PREDATORS, PARASITOIDS, AND PATHOGENS AS MORTALITY AGENTS IN PHYTOPHAGOUS INSECT POPULATIONS

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Abstract. We compiled life tables for 78 holometabolous herbivorous insect species to quantify levels of apparent enemy-induced mortality of immature insects. Enemies were classified by type (predator, parasitoid, or pathogen), and mortalities caused by each type in each herbivore immature stage were tested with Analysis of Deviance for differences associated with four ecological characteristics of preadult herbivores: feeding biology, invasion status, and the cultivation status and latitudinal zone of the habitat. Total enemy-induced mortality is higher in the late developmental stages, and overall, parasitoids kill more herbivores than do either predators or pathogens. Among the ecological variables, both feeding biology and latitude showed significant enemy effects in at least one late developmental stage, whereas neither cultivation status nor invasion status was associated with enemy-induced mortality in any stage. Bonferroni adjustment of probabilities for multiple comparisons resulted in few significant interactions between enemy type and the ecological variables. However, raw probabilities and comparisons across herbivore immature stages suggest several patterns that deserve attention in future studies: (1) endophytic herbivores suffer lower mortality by predators and pathogens than exophytics, and endophytic leaf miners suffer the greatest parasitoid-induced mortality, while endophytic gallers/borers/root feeders suffer the least; (2) overall enemy-induced mortality is similar in natural and cultivated habitats; (3) exotic insects do not suffer lower enemy-induced mortality rates than natives; and (4) predation and disease may be greater in tropical/subtropical habitats, whereas parasitism is greater in the temperate zone. These results identify several general patterns in insect demographics that should be useful for hypothesis testing.

Key words: herbivores; life tables; mortality; natural enemies; parasitoids; pathogens; phytophagous insects; population dynamics; predators.

INTRODUCTION

Insect herbivores are killed by a taxonomically and ecologically diverse collection of natural enemies that includes vertebrate and invertebrate predators, insect parasitoids, nematodes, fungi, protists, bacteria, and viruses. Further, natural enemies represent an important and ubiquitous source of herbivore mortality. However, not all herbivores suffer enemy attacks to the same degree. Mortality due to enemies can be severe enough to cause extinctions of local populations (Washburn and Cornell 1981, Eber and Brandl 1994, Lei and Hanski 1997), but in other cases it can be trivial (Embree 1965, Price and Craig 1984). Given this variable impact, the ecological and biological factors that influence enemies need to be identified in order to predict when and where they are likely to be significant and to test conventional wisdom about the factors influencing insect population dynamics. Much of the information required to identify these factors is provided by life table studies.

In a previous study, Cornell and Hawkins (1995)

compiled 530 life tables for 124 holometabolous herbivore species to analyze causes of mortality. Mortality was classified into six sources and the frequency with which each source appeared in life table data grouped by ecological category and victim developmental stage was determined. Two patterns emerged: (1) sources of mortality shift as herbivores grow (physiological factors, weather and plant factors more frequently kill early stages, whereas enemies more frequently kill later stages), and (2) the herbivore's feeding biology exerts a strong influence on mortality sources (natural enemies more frequently kill insects feeding externally on the plant [exophytics], whereas plant factors are relatively more frequent killers of insects feeding within plant tissues [endophytics]). In contrast, the successional stage and cultivation status of the habitat, the invasion status of the herbivore, and the latitudinal zone of the study site showed only feeble relationships with mortality. This does not necessarily mean that these latter factors are not important, only that consistent relationships with mortality sources could not be found using the frequency-based methodology employed. Nevertheless, the differences found between exophytic and endophytic feeders suggest that this ba-

sic trait exerts a potent influence on herbivore demographics relative to the other factors tested.

Cornell and Hawkins (1995) also found that enemy attack was the most frequent cause of death for immature herbivores and was more frequent than all other factors combined for late immature stages (late-instar larvae and pupae). However, the different types of enemies were not distinguished in this analysis. Instead, they were pooled into a single category, which was compared against a variety of other mortality sources (competition, plant factors, weather, developmental failure, and miscellaneous/unknown). This method obscured any differences in the way parasitoids, predators, and pathogens might respond to the ecological settings of herbivore populations. For example, compared to their native counterparts, recently introduced herbivores might be attacked by generalized predators to a greater extent than by more specialized parasitoids, because generalists are able to switch to novel prey/hosts more quickly and easily than specialists (e.g., Cornell and Hawkins 1993). Or the concealment of endophytic herbivores may protect them from attack by predators, but their immobility may make them highly vulnerable to parasitoids. It is therefore possible that ecological and biological differences among herbivores could result in differences in attack rates by different types of enemies, even if overall rates are similar.

In this paper we examine in more detail enemy-induced mortality of herbivorous insects, as revealed by life table studies. Specifically, we distinguish mortality caused by the three basic types of enemies: predators, parasitoids, and pathogens. Further, we quantify the levels of apparent mortality caused by each type of enemy to test for differences associated with four ecological characteristics of herbivores: feeding biology (exophytic folivores vs. two classes of endophytics, leaf miners, and gallers/borers/root feeders), cultivation (natural/semi-natural vs. cultivated habitats), invasion status (native vs. exotic species) and latitudinal zone (tropical/subtropical vs. temperate habitats). These represent four of the five variables previously examined by Cornell and Hawkins (1995). The successional stage of the habitat is excluded here.

Our goal is to determine if the ecological characteristics that might influence the overall prevalence of enemies affect all enemies equally, or if trade-offs exist such that reductions in the rate of attack by one type of enemy are offset by increased attack by other types. Although the characteristics that influence the susceptibility of herbivores to parasitoids have received considerable attention (Askew 1961, Askew and Shaw 1986, Gross 1991, Cornell and Hawkins 1993, Mills 1993, Hawkins 1994), interactions among parasitoids and predators or pathogens have been more sporadically studied (Tostowaryk 1971, Hochberg and Lawton 1990, Tscharntke 1992, 1997, Weis et al. 1992, Memmott et al. 1993, Hoelmer et al. 1994, Weis and Ka-

pelinski 1994), and it is uncertain how mortality rates due to different types of enemies covary. It is clear that herbivores are frequently faced with opposing selection pressures exerted by their food plants and their natural enemies (Lawton and McNeill 1979, Gross and Price 1988, Clancy and Price 1989, Abrahamson and Weis 1997). We can similarly ask if herbivores may escape one type of enemy only to succumb to another. If so, the already complex range of dynamics that have been identified for the interacting effects of food plants and enemies may be enriched by additional interactions among the enemies themselves.

METHODS

The data were extracted from life tables for 78 holometabolous phytophagous insects compiled from the literature. In five cases, tables were available for insect species in both native and exotic locations, providing 83 cases in total. The herbivores are distributed across four orders with the following percentages; 64% Lepidoptera, 23% Coleoptera, 6% Diptera, and 6% Hymenoptera. The Lepidoptera and Diptera are overrepresented and the Coleoptera are underrepresented relative to their occurrence in the world herbivore fauna (43% Lepidoptera, 39% Coleoptera, 10% Diptera, 6% Hymenoptera; Weis and Berenbaum 1989). However, a more comprehensive analysis of life table data has shown that taxonomic category has no significant effect on cause of mortality (Cornell and Hawkins, *unpublished manuscript*). The ecological distribution of the herbivores is as follows: 32% forest, 23% agricultural field, 15% grassy field, 16% plantation, 10% orchard, and 4% park.

Although we perused government reports, experiment station bulletins, and other gray literature as well as journals and books, 98% of the data for this study were extracted from the peer reviewed literature. Life tables for each species were taken from single studies, but 73% of the studies included more than one table for that species. Multiple tables were generated at different sites, over different years for univoltine species, or for different generations within the same year for some multivoltine species. Sample sizes of initial cohorts varied widely from <100 to >10^6, but usually comprised at least several hundred individuals. Protocols demanding large samples to reduce sampling error were laid down in Morris's (1955) original article on technique and have been scrupulously adhered to in a large proportion of life table studies. We believe we have uncovered a large proportion of the published life tables of holometabolous herbivores, but life tables that appear in the literature are not a random sample of herbivorous insects. The bias towards abundant and economically important species has meant that rare species are underrepresented and need more attention to provide a balanced view. Caution dictates that we be aware of this bias when generalizing beyond the literature.

For the present study, a life table was considered usable only if there was a clear attempt to implement a formal sampling scheme to prevent bias in mortality estimates, and when it provided counts of the numbers of herbivores killed by parasitoids (including parasitic Hymenoptera, Diptera, and nematodes), predators (including birds, mammals, and arthropods), and pathogens (including protists, bacteria, viruses, and fungi) for at least one immature stage (egg, early larval, mid-larval, late larval, or pupal), as well as the number of immatures entering that stage. When multiple life tables for a herbivore species were generated in a single study, counts were summed over all tables.

In compiling the data set we included data for each type of enemy only when we considered it unlikely that any mortality for that type may have been missed. For example, we excluded predation for any stage in which authors listed any "disappearance", and we excluded both parasitism and disease for any stage in which authors listed "developmental failure". On the other hand, when all sources of mortality had been fully documented, or it was otherwise clear that a stage did not suffer mortality by one or more of the three enemy types, mortality due to the absent types was scored as a "0". If all of the life tables had identified and quantified all mortality sources across all herbivore life stages, the data set could have comprised a maximum of 1245 values (83 cases × 5 stages × 3 enemy types). Since many life tables did not fully document mortality sources we were able to extract only 663 values (comprising 315 zeros and 348 nonzero values), 53% of the maximum. Values for the independent variables were assigned based on information given in the life table studies or from other articles describing the biology or bionomics of the herbivores and are provided in Cornell and Hawkins (1995).

The proportions of herbivores killed were analyzed using GLIM 3.77 (NAG, Oxford, UK, 1985), which uses maximum likelihood estimators for fitting general linear models. All analyses assumed a binomial error distribution (appropriate for proportions; using the number of herbivores killed as the response variable, and the stage-specific cohort size as the binomial denominator) and a logit link function (which bounds the linear predictor of the proportion killed between 0 and 1) (see Crawley 1993). Because of the large numbers of 0s, the data were overdispersed relative to the binomial distribution. Consequently, the scale parameter (which adjusts the error mean square for overdispersion) was estimated using the residual variance (Crawley 1993).

The ecological characteristics were tested with two-way linear logistic Analyses of Deviance (ANODEV; a GLIM analogue of Analysis of Variance that permits specification of non-normal error distributions and a range of link functions). Each ANODEV included one ecological variable and enemy type, with each of the five immature stages analyzed separately, for a total of 20 analyses. An ideal analysis would generate models of increasing complexity by sequentially adding factors to determine their abilities to account for variability in mortality. However, limited data precluded any models containing more than two factors. Further, each immature stage had to be analyzed separately due to a lack of independence in the data among stages (i.e., the same herbivore populations were sampled repeatedly as they developed), but repeated measure models could not be tested because of large amounts of missing data. The ANODEVs produced a total of 60 probabilities, including main effects and interactions. To adjust for multiple comparisons, we set our significance level at 0.0008 (0.05/60); using less conservative adjustments, such as sequential Bonferroni or Dunn-Sidak, did not affect interpretation of the results. Due to the non-normal distributions of the data, the results of the ANODEVs were interpreted by plotting median mortality rates and approximate 95% confidence intervals, based on the sign test (Daniel 1978).

A potential problem inherent to all life table studies is that mortality rates among the enemy types both within and between life stages may not be independent. Life tables measure only the factor that is thought to have actually killed the herbivore, but individual insects might have been attacked by more than one enemy type. For example, a sick or parasitized, but still active host can be eaten by a predator, which would be credited with the kill even though the host would have eventually died from parasitism or disease. Consequently, attack rates by some natural enemies may be partially masked by the effects of other types of enemies. Furthermore, individuals removed from the population at an early stage by predators or idiobiont parasitoids (that kill or permanently paralyze the host during oviposition) are unavailable to natural enemies at later stages, whereas diseased immatures and those parasitized by koinobiont parasitoids (that permit continued host development following oviposition) may remain in the population for some time and be eaten by predators or killed by some non-enemy factor. Consequently, stage-specific mortality rates may not reflect attack rates at that stage, particularly for pathogens and koinobionts that attack early stages but kill later stages. All of these potential interactions among different types of natural enemies can, and probably do, influence observed mortality rates. In addition, such interactions are possible among enemies and other sources of mortality, and all mortality factors are ultimately compensatory, since all insects must eventually die of something. Correcting for hidden interactions among mortality sources requires information generally unobtainable in the field. Thus, this problem is not unique to our study but is likely to influence to some extent virtually any study of mortality in natural populations.

RESULTS

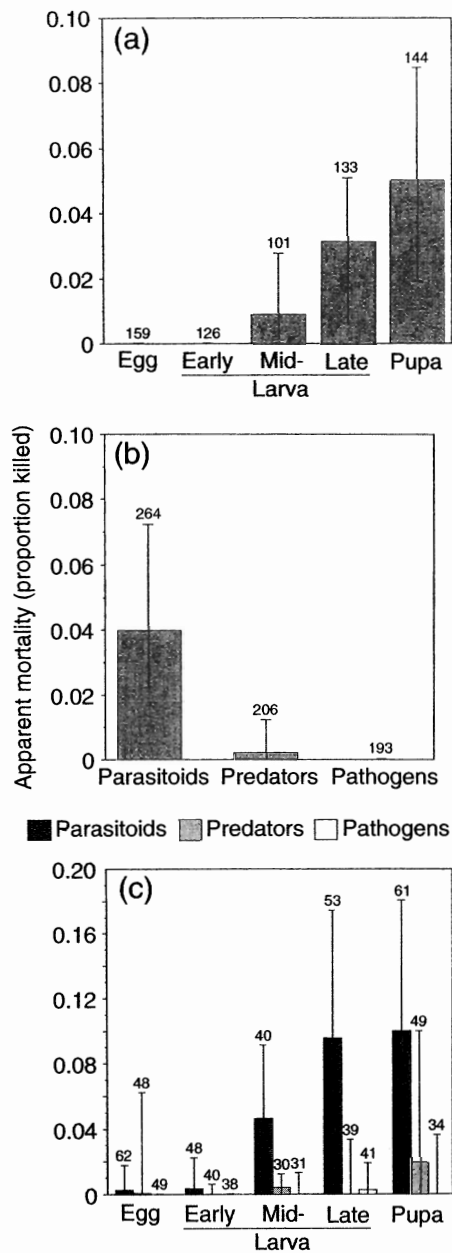The general structure of the data indicates that enemy-induced mortality increases with herbivore age

FIG. 1. Relationships between median (and 95% CI) mortality levels and (a) herbivore immature stage, (b) type of natural enemy, and (c) stage × enemy interaction. Numbers above confidence interval bars are the number of cases at each level.

(Fig. 1a), and that, across all stages, parasitoids kill more herbivores than either predators or pathogens (Fig. 1b). The dominance of parasitoids as mortality agents is most pronounced in the mid/late larval and pupal stages of their hosts (Fig. 1c).

Analyses of the four ecological characteristics, followed by Bonferroni adjustment of the critical α, identified enemy type as the only consistently significant main effect (Table 1), in all cases reflecting the dom-

inance of parasitoids and the low mortality rates caused by pathogens (Fig. 1c). Although parasitoids also dominate in hosts' mid-larval stages across all species (Fig. 1c), the enemy main effect is not statistically significant when herbivores are classified into subgroups (Table 1).

Among the ecological variables, feeding biology emerged as having unambiguously significant relationships with enemy-induced mortality in both the late larval and pupal stages, when mortality is greatest (Table 1a, Fig. 1a). The significant enemy × biology interaction in the egg stage reflects that the eggs of exophytics suffer higher parasitism rates than do the eggs of endophytics (Fig. 2a), at least partially due to the latter's inaccessibility when inserted into plant tissues. Although there were no significant interactions between biology and enemy type in post-egg immature stages following adjustments of probabilities, the raw probabilities and comparisons across herbivore life stages (which cannot be tested statistically) suggest differential effects of feeding biology on predators, parasitoids, and pathogens. Relative to exophytics, endophytics suffer lower mortality rates due to both predators and pathogens in all post-egg immature stages (Fig. 2b–e). Further, gallers/borers may benefit somewhat from protection from parasitoids, at least in the egg and pupal stages (Fig. 2a, e). In stark contrast, leaf miners are more vulnerable to parasitoids in both the mid-larval (Fig. 2c) and late-larval stages (Fig. 2d).

Cultivation practices differentially disrupt egg predators (Table 1b, Fig. 3a), and insects in agricultural situations may suffer marginally higher overall mortality in late developmental stages (Table 1b, Fig. 3d, e), but natural enemies generally appear little affected in cultivated habitats relative to natural ones.

Our sample of exotic insects does not suffer significantly lower enemy-induced mortality rates than native insects in any life stage (Table 1c). Indeed predation rates, and perhaps disease rates, of exotics are higher over most of their immature lives (Fig. 4).

The pupae of tropical/subtropical insects suffer significantly higher mortality rates than do temperate insects (Table 1d, Fig. 4e). Further, predators represent the dominant natural enemy of post-egg stages in the tropics and subtropics, whereas parasitoids are dominant in the temperate zone (Fig. 5). Higher death rates of eggs in the tropics are equally due to predators and parasitoids (Fig. 5a). Finally, pathogens show a slight increase in activity into the tropics.

DISCUSSION

The clearest result to emerge from our analysis is that basic developmental and feeding characteristics of herbivores are more strongly associated with enemy-induced mortality rates than are habitat/ecological variables. As found in our frequency-based study (Cornell and Hawkins 1995), the risk of mortality due to natural enemies shifts as herbivores develop: enemies kill few-

TABLE 1. Summaries of two-way ANODEVs, each including an ecological characteristic and the type of natural enemy. Because data are not independent across stages, each herbivore immature stage was analyzed separately.

Source	Egg F	Egg P	Early larva F	Early larva P	Mid-larva F	Mid-larva P	Late larva F	Late larva P	Pupa F	Pupa P
a) Feeding biology (35 exophytic vs. 25 gallers/borers/root feeders vs. 11 leaf miners)										
Biology	4.9	0.009	1.4	0.264	2.5	0.090	11.1	<0.0008	27.2	<0.0008
Enemy	893	<0.0008	9.6	<0.0008	5.0	0.009	14.2	<0.0008	687	<0.0008
Biology × Enemy	17.6	<0.0008	4.5	0.002	0.5	0.758	3.3	0.014	3.2	0.017
b) Cultivation status (39 natural vs. 44 cultivated)										
Cultivation	1.5	0.222	0	1.000	0.8	0.369	4.4	0.038	3.8	0.053
Enemy	399	<0.0008	7.4	<0.0008	1.4	0.252	9.1	<0.0008	403	<0.0008
Cult. × Enemy	16.8	<0.0008	1.3	0.276	0.1	0.942	1.5	0.227	0.8	0.475
c) Invasion status (63 native vs. 20 exotic)										
Status	4.5	0.070	0	1.000	1.7	0.166	6.7	0.011	0.7	0.413
Enemy	294.5	<0.0008	7.4	<0.0008	2.0	0.144	12.0	<0.0008	406	<0.0008
Status × Enemy	1.2	0.320	2.3	0.104	4.0	0.022	0.9	0.416	0.9	0.389
d) Latitudinal zone (11 tropical/subtropical vs. 72 temperate)										
Latitude	0	1.000	4.4	0.038	<0.1	0.865	1.3	0.262	16.7	<0.0008
Enemy	300	<0.0008	5.6	0.004	1.2	0.307	10.7	<0.0008	458.5	<0.0008
Lat. × Enemy	3.5	0.033	3.4	0.038	1.2	0.269	4.1	0.011	4.4	0.014

Note: F statistics and probabilities are approximate due to use of binomial error distributions in analyses (Crawley 1993). Probabilities in bold are significant after Bonferroni adjustment ($\alpha = 0.0008$).
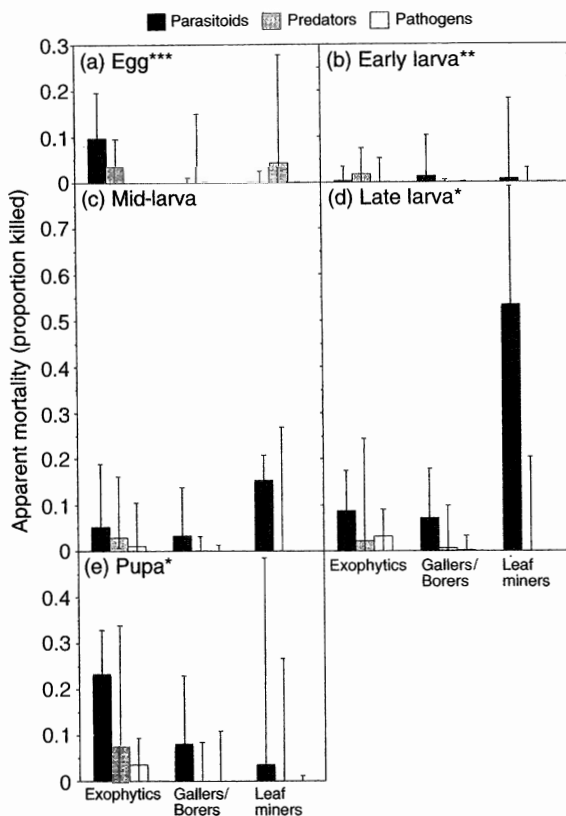

FIG. 2. Relationships between herbivore feeding biology and median (and 95% CI) apparent mortality levels due to three types of natural enemies at each herbivore immature stage. Asterisks represent unadjusted significance levels for enemy type × feeding biology interaction in each stage (from Table 1): * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

er early-instar larvae but increasingly more late-instar larvae and pupae. This pattern may derive from the relative unprofitability of small, early-instar larvae to predators (but see Weseloh [1989] for a counter example involving ants), coupled with difficulties in the location of small prey. It may also be exaggerated,
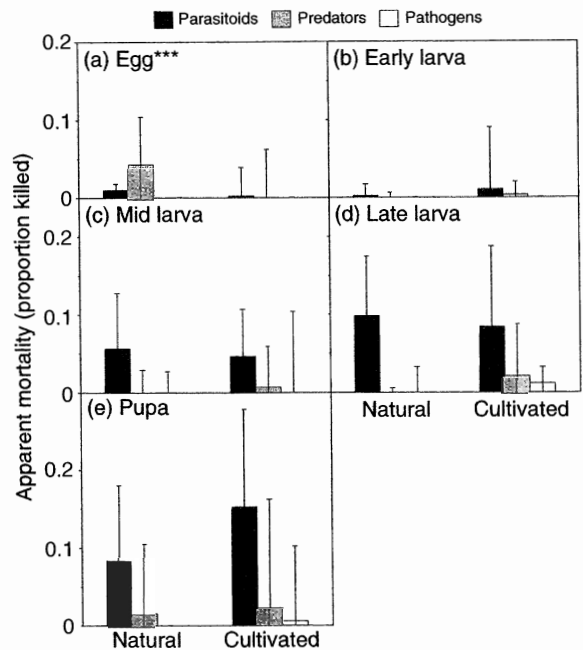

FIG. 3. Relationships between cultivation status of the habitat and enemy-induced apparent mortality. Presentation is as in Fig. 2.
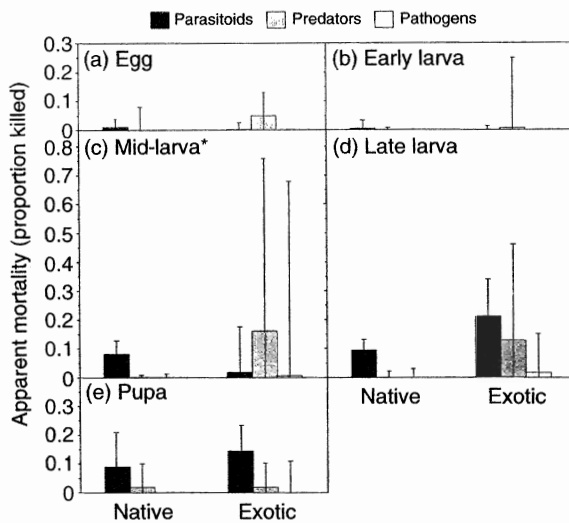
FIG. 4. Relationships between the invasion status of herbivores and enemy-induced apparent mortality. Presentation is as in Fig. 2.

FIG. 5. Relationships between the latitudinal zone of the habitat and enemy-induced apparent mortality. Presentation is as in Fig. 2.

because attack rates on early instars by pathogens and koinobiont parasitoids are undoubtedly underestimated during life table studies (see also Bellows et al. 1992). Many koinobionts oviposit in early-instar larvae but do not kill the host until the late-larval, prepupal, or pupal stage. These parasitoids often represent the most speciose portion of parasitoid complexes (Mills 1994), so the underestimation of parasitoid attack on early host stages can be substantial. Herbivore mortality rates thus increase through host development, but this increase comprises both delayed mortality from koinobionts that attacked hosts earlier in their life cycle as well as immediate mortality by later attacks from both predators and idiobiont parasitoids that require fully grown larvae and pupae for development.

Regardless of biases in perceived koinobiont attack rates on early host stages, parasitoids unequivocally kill more herbivores over the entire herbivore immature life cycle than predators. This partially reflects that parasitoids are found in most herbivorous insect populations, whereas predators are frequently absent from populations of endophytic herbivores. Further, delayed mortality by koinobionts should make parasitoids appear less abundant than they actually are, because predators may remove parasitized hosts from populations (e.g., Tscharntke 1992), whereas parasitoids can never mask a predation event. On the other hand, many predators, unlike the vast majority of parasitoids, also kill adult insects, so predation rates are underestimated to an unknown extent in life tables focused on immature stages.

Pathogens kill fewer herbivores than either parasitoids or predators. As with parasitoids, quantitative estimates of their abundance could be underestimated due to the actions of predators, and life table studies can miss sublethal effects entirely (Sait et al. 1994). Even
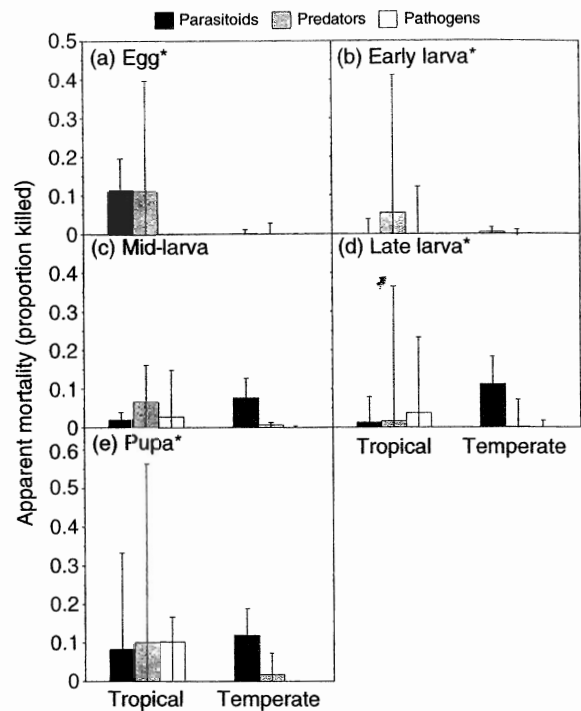
so, many herbivores, particularly endophytics, suffer little or no mortality from pathogens. Thus, although disease can be important in some groups of insects, such as forest Lepidoptera (Dwyer and Elkinton 1993, Myers 1993), on average it does not represent a potent mortality source in phytophagous insect populations.

Another pattern to emerge is that feeding biology influences the susceptibility of herbivores to attack by natural enemies. Comparative analyses of parasitoid communities have identified herbivore feeding biology as the primary correlate of species richness (Askew 1980, Hawkins and Lawton 1987, Hawkins and Gagné 1989, Mills 1993, Hawkins 1994). Subsequent studies have found that feeding biology also influences levels of parasitoid-induced mortality (Hawkins 1994) and the probability that pests can be controlled biologically by means of parasitoids (Gross 1991, Hawkins 1994). Here we find that it influences predator and pathogen activity as well.

Endophytic feeding is believed to protect herbivores from general predation, a pattern confirmed by the life table data. Similarly, pathogens rarely kill endophytic herbivores, probably because endophagy limits pathogen transmission. In contrast, parasitoids are not deterred by endophagy per se. Gallers/borers may suffer reduced parasitoid-induced mortality, but leaf miners actually suffer more. The increased risk of parasitism for leaf miners is particularly evident in the late-larval stage, when the bulk of idiobiont attacks occur and

when many early-attacking koinobionts finally kill their hosts. Thus, all forms of endophagy reduce mortality by pathogens and many predators, but protection from parasitoids requires that endophages develop within relatively tough plant structures, such as galls or stems (see also Askew and Shaw 1986, Hawkins 1994). The flimsy structures in which leaf miners develop increase their vulnerability to parasitoids to a degree that more than compensates for relatively small decreases in predation and disease. When all types of enemies are considered, leaf miners on average suffer higher mortality rates than other types of herbivores.

Although enemy-induced mortality showed strong relationships with herbivore developmental stage and feeding biology, it showed few relationships with the ecological variables, although some interactions may be present. Cultivation has little or no effect on larval or pupal enemy-induced mortality, consistent with other data suggesting that parasitoid impact on host populations is similar in cultivated and natural habitats (Hawkins 1994). It is unclear why the enemy × cultivation interaction was significant for the egg stage (see Table 1, Fig. 3a) since there are few reasons why egg predators should be affected by cultivation, whereas larval and pupal predators are not.

Invasion status has no detectable impact on parasitoid-induced mortality, although predation actually appears higher on exotic species. This pattern is unexpected in light of the historical record of biological control, which indicates that some introduced species escape their enemies and reach high densities. Furthermore, paired comparisons show that parasitoid-induced mortality for exotics is typically lower than when the same species are native (Cornell and Hawkins 1993). Given these contradictions, our results should not be taken as evidence that pest status for exotic insects is unrelated to natural enemies. On the other hand, they do suggest that there are few fundamental differences between our sample of native and exotic insects, and natives can also suffer little enemy-induced mortality or be very abundant.

Mortality levels due to different types of enemies may vary with latitude. Tropical samples are few, but the increase in predation at lower latitudes supports the conventional wisdom that predation pressures are greater in the tropics (Dobzhansky 1950, Elton 1973, Rathcke and Price 1976, Pianka 1978). It is not clear why parasitism does not show similar increases, but it may be related to patterns of diversity. Both invertebrate and vertebrate predators are more diverse in the tropics, but the largest group of parasitoids, the Ichneumonidae, are not (Hawkins 1994, and references therein). The mechanisms determining parasitoid diversity patterns are complex (Hawkins et al. 1992, Gauld and Gaston 1994, Hawkins 1994, Hochberg and Hawkins 1994), though it has been hypothesized that tropical parasitoid diversity is constrained by predation (Rathcke and Price 1976). In response to the predation

hypothesis, Morrison et al. (1979) argued that in contrast to larval and pupal parasitoids, egg parasitoids should be more diverse and abundant in the tropics due to their small size and rapid developmental rates. Consistent with their prediction, we found that egg parasitism is on average an order of magnitude greater in the tropics/subtropics than in the temperate zone (see Fig. 5). Across all stages, however, our results suggest that parasitoids represent a more potent source of mortality in the temperate zone than in the tropics, whereas predation pressures are greater in the tropics.

In sum, our analysis identifies basic developmental and biological traits of herbivores as important influences on natural enemy attack, whereas factors related to the herbivores' ecological setting have more limited effects. This suggests that theories of insect population dynamics that do not incorporate information on the feeding biologies of herbivores will be less predictive than are those that do. We also note in closing that the results of the quantitative analysis mirror closely the patterns for natural enemies Cornell and Hawkins (1995) found using frequency-based mortality. The results of the frequency-based study thus appear robust, and both studies taken together suggest that despite much complexity and unexplained variation, it is possible to identify general patterns in insect demographics using either semiquantitative or quantitative techniques.

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