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SHORT COMMUNICATION

Is fecundity correlated with resistance to viral disease in the western tent caterpillar?

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Introduction

Reduced fecundity following high larval densities is a common feature of lepidopteran populations and may contribute to population declines (Myers, 1988; Munster-Swendsen, 1991). Species exhibiting density-related reductions in fecundity include the pine looper, *Bupalus piniarius* (Gruys, 1970; Barbour, 1988), the Douglas-fir tussock moth, *Orgyia pseudotsugata* (Mason *et al*., 1977), the larch budmoth, *Zeiraphera diniana* (Baltensweiler *et al*., 1977), the eastern spruce budworm, *Choristoneura fumiferana* (Miller, 1963), the gypsy moth, *Lymantria dispar* (Campbell, 1978) and the spruce needleminer, *Epinotia tedella* (Munster-Swendsen, 1991). Although most often attributed to changes in host food plant quantity or quality, viral disease may play a role in these observed fecundity changes (Myers, 1988, 1993; Rothman & Myers, 1996).

In the western tent caterpillar, *Malacosoma californicum pluviale* (Dyar), fecundity tends to decrease following peak larval densities, and remains low for several generations during the population decline (Myers, 1990; Myers & Rothman, 1995; Myers & Kukan, 1995). On average, mean fecundity of female moths is reduced by 35% during this period compared with mean fecundity of moths prior to peak population densities (range = 18–65%, SE = 9%, $n = 5$ populations) (see Rothman, 1995). Myers (1990) proposed the 'disease defence hypothesis' to explain this pattern, as nuclear polyhedrosis virus (NPV) is a common feature of high-density tent caterpillar populations. If reduced fecundity were a correlated characteristic of resistance to disease, fecundity might be expected to decline in populations after a viral epizootic at high host densities (Myers & Kukan, 1995). Recovery of fecundity to pre-peak levels would be delayed during the population decline if disease resistance and fecundity were heritable traits.

A prediction of this hypothesis is that caterpillars from small egg masses will be more resistant to disease than caterpillars from large egg masses (Myers & Kukan, 1995). This prediction was tested by treating individuals from a wide range of egg mass sizes with a NPV, and relating the percentage mortality per family (egg mass) to maternal fecundity (number of eggs per egg mass).

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Methods

Malacosoma c. pluviale females lay eggs (100–300) in a single mass on twigs of the host plant [often red alder, *Alnus rubra* (Bong.)] after mating in mid-summer (July). First instars hatch from the eggs in April or May and pupate in June or July. For a more detailed description of tent caterpillar biology see Myers (1993).

Tent caterpillar egg masses were collected from a high density population on Saturna Island, British Columbia, Canada in the early spring of 1995 and stored at 4 °C. On 3 April 1995, egg masses were rinsed in a bleach solution (3% sodium hypochlorite) to remove any possible contamination with NPV and tied to host alder trees at a site on the University of British Columbia campus.

After hatch, the number of eggs per egg mass was counted. Larvae from these masses were brought indoors within 24 h of moulting to third instar (beginning 13 May) and reared individually in 60-mL plastic cups in a naturally lit room at room temperature (17–28 °C) (photoperiod and humidity were not controlled). Larvae were starved for 24 h and then fed an alder leaf disc treated with NPV ($n = 25$ per family) or distilled water ($n = 15$ per family). Controls were reared to account for any families that came into contact with NPV in the field before third instar, or NPV on egg masses not removed by bleaching. For treated larvae, 5 μL of distilled water containing NPV at a concentration of 1.6×10^5 PIBs/mL were applied to the leaf disc. This dose was expected to kill approximately 30% of treated larvae at third instar. Larvae (control and treated) not eating the entire leaf disc within 48 h were discarded. Treatments were applied at third instar because individuals prior to this stage will usually only feed in groups.

NPV for this experiment was originally extracted from diseased *M. c. pluviale* larvae using a discontinuous sucrose

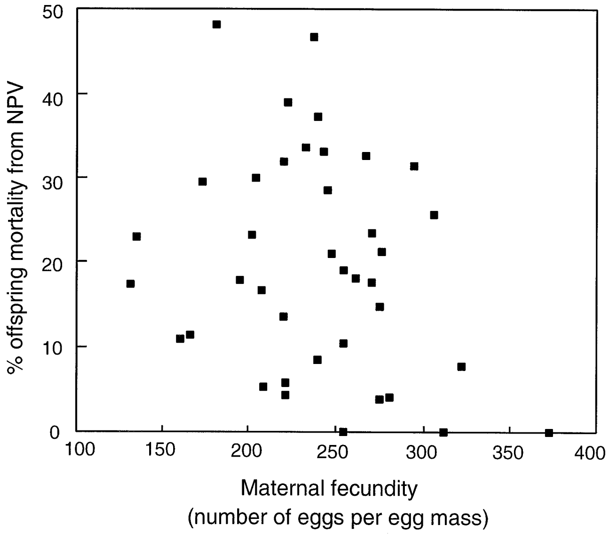

Fig. 1. Relationship between maternal fecundity and offspring mortality from NPV.

gradient (see Kalmakoff & Wigley, 1980). For this study, NPV was obtained from laboratory reared *M. c. pluviale* caterpillars that died following inoculation and infection with this virus. For details of NPV extraction see Rothman & Myers (1994).

Caterpillars were fed every other day with alder leaves collected from an area with no prior history of tent caterpillar infestation. These leaves were rinsed in a bleach solution (0.6% sodium hypochlorite) to remove any possible NPV contamination. Individuals dying before fifth instar were smeared on slides and examined under the light microscope for the presence of polyhedral inclusion bodies. Percentage mortality of individuals showing presence of NPV was calculated for each family. The experiment was terminated when individuals reached fifth instar because mortality after this time was likely to be from other causes. Mortality from NPV was detected in the controls in four of the thirty-nine families (an average of 1.5 individuals per contaminated family). For these families, percentage mortality from NPV in treated larval groups was adjusted using Abbott's formula (see Kalmakoff & Wigley, 1980).

The relationship between percentage mortality from NPV and fecundity was examined using regression. Because both positive or negative relationships between fecundity and viral disease might be expected, two-tailed significance testing was employed. To satisfy the assumptions of significance testing, percentage mortality data were first arcsin and then log (+ 1) transformed (Zar, 1984). To improve the arcsin transformation, zero values were converted to $1/4n$ (where n = the number of NPV treated larvae) (see Zar, 1984).

Results and discussion

Results do not support the disease defence hypothesis. A non-significant relationship (at the 5% level) was observed between fecundity and percentage mortality of larvae from NPV (Fig. 1) ($\log(Y + 1) = 1.67 - 0.013X$, $r^2 = 0.09$, $P = 0.063$, $n = 39$). Individuals from large egg masses were not less resistant, and in fact tended to be more resistant, to NPV than individuals from small egg masses.

Other studies that look for correlations between disease resistance and size or reproductive capacity amongst Lepidoptera have yielded variable results, and both positive (Boots & Begon, 1994) and negative correlations (Boots & Begon, 1993) might be expected. Fuxa & Richter (1990) found reduced fecundity in a strain of *Spodoptera frugiperda* selected for resistance to a NPV. Boots & Begon (1993) found greater pupal weights in laboratory populations of *Plodia interpunctella* selected for resistance to a granulosis virus (GV) than in control populations. However, the total number of eggs laid did not differ between resistant and control populations and resistant populations had higher rates of egg failure. In a comparative study of six populations of *P. interpunctella*, Vail & Tebbets (1990) observed that females in the two populations exhibiting significantly greater resistance to GV did not differ from the less resistant populations with respect to pupal weight, fecundity or eggs produced per mg of body weight.

Studies on *M. c. pluviale* do not support the disease defence hypothesis. Rothman & Myers (1994) found that families composed of fecund females were not less resistant to viral disease than those composed of less fecund females. Sample size was small for this study but the trend was consistent with the results of the present study and was toward greater resistance to NPV in families composed of fecund females. Females from caterpillars surviving exposure to virus in the last larval instar were less fecund than control females, suggesting that sublethal infection rather than selection could reduce fecundity (Rothman & Myers, 1994). Myers & Kukan (1995) observed that recovery of fecundity in field populations of *M. c. pluviale* was likely to be too rapid to be explained by selection on genetically determined traits. Further, the size distribution of egg masses in the population decline was more consistent with sublethal disease than with selection caused by mortality from virus. Finally, results of this direct test of the disease defence hypothesis illustrate that offspring of fecund females are not less likely, and if anything may be more likely, to be resistant to viral disease.

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References

Baltensweiler, W., Benz, G., Bovey, P. & Delucchi, V. (1977) Dynamics of larch bud moth populations. *Annual Review of Entomology*, **22**, 79–100.

Barbour, D.A. (1988) The pine looper in Britain and Europe. *Dynamics of Forest Insect Populations* (ed. by A.A. Berryman), pp. 291–308. Plenum, New York.

Boots, M. & Begon, M. (1993) Trade-offs with resistance to a granulosis virus in the Indian meal moth examined by a laboratory evolution experiment. *Functional Ecology*, **7**, 528–534.

Boots, M. & Begon, M. (1994) Resource limitation and the lethal and sublethal effects of a viral pathogen in the Indian meal moth, *Plodia interpunctella*. *Ecological Entomology*, **19**, 319–326.

Campbell, R.W. (1978) Some effects of gypsy moth density on rate of development, pupation time, and fecundity. *Annals of the Entomological Society of America*, **71**, 442–448.

Fuxa, J. & Richter, A.R. (1990) Reversion of resistance by *Spodoptera frugiperda* to nuclear polyhedrosis virus. *Journal of Invertebrate Pathology*, **53**, 52–56.

Gruys, P. (1970) Growth in *Bupalus piniarius* (Lepidoptera, Geometridae) in relation to larval population density. *Verh. Rijksinstitut Natuurbeheer*, **1**, 1–127.

Kalmakoff, J. & Wigley, P.J. (1980) Purification of NPV from *Heliothis armigera* larvae and serological detection of infection. *Microbial Control of Insect Pests* (ed. by J. Kalmakoff and J.F. Longworth), pp. 26–42. New Zealand Department of Industry and Research, Bulletin No.228.

Mason, R.R., Beckwith, R.C. & Paul, H.G. (1977) Fecundity reduction during collapse of a Douglas-fir tussock moth outbreak in northeast Oregon. *Environmental Entomology*, **6**, 623–626.

Miller, C.A. (1963) The analysis of fecundity proportion in the unsprayed area. *The Dynamics of Epidemic Spruce Budworm Populations* (ed. by R.F. Morris), pp. 75–87. Memoirs of the Entomological Society of Canada, No. 31.

Munster-Swendsen, M. (1991) The effect of sublethal neogregarine infections in the spruce needleminer, *Epinotia tedella* (Lepidoptera: Tortricidae). *Ecological Entomology*, **16**, 211–219.

Myers, J.H. (1988) Can a general hypothesis explain population cycles of forest Lepidoptera? *Advances in Ecological Research*, **18**, 179–242.

Myers, J.H. (1990) Population cycles of western tent caterpillars: experimental introductions and synchrony of fluctuations. *Ecology*, **71**, 986–995.

Myers, J.H. (1993) Population outbreaks in forest Lepidoptera. *American Scientist*, **81**, 240–251.

Myers, J.H. & Kukan, B. (1995) Changes in the fecundity of tent caterpillars: a correlated character of disease resistance or sublethal effect of disease? *Oecologia*, **103**, 4755–480.

Myers, J.H. & Rothman, L.D. (1995) Field experiments to study regulation of fluctuating populations. *Population Dynamics: New Approaches and Synthesis* (ed. by N. Cappuccino and P.W. Price), pp. 229–250. Academic Press, San Diego, U.S.A.

Rothman, L.D. (1995) *Effects of a nuclear polyhedrosis virus of the western tent caterpillar on individual performance and population dynamics*. PhD thesis. University of British Columbia.

Rothman, L.D. & Myers, J.H. (1994) Nuclear polyhedrosis virus effects on tent caterpillar reproductive potential (Lasiocampidae). *Environmental Entomology*, **23**, 864–869.

Rothman, L.D. & Myers, J.H. (1996) Debilitating effects of viral diseases on host Lepidoptera. *Journal of Invertebrate Pathology*, **67**, 1–10.

Vail, P.V. & Tebbets, J.S. (1990) Comparative biology and susceptibility of *Plodia interpunctella* (Lepidoptera: Pyralidae) populations to a granulosis virus. *Environmental Entomology*, **19**, 791–794.

Zar, J.H. (1984) *Biostatistical Analysis*. Prentice Hall, Englewood Cliffs, New Jersey.

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