Are sawflies adapted to individual host trees?
A test of the adaptive deme formation hypothesis

Haike Ruhnke,[1]* Martin Schädler,[2] Diethart Matthies,[3]
Stefan Klotz[1] and Roland Brandl[2]

[1]*Department of Community Ecology, Centre for Environmental Research Leipzig-Halle (UFZ),
Theodor-Lieser-Str. 4, D-06120 Halle,* [2]*Department of Animal Ecology and* [3]*Department of Plant
Ecology, University of Marburg, D-35032 Marburg, Germany*

ABSTRACT

Question: Are populations of two sawfly species adapted to individual host trees?

Hypothesis: The adaptive deme formation hypothesis suggests that selection may lead to populations (demes) adapted to host individuals.

Organisms: Larvae of the black sawfly *Tomostethus nigritus* and the privet sawfly *Macrophya punctumalbum* (Hymenoptera: Tenthredinidae) living on ash (*Fraxinus excelsior*).

Methods: We reciprocally transferred larvae of the two sawfly species to leaves of different ash individuals of a floodplain forest in Central Germany. After 24 h, we assessed the relative growth rate of the larvae.

Conclusions: There was no effect of the transfer between host individuals on the relative growth rates of sawfly larvae. Based on our results, together with published literature, we conclude that under certain conditions local adaptations may fine-tune herbivore populations to individual hosts. However, the formation of adaptive demes does not appear to be a general phenomenon in herbivorous insects.

Keywords: adaptive deme formation, feeding trial, herbivory, intraspecific variation, local adaptation, relative growth rate, *Macrophya punctumalbum, Tomostethus nigritus*.

INTRODUCTION

Several studies have demonstrated genetic variation within and among populations of phytophagous insects (Mopper, 1996). Genetic structure may occur even among herbivorous insects occupying different branches of the same tree (Alstad and Corbin, 1990). The mechanisms behind this structure, however, are poorly understood. One possible mechanism is the adaptation of insects to host individuals.

The quality of leaf tissue differs not only among plant species, but varies also among plant individuals within a species (Howard, 1990; Laitinen *et al.*, 2000; Osier *et al.*, 2000b). This variation in the quality of plant tissue may influence feeding behaviour and development of insect

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* Author to whom all correspondence should be addressed. e-mail: ruhnke@genalis.de
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herbivores (Ayres *et al.*, 1987; Howard, 1990; Fortin and Mauffette, 2002; Glynn and Herms, 2004). Based on transfer experiments with a herbivorous insect species, Edmunds and Alstad (1978) formulated the adaptive deme formation hypothesis. According to this hypothesis, selection forms populations (demes) of herbivorous insects adapted to the specific defensive and nutritional characteristics of a host plant individual. Of course, such selection can only work within a framework of preconditions, set by the host as well as the herbivore.

First, the life span of a host individual must sustain several generations of the herbivore. Therefore, adaptive demes are most likely to occur in insects living on trees. Another important precondition is predictability of host quality. At least the ranking of the quality of leaf tissue across individuals should remain constant over time. One important attribute of the insect's biology, which might influence the formation of adaptive demes, is mobility. Gene flow between insect populations on individual trees counteracts local adaptations. The particular defence system of a host individual may result in physiological trade-offs in the insect, which may lead to disadvantages on other host individuals. In turn, this will select for a reduced gene flow between insect populations on different host individuals, which would reinforce the formation of genetically distinct groups [adaptive demes (Edmunds and Alstad, 1978)]. However, low gene flow among populations may also preclude adaptation to host plants by limiting genetic variation upon which selection can act (Slatkin, 1987). Besides mobility, the breeding system and the feeding mode of herbivorous insects may affect the formation of adaptive demes. In a meta-analysis, however, van Zandt and Mopper (1998) found no evidence that mobility constrained local adaptation. In addition, they found no convincing effect of the feeding mode (exophagous vs. endophagous) or the breeding system on the formation of adaptive demes.

Tests of the adaptive deme formation hypothesis failed to produce consistent results (van Zandt and Mopper, 1998, Table 2). Nevertheless, based on their meta-analysis van Zandt and Mopper (1998) suggested that endophagous, parthenogenetic, and diplodiploid herbivorous insects are most likely to form adaptive demes. But different authors have arrived at very different conclusions. Whereas Boecklen and Mopper (1998) suggested that adaptive deme formation is an important evolutionary phenomenon, Cobb and Whitham (1998) doubted that adaptations to individual trees occur at all. We tested the adaptive deme formation hypothesis for populations of the black sawfly *Tomostethus nigritus* and the privet sawfly *Macrophya punctumalbum* in a floodplain forest in Central Germany. These two species differ in biological characteristics, which should affect the formation of locally adapted demes. The parthenogenetic *M. punctumalbum* should show stronger adaptation to host individuals than the haplodiploid and sometimes outbreaking species *T. nigritus* (cf. Price *et al.*, 1990; van Zandt and Mopper, 1998).

METHODS

The study was carried out in the 'Leipzig floodplain forest' (city of Leipzig, Saxony, Germany). In spring 2001, a construction crane was installed in the forest. Equipped with a gondola, the crane allowed us to work in the canopy so that we could investigate mature tree individuals within an area of 1.6 ha. The vegetation around the crane is a typical floodplain forest of the upper alluvial zone on nutrient-rich loamy soils [Querco-Ulmetum (Morawetz and Horchler, 2004)]. The forest is rich in plant species. The dominant tree species are ash (*Fraxinus excelsior*), oak (*Quercus robur*), sycamore (*Acer pseudoplatanus*), lime (*Tilia cordata*), and hornbeam (*Carpinus betulus*).

The experiments were performed with larvae of the black sawfly *Tomostethus nigritus* (F.) (Hymenoptera: Tenthredinidae, Blennocampinae) and the privet sawfly *Macrophya punctumalbum* (L.) (Hymenoptera: Tenthredinidae, Tenthredininae) on ash (*Fraxinus excelsior*). These sawfly species are univoltine. Females of the two species oviposit under the epidermis of leaves. The larvae are, however, solitary and free-feeding leaf chewers.

Tomostethus nigritus appears to be monophagous on ash (Lorenz and Kraus, 1957; Mrkva, 1965) and has a haplodiploid breeding system. One female can lay 80–120 eggs, which are placed singly into young leaves (Mrkva, 1965). Larvae develop fairly fast. Gradations of the species are known to defoliate ash populations (Mrkva, 1965). However, no outbreaks have been observed in the 'Leipzig floodplain forest' during the last 40 years (A. Sickert and L. Fischer, personal communication). *Macrophya punctumalbum* feeds on several species of the family Oleaceae, in particular on *Fraxinus excelsior* and *Ligustrum vulgare* (Hoebeke and Johnson, 1985; Chevin, 1995). Males of *M. punctumalbum* are extremely rare. The species is therefore considered to be parthenogenetic (Hoebeke and Johnson, 1985; Chevin, 1995). The females usually oviposit groups of about 2–8 eggs into fully expanded leaves. Compared with *T. nigritus*, *M. punctumalbum* larvae have a slow growth rate. Outbreaks are not known for *M. punctumalbum*.

We performed reciprocal transfer experiments with larvae of the two species of sawflies collected from individual host trees. The ash trees sampled during our study were mature (height 29–34 m) and showed phenotypic variation in bud burst (personal observations). Furthermore, in a preliminary study we found significant differences in the palatability of leaf tissue among individual ash trees of our study area using a generalist herbivorous insect (unpublished data). We collected eggs and early instars of the sawflies from the canopy of several ash individuals within the crane area. Larvae were reared in the laboratory on leaves collected from the same branch on which we had sampled the particular insect individual. Every 2 days we provided freshly collected leaves. When the larvae had reached the third larval stage, we reciprocally transferred them between leaves of certain pairs of ash trees. Half of the larvae remained as controls on the original trees. We used two pairs of trees and 339 larvae for the experiments with *T. nigritus* and four pairs of trees and 1550 larvae for the experiments with *M. punctumalbum*. The distance between the ash individuals of a pair was about 30 m and 90 m respectively for the trees used in the experiments with *T. nigritus*. For *M. punctumalbum*, the distance between ash individuals of a pair was 10 m (one pair) and about 130 m (the other three pairs).

The experiments with *T. nigritus* were carried out between 24 May and 9 June 2004 in a climate chamber (18°C and 16 h light), and with *M. punctumalbum* between 15 June and 5 July 2004 (22°C and 16 h light). Before the experiments, larvae were weighed and placed individually in petri dishes with moist filter paper. Non-transferred larvae were provided *ad libitum* with leaves from the branch on which they had been sampled. Transferred larvae received leaves of the corresponding novel tree individual of the tree pair. After 24 h, the larvae were re-weighed.

Before all analyses, initial and final mass of larvae were log-transformed. The effects of tree pair, natal tree, novel tree, and home versus away on larval mass at the end of the experiment were analysed by analysis of covariance [ANCOVA; Proc GLM (Version 8.02); SAS Institute]. Initial larval mass had a significant effect on the growth of larvae for both sawfly species and was therefore used as the covariate. By using Type I sums of squares, the confounding effects of initial larval mass were removed. Thus, after removing the effects of initial mass, we obtained for our analyses an estimate of the relative growth rate of the larvae (Raubenheimer and Simpson, 1992; Horton and Redak, 1993). In our statistical model, the factor 'tree

pair' tested the effect of the specific tree pairs, 'natal tree' the genetic differentiation of the sawfly populations between trees, and 'novel tree' the quality of the ash individuals. The factor 'home versus away' tested whether larvae were adapted to the tree on which they had been sampled.

We decided to measure the growth of larvae in the laboratory, not in the field, because microclimatic differences between host individuals could have compromised the test of whether differences in host quality had an effect on the growth rate of insect larvae. A drawback of such laboratory experiments, however, is that we had to remove leaves from the tree, which could have affected tissue quality. However, Osier *et al.* (2000a) showed that the growth of caterpillars reared in bags on trees was highly correlated with the growth of larvae reared in the laboratory with leaves of the same tree. Furthermore, over 2 days, leaves removed from the tree do not show significant changes in nutritional quality (Kleiner, 1991).

RESULTS

Larvae of *M. punctumalbum* sampled from different tree individuals had different relative growth rates (ANCOVA; Table 1, Fig. 1a). This indicates genetic differences among populations living on different individuals of host trees. However, we found no adaptation to the leaves of the tree on which larvae were sampled. The transfer of larvae from one ash individual to another had no significant negative effect on their relative growth rate (ANCOVA; Table 1, Fig. 1b). Instead, sawfly larvae on the four tree pairs tended to respond to the transfer differently (ANCOVA, interaction of tree pair and home versus away; Table 1). Growth of the larvae of *M. punctumalbum* on leaves of novel trees was not different from that of larvae on leaves of the trees they originated from.

For *T. nigritus*, the relative growth rate of sawflies from different tree individuals was not significantly different (ANCOVA; Table 1). However, the identity of the novel host tree affected the relative growth rate of the larvae (ANCOVA; Table 1, Fig. 1c). This indicates that the quality of leaves differed between ash individuals. Again, the transfer of larvae had no negative effect on relative growth rate (ANCOVA, home versus away; Table 1, Fig. 1d).

Table 1. Results of two analyses of covariance of the effects of tree pair, natal tree, novel tree, and transfer (home vs. away) on the relative growth rate (effect after incorporating the covariate) of the larvae of *Macrophya punctumalbum* and *Tomostethus nigritus*

Source of variation	*M. punctumalbum*			*T. nigritus*		
	d.f.	MS	*F*	d.f.	MS	*F*
Initial larval mass	1	119.099	5730.95 ***	1	16.995	1396.02 ***
Tree pair	3	0.099	4.78 **	1	0.001	0.09
Natal tree	4	0.528	25.41 ***	2	0.016	1.36
Novel tree	4	0.031	1.51	2	0.100	8.21 ***
Home vs. away	1	<0.001	0.04	1	<0.001	0.01
Tree pair × home vs. away	3	0.054	2.58 (*)	1	0.024	2.02
Residual	1533	0.021		330	0.012	

Note: The table presents the results of Type I analyses. (*) $P < 0.10$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.
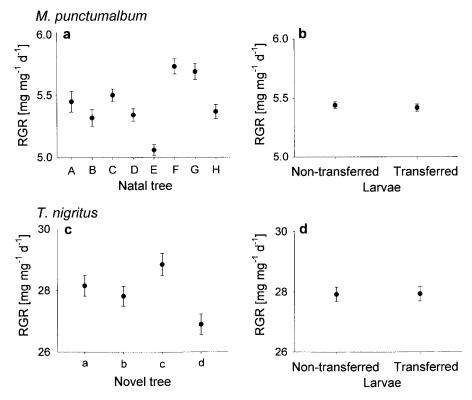
Fig. 1. Effect of natal tree, novel tree, and host transfer on the relative growth rate of larvae of *Macrophya punctumalbum* (a, b) and *Tomostethus nigritus* (c, d). We give relative growth rates (RGR) measured across 24 h from an ANCOVA (back-transformed least squares means; error bars provide back-transformed values of the mean ± standard error, hence the error bars are not symmetric).

DISCUSSION

We tested the adaptive deme formation hypothesis (Edmunds and Alstad, 1978) with two species of sawflies. In reciprocal transfer experiments with larvae of *T. nigritus* and *M. punctumalbum* on ash trees, we did not observe any effect of the transfer: for both species, relative growth rate did not differ significantly between transferred and non-transferred larvae. Therefore, we found no evidence for local adaptation of the insects to individual host plants. Our results are in line with those of several previous studies that tested the adaptive deme formation hypothesis using transfer experiments (Table 2).

As noted in the Introduction, the ability to form locally adapted demes may depend on the mobility, the feeding mode, and the breeding system of the herbivorous species (Edmunds and Alstad, 1978). The adaptive deme formation hypothesis was originally formulated for herbivores with low dispersal. Therefore, half of the published studies used sedentary scale insects. However, in their meta-analysis van Zandt and Mopper (1998) found no evidence that adaptive demes are more common in sedentary than in mobile herbivorous insects. Nevertheless, some authors consider spatial segregation as an important precondition for the formation of local demes (Hanks and Denno, 1994). The species we used in our experiments

Table 2. Results of published experiments that tested the formation of adaptive demes

Herbivorous insect	Host plant	Local adaptation	Source
Apterothrips seticornis	*Erigeron glaucus*	Yes	Karban (1989)
Stilbosis quadricustatella	*Quercus geminata*	Yes	Mopper *et al.* (1995)
Asphodylia borrichiae	*Borrichia frutescens*	Yes	Stiling and Rossi (1998)
Cryptococcus fagisuga	*Fagus sylvatica*	Yes/No	Wainhouse and Howell (1983)
Pseudaulacaspis pentagona	*Morus alba*	Yes/No	Hanks and Denno (1994)
Nuculaspis californica	*Pinus lambertiana*	No	Rice (1983)
Matsucoccus acalyptus	*Pinus monophylla*	No	Unruh and Luck (1987)
Matsucoccus acalyptus	*Pinus edulis*	No	Cobb and Whitham (1993, 1998)
Cinara cupressi	*Cupressus lusitanica*	No	Memmott *et al.* (1995)
Daktulosphaira vitifoliae	*Vitis arizonica*	No	Kimberling and Price (1996)
Adelges japonicus	*Picea jezoensis*	No	Ozaki and Itahana (1997)
Blepharida rhois	*Rhus glabra*	No	Strauss (1997)
Chionaspis pinifoliae	*Pinus resinosa*	No	Glynn and Herms (2004)

have the potential to fly. The prepupae of the two species hibernate in the soil. After hatching, adults need to fly into the canopy for oviposition. Thus, active dispersal or passive transport may cause a mixing of populations among nearby host individuals. Nevertheless, when the selection pressure is sufficiently high, adaptive demes may form despite some gene flow (see Feder *et al.*, 1994). For *M. punctumalbum*, our results are consistent with genetic differentiation between populations on different trees, but there was no evidence for specific adaptations of these demes. Hence, genetic differentiation is not necessarily an indicator for the adaptive deme formation hypothesis. The processes that generate this genetic differentiation are not necessarily related to differences in the selection regime among tree individuals. Microclimatic differences or microclimatic barriers together with variations in host plant phenology may isolate insect populations living on different host individuals, and genetic differences between host trees are due to genetic drift.

Edmunds and Alstad (1978) developed their hypothesis for a specialist and, indeed, a limited host range has been shown to be an important precondition for adaptive demes. Parasites and herbivores with a broad host range are less likely to show local adaptation than parasites with a narrow host range (Lajeunesse and Forbes, 2002). The feeding mode of herbivorous insects is also thought to affect the probability of the formation of adaptive demes. Endophagous insects are not able to escape from unfavourable plant tissues. Therefore, they should have a higher probability to form adaptive demes than exophagous insects. However, van Zandt and Mopper (1998) found no significant effect of feeding mode on the probability of adaptation. Nevertheless, the effect size for the endophagous insects was larger than that for exophagous species and van Zandt and Mopper (1998) interpreted this as tentative support for the influence of feeding mode on the formation of adapted demes. In our experiments, we used larvae both of a monophagous and an oligophagous sawfly species. Females of the two species of sawflies oviposit under the epidermis of leaves. The larvae are, however, free-living leaf chewers. Thus, the species may display an intermediate mode of feeding behaviour. Although the sawflies used in our experiments should have had a considerable propensity to form adaptive demes, we found no evidence for the formation of locally adapted populations.

Compared with parthenogenetic species, a sexual breeding system may increase genetic variation and should thereby allow for an effective evolution of adaptations by selection (Weismann, 1904; Strauss and Karban, 1994; Goddard *et al.*, 2005; but see Lushai *et al.*, 2003). In addition, haplodiploid insects are usually assumed to adapt more easily than diplodiploid insects (Alstad, 1998; Haccou and Schneider, 2004; Schoustra *et al.*, 2005). In contrast to these expectations, van Zandt and Mopper (1998) found no significant effect of the breeding system in their meta-analysis. Moreover, they suggest from the magnitude of the effect sizes that parthenogenetic and diplodiploid insects may even be more likely to form locally adapted demes than haplodiploid herbivores. During our experiments we used the haplodiploid *T. nigritus* and the probably parthenogenetic *M. punctumalbum* (Hoebeke and Johnson, 1985; Chevin, 1995). *Tomostethus nigritus* has not only a haplodiploid breeding system but also tends to have eruptive population dynamics with fast development of the larvae (Mrkva, 1965), whereas larvae of *M. punctumalbum* have a slower growth rate. Together, these differences between the two species should mean that it is less likely for adaptive demes to be formed by *T. nigritus* than *M. punctumalbum* (cf. Price *et al.*, 1990; van Zandt and Mopper, 1998). However, we found no evidence for differences in the formation of adaptive demes in the two species.

An important prerequisite for the formation of demes adapted to host individuals is that resource heterogeneity within individual hosts has to be much lower than among host individuals. In addition, the quality of leaf tissue of host individuals needs to be predictable for the herbivores over generations (see Edmunds and Alstad, 1978). Mopper *et al.* (2000) reported for a leafminer that it could take ten generations to form demes. At least across such temporal scales host individuals should have predictable properties to which the insects can adapt. But there may be variation in leaf tissue quality within plant individuals (Hollinger, 1989; Dudt and Shure, 1994) and these variations may affect the feeding behaviour and development of associated herbivorous insects (Howard, 1990; Fortin and Mauffette, 2002). Furthermore, large variations in leaf quality occur within and between years (Laitinen *et al.*, 2000; Osier *et al.*, 2000b; Covelo and Gallardo, 2001), although the ranking among host individuals is sometimes consistent across years (Riipi *et al.*, 2004). The leaf quality of a single plant can rapidly change with age such that a tenfold change in resistance can occur over a 2-year period (Kearsley and Whitham, 1989). Overall, the published evidence suggests that fluctuations in host quality within and between years may prevent local adaptations. Instead, the variability of leaf quality may select for genotypes that can cope with a variety of leaf qualities (Whitham, 1983; Cobb and Whitham, 1998).

In our opinion, the variability of leaf quality within and between years, together with the conflicting results from transfer experiments, indicate that generalizations about the formation of adaptive demes are premature. Following Hanks and Denno (1994), we conclude that local adaptation may fine-tune herbivore populations to host individuals under very specific conditions. However, it appears that adaptive demes do not play a general role in the evolution of herbivorous insects. Mopper (2005) suggested recently that demes will evolve when variation in host phenology is coupled with endophagy of the herbivore. Further studies are needed to evaluate this hypothesis.

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