chiefly a consequence of "psychological" factors (that is, lack of control) rather than a consequence of the shock itself. Second, it demonstrates a behavioral manipulation that both impairs learning and modulates the induction of LTP, thereby providing further evidence that LTP may be involved in behavioral learning processes.

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Seasonal Microhabitat Selection by an Endoparasitoid Through Adaptive Modification of Host Behavior

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Differences in the distribution of parasitized and unparasitized hosts has been used to infer modification of host behavior by insect parasitoids. Data are presented showing that not only do parasitized hosts behave differently from unparasitized ones, but that the behavior of parasitized hosts varies in function of the physiological state of the parasitoid. Aphids containing nondiapausing parasitoids leave the aphid colony and mummify on the upper surface of the leaves, whereas those containing diapausing parasitoids leave the host plant and mummify in concealed sites. Modification of host behavior by diapausing parasitoids results in the selection of a suitable microhabitat that reduces the incidence of hyperparasitism and should decrease the action of adverse climatic conditions during the lengthy dormant period.

THERE IS CONSIDERABLE EVIDENCE that true parasites can modify the behavior of their intermediate host, thereby increasing the probability of transmission to their final host (*1*). In the case of insects, parasitoid modification of host behavior has been inferred on the basis of differences in the distribution of parasitized and nonparasitized hosts within a habitat (*2*). However, these distributions may be unrelated to modified host behavior and instead reflect patterns of parasitoid foraging behavior (*3*). The mechanisms and adaptive significance of induced behavioral modification have received little attention, even though the ability to modify host behavior has been considered as an important aspect involved in the process of successful parasitism by parasitoids (*4*). The parasitic wasp *Aphidius nigripes* (Hymenoptera: Aphidiidae), an endoparasitoid of the potato aphid *Macrosiphum euphorbiae* (Homoptera: Aphididae), completes pupal development and facultative prepupal diapause within the mummified host. We hypothesized that if there is a selection of a suitable mummification habitat by endoparasitoid larvae under these distinctive developmental conditions, it could only occur through the modification of host behavior.

In the laboratory we noted that the position of nonparasitized aphids on potato plants differ from that of nondiapausing *A. nigripes* mummies. Detailed observation of the distribution of aphids throughout their lives showed that, under greenhouse conditions, unparasitized aphids ($n = 25$) generally remained on the undersurface of leaves [the preferred feeding area (*5*)], whereas parasitized ones ($n = 51$) often moved to the upper surface 24 to 36 hours before death (Fig. 1). This strongly supports the hypothesis that *A. nigripes* has the ability to modify host behavior before the host mummifies. However, the principal objective of our study was to examine the possibility of differential modified host behavior by nondiapausing or diapausing parasitoids, as preliminary observations suggested that the distribution of dark brown, diapausing *A. nigripes* mummies differed from that of light brown, nondiapausing ones. Experiments were therefore designed to test this

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Table 1. Incidence of hyperparasitism of diapausing and nondiapausing *Aphidius nigripes* mummies by the hyperparasitoid *Asaphes vulgaris*.

Location of mummies	Nondiapausing parasitoids		Diapausing parasitoids		G	P
	n	Hyperparasitized (%)	n	Hyperparasitized (%)		
On plant	140	32.9	51	33.3	0.006	>0.950
Off plant	23	47.8	49	12.2	10.432	<0.005
Total	163	35.0	100	23.0	4.298	<0.050

hypothesis and determine the adaptative value of such behavior.

Laboratory colonies of both the aphid and the parasitoid were established from field-collected individuals and maintained at 20°C, 14 hours light:10 hours dark (14L:10D) photoperiod, and 65% relative humidity. Third instar aphids ($n = 320$) were parasitized and then placed on eight potato plants (cv. Norland) in a cage at 20°C under a 12L:12D photoperiod, conditions known to induce approximately 50% diapause in the parasitoid (*6*). Once all aphids had mummified, the distribution of mummies containing diapausing and nondiapausing parasitoids was recorded as being on the upper, median, or basal sections of the plant; on or under the pot; or on the upper or lower parts of the cage. Mummies were then collected and held in gelatine capsules. Ten days after peak parasitoid emergence all remaining mummies were dissected and classified as diapausing or nondiapausing on the basis of whether they contained healthy prepupae, or dead pupae and adults, respectively. This experiment was repeated four times (*7*). A total of 1004 mummies were obtained, and the distribution of diapausing and nondiapausing *A. nigripes* (Fig. 2) differed significantly ($G = 296.97$, 6 df, $P < 0.001$; 566 nondiapausing, 438 in diapause). Aphids containing diapausing parasitoids tended to leave the host plant and mummify in more concealed sites, whereas those containing nondiapausing parasitoids tended to remain on the plant. Furthermore, nearly a quarter of diapausing individuals that remained on the plant were found inside the curled-up basal leaves. No mummies were found in or on the soil. Only the proportion of mummies recovered on the pot did not differ significantly between the two groups ($G = 0.6$, 1 df, $P > 0.5$; 29 nondiapausing, 23 in diapause).

The majority of insects entering diapause select sheltered overwintering sites (*8*), which may result in lower mortality due to either mechanical and physiological damage (*9*), or the actions of natural enemies (*10*). Important behavioral changes are often associated with the selection of a suitable overwintering site, including increased wandering and digging, as well as changes in hygro-, thermo-, photo-, geo-, and thigmoresponses (*11*). Field observations indicated that the seasonal biologies of *M. euphorbiae* and *A. nigripes* are closely synchronized, with the majority of diapausing parasitoids passing the winter outside the potato agroecosystem, on shrubs and trees that serve as the primary host for the potato aphid (*12*). Thus, the tendency of aphids containing diapausing parasitoid larvae to find protected sites prior to mummification would result in *A. nigripes* mummies being concentrated in crevices on the branch or trunk, a preferred microhabitat for some insects in diapause (*13*), rather than remaining exposed on the bark surface. Individuals mummifying in exposed sites would undoubtedly suffer higher mortality, due to the negative effects of freezing rain and hail, than those in protected habitats, so one could envisage strong selection against such behavior. A suitably protected microhabitat may also result in diapausing insects being subjected to less drastic fluctuations in temperature and humidity (*8*).

Another possible advantage of diapausing in well-protected sites is the reduction in mortality due to the action of natural enemies. Fritz (*14*) predicted that the degree to which host behavior is modified by the parasitoid, for its own advantage, will be proportional to the intensity of pressure exerted by its natural enemies. Confined within the mummified host, diapausing parasitoid larvae are exposed to the actions of predators and other secondary parasitoids for an extended period of time. Foraging activities of some predators and hyperparasitoids will overlap the dormancy period of *A. nigripes*, at least during the fall period (*15*). This, like adverse climatic conditions, should result in a strong selection for diapausing *A. nigripes* individuals that alter host behavior in a way that favors suitable overwintering microhabitat selection. We tested the prediction that well-hidden mummies would be less susceptible to attack in the laboratory with *Asaphes vulgaris,* a common pteromalid hyperparasitoid of *A. nigripes* in the potato ecosystem. Parasitized aphids ($n = 270$) were reared on potato plants at 20°C, 12L:12D, and 48 hours prior to mummification they were distributed randomly on 15 potato plants in a large cage (2.36 × 0.76 × 0.72 m) at 20°C under 18L:6D. Once mummification had been completed, 30 3-day-old, mated hyperparasitoid females were introduced into the cage for 24 hours, after which the exact position of all mummies was noted. These were then collected and held in gelatine capsules until parasitoids or hyperparasitoids emerged. Mummies from which nothing emerged were dissected and the contents determined.

Overall hyperparasitism was significantly lower in mummies containing diapausing parasitoids (Table 1). As the incidence of hyperparasitism was similar for all mummies found on the potato plant, the difference resulted from a greater proportion of aphids

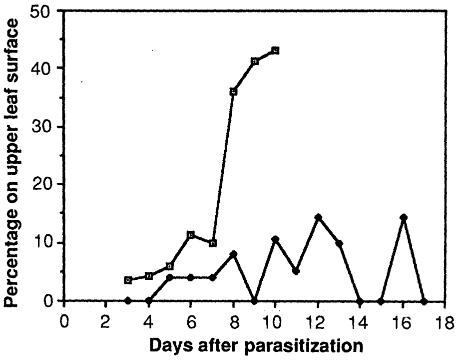

Fig. 1. The effect of parasitism by nondiapausing *Aphidius nigripes* larvae on the distribution of *Macrosiphum euphorbiae* adults. ⊡, Parasitized; ●, nonparasitized.

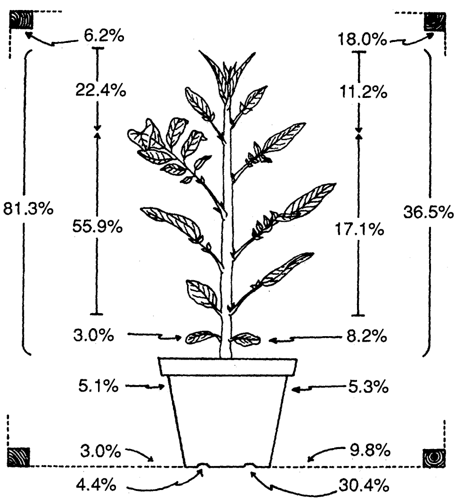

Fig. 2. The distribution of *Macrosiphum euphorbiae* mummies containing diapausing ($n = 438$) and nondiapausing ($n = 566$) individuals of the primary parasitoid *Aphidius nigripes* at 20°C, 12L:12D. The proportion of diapausing (18.0%) and nondiapausing (6.2%) mummies found on the cage walls are indicated at the top right and left corners, respectively.

containing diapausing parasitoids leaving the host plant. Furthermore, on leaving the plant, aphids containing diapausing parasitoids selected much more protected mummification sites (under the pot, in crevices in the cage), and suffered a lower incidence of hyperparasitism (12.2%), than those on exposed sites containing nondiapausing individuals (47.8%). The results of this experiment support the hypothesis that the observed change in the behavior of aphids containing diapausing parasitoids would favor parasitoid survival.

Behavioral changes observed in newly parasitized aphids, which were detrimental to the parasitoid (*16*), have been taken as evidence supporting the host suicide hypothesis (*17*). Our work has shown that later in parasitoid larval development behavior of the host aphid is also modified, but in this case clearly to the advantage of the parasitoid. Furthermore, we report a differential modification of host behavior that has evolved within the same host-parasitoid association, responding to the specific ecological and physiological requirements of diapausing and nondiapausing parasitoids. The observed relation between *A. nigripes* and *M. euphorbiae* provides evidence that the ability to modify host behavior may represent a crucial aspect of successful parasitism for insect parasitoids, in addition to the physiological interactions described in many host-parasitoid systems (*4, 18*).

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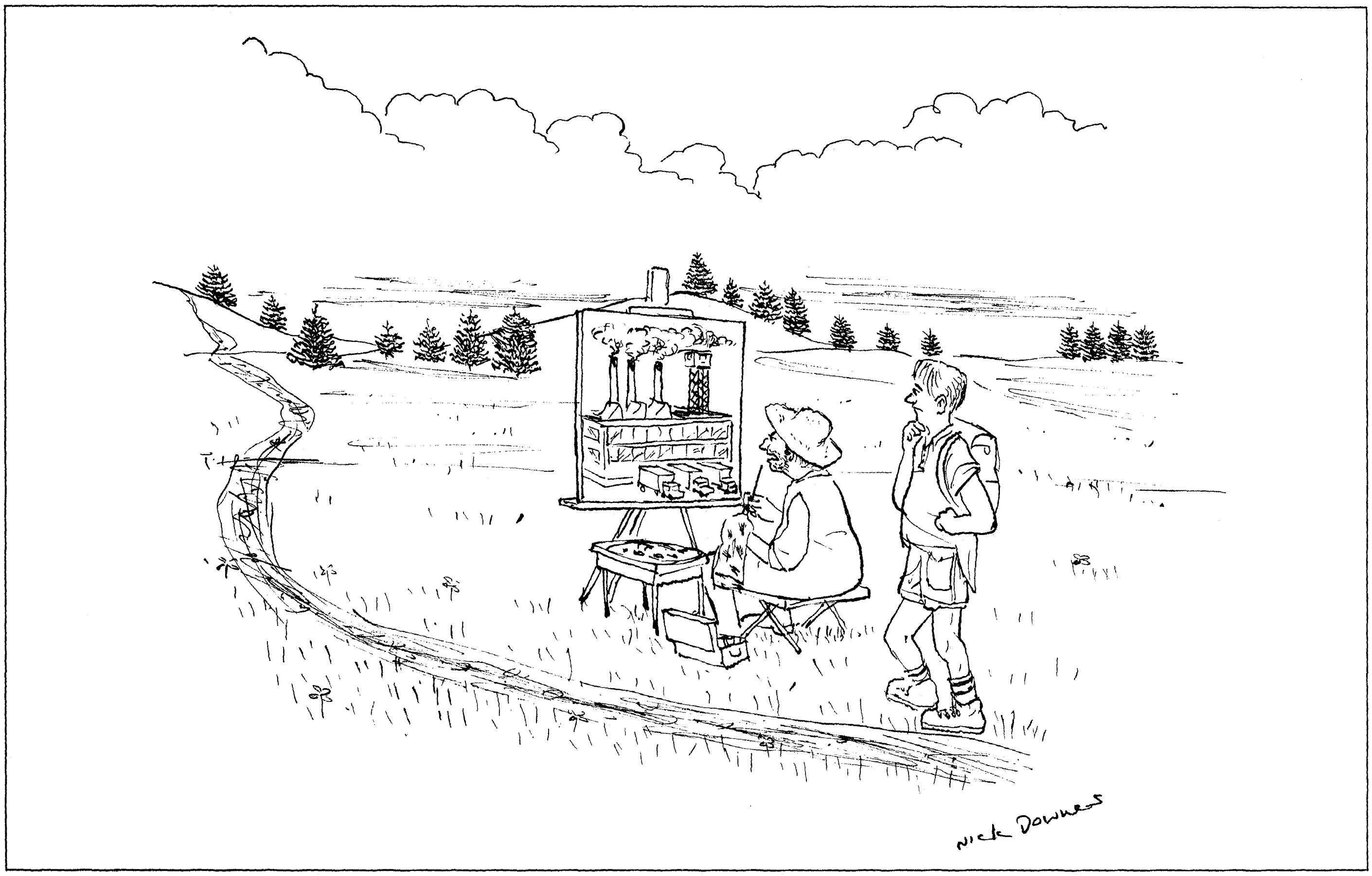

"I paint what I smell."