (GV) before rearing them for a further 36 days under either solitary or crowded conditions. They found that larvae reared at high densities (twenty per container) were about fourfold more resistant to GV than those reared singly. Thus, in this species at least,

density-dependent resistance to baculoviruses appears to be manifested not only in the reduced establishment of an infection, but also its development.

A. F. Reeson *et al.* (in prep.) observed a similar phenotypically plastic response to larval density in the African armyworm moth (*Spodoptera exempta*): caterpillars reared at a density of six larvae per container were about eightfold more resistant to NPV than those reared solitarily. Goulson & Cory (1995) observed significantly lower resistance to NPV in isolated caterpillars of the cabbage moth (*Mamestra brassicae*) than in individuals reared at densities ranging between two and ten larvae per container. However, in this experiment there was a decline in resistance when caterpillars were crowded at unnaturally high densities (twenty larvae per 15 ml container). Density-dependent prophylactic resistance may also explain the results of a recent study of the western tent caterpillar (*Malacosoma californicum pluviale*). Rothman & Myers (1996) allowed caterpillars from egg masses ranging in size between 130 and 375 eggs to associate with their siblings for the first two larval instars before orally inoculating them with NPV. They found that there was a trend ($P > 0.06$) for individuals from naturally large egg masses to be more resistant to NPV than those from smaller ones. This result may be a consequence of a relatively higher proportion of resources being directed into resistance by individuals experiencing the highest densities during their early larval instars (though the possibility that it was a consequence of differences in maternal condition cannot be excluded). Finally, adaptive responses to larval density may also explain why D'Amico *et al.* (1996) found that the transmission coefficient of NPV was a declining function of larval density in the gypsy moth (*Lymantria dispar*).

The preceding discussion suggests that density-dependent prophylaxis may be a widespread phenomenon in Lepidoptera. However, we believe that it is likely to be particularly well expressed in species for which larval density (and hence the risk of pathogen attack) is highly variable and frequently high. Typically, this will include those species that exhibit density-dependent phase polyphenism, such as *S. exempta*, *M. separata* and *M. brassicae*. However, by definition, it is also likely to

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include most of those species we refer to as outbreak pests, including *L. dispar* and *M. c. pluviale*. It could be argued that in tent caterpillars and other species that feed in sibling aggregations (including *M. c. pluviale*), local density provides little information about the risk of pathogen attack. However, even if sibling group size is independent of the number of sibling groups, large families will tend to consume more foliage overall than small families. There is, therefore, a greater chance that one or more individuals from these families will become infected with the pathogen, which they may then pass on to their siblings at the tent site. Thus, all else being equal, there is likely to be a selective advantage to individuals that increase resources directed towards pathogen resistance in response to increasing sibling group size. If interactions between family groups are also common, then prophylactic responses to these will also be favoured.

Hochberg (1991) performed a comparative analysis of viral-bioassays that suggested that Lepidopteran species whose larvae feed in aggregations (e.g. *M. c. pluviale*) have evolved higher resistance to pathogens than those that feed solitarily. However, this observation does not preclude the possibility of density-dependent prophylaxis having also evolved, with different *norms of reaction* (Stearns, 1989) being exhibited by species with solitarily and gregariously feeding larvae. An analogous situation is observed in studies of wing-dimorphic insects. Although species or populations that live in temporary habitats tend to have higher frequencies of winged-morphs than those that live in more permanent habitats, both tend to exhibit increased rates of winged-morph production when suitable cues indicate that habitat deterioration is imminent (for some examples, see Wilson, 1995).

The possible mechanisms behind any density-dependent prophylactic response are not yet understood. Both behavioural and physiological mechanisms are possible, but the bioassay results reported here shed light only on physiological responses. Kunimi & Yamada (1990) showed that when non-occluded NPV was injected into sixth-instar larvae that had been reared in isolation or in crowded conditions, there was no significant difference between the mortalities of the two groups of insects. This suggests that whatever is determining the relative susceptibilities of solitary and crowded caterpillars in this species, its biggest impact probably occurs at sites other than the haemocoel. A major challenge for future studies of this phenomenon is to elucidate the precise mechanisms involved.

Finally, although we have restricted our discussion to Lepidoptera, we believe that density-dependent prophylaxis may extend to any invertebrate taxon that regularly experiences wide fluctuations in population density between generations. Moreover, we believe that these responses are likely to be particularly well expressed in those species exhibiting density-dependent phase polyphenism, including many species of aphids, planthoppers and locusts. Only further experimentation can clarify the ubiquity of this phenomenon.

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