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PREDICTING NATURAL-ENEMY RESPONSES TO HERBIVORES IN NATURAL AND MANAGED SYSTEMS

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Abstract. One underutilized approach for bridging the gap between basic research on plant–insect–enemy interactions and applied research on biological control is to examine prey defensive characteristics as predictors of successful pest eradication by specific natural enemies. We used such a prey-based approach to compare predictors of predator and parasitoid response in natural systems to predictors of success of biological control. To construct predictive models based on defensive characteristics, we used data from predation (34 prey species) and parasitism (98 host species) studies on lepidopteran larvae in natural systems. To compare efficacies of defenses in natural vs. biocontrol systems and to test the predictions from natural systems, we examined data from 150 biological control programs that used predators and parasitoids as control agents. Predictors were different for each type of natural enemy, yet the patterns of association were similar in natural and biocontrol systems. Specialists and gregarious larvae had high levels of parasitism in natural systems and were successfully controlled by biocontrol programs using parasitoids. Cryptic and smooth larvae had high levels of predation in natural systems and were successfully controlled by predators in biological control programs. Predictions derived from the natural-system models explained 53% of the variation in success of biocontrol efforts.

Key words: antiparasitoid; antipredator; biological control; Coleoptera; Hymenoptera; interactions, tritrophic; Lepidoptera; parasitoids as control agents; pest control; pest eradication, predicting success; predators as control agents; refuge theory.

INTRODUCTION

Divisions between ecological theory and practical application in biological control programs (Kareiva 1996) lead to underutilization of current advances in ecological theory as sources of useful biocontrol guidelines (Murdoch et al. 1985, Waage 1990, Murdoch and Briggs 1996). Part of the failure of ecological theory to inform biocontrol projects stems from the dearth of easily measured host or parasitoid parameters with good predictive power (Hawkins et al. 1993). This lack of reliable predictive models often forces biological control projects to use empirical or ''trial and error'' methods (e.g., van Lenteren 1980).

Several authors have uncovered pest characteristics that are good general correlates of biological control success (Hall and Ehler 1979, Hall et al. 1980, Stiling 1990, Waage 1990, Gross 1991, Hawkins and Gross 1992, Hawkins 1993, Hawkins et al. 1993, Hawkins 1994, Hawkins and Cornell 1994). For example, Stiling (1990) and Gross (1991) used biocontrol data to uncover associations between successful control and host attributes such as diet breadth (biocontrol is more successful against specialists than against generalists; Stiling 1990) and feeding niche (biocontrol is more successful against exposed than against concealed feeders; Stiling 1990, Gross 1991). The idea that host characters are associated with success of biocontrol has been expanded into a model with prey refuges as predictors of biocontrol success: when pests have high maximum levels of parasitism (a small refuge) biocontrol will be successful (Hawkins and Gross 1992, Hawkins et al. 1993, Hawkins 1994, Hawkins and Cornell 1994). Although similar associations have been uncovered in natural systems (Hawkins and Lawton 1987, Price and Pshorn-Walcher 1988, Hawkins et al. 1990, Hawkins 1993, 1994), predictions have not been explicitly tested with independent data sets (i.e., quantitative predictions of biocontrol data using models from natural systems), nor have comparisons been made with enemies other than parasitoids. Despite the fact that enemy–prey interactions are often very different in agricultural systems (Price et al. 1980, Price 1991, 1994), predictions from ecological models (constructed with data independent of biocontrol data sets) could provide useful guidelines for biocontrol.

Here, we use independently derived data from natural systems to construct predictive models useful to the practice of biological control. Instead of using traditional predator-/parasitoid-based characters (e.g.,

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TABLE 1. Larval defensive mechanisms examined in natural systems using multiple species comparisons (Sheehan 1991, Dyer 1995, 1997; L. Dyer and G. Gentry, *unpublished data*).

Defensive characteristics†	Categories‡	Deterrence§
Appearance	**brightly colored,** cryptic, other	ants, **wasps, bugs,** parasitoids
Behavior (after prey is encountered)	thrashing, biting, dropping, **nothing**	**ants**
Chemistry	**unpalatable,** neutral, palatable	**ants, wasps, bugs**
Diet breadth	**specialist,** generalist	**ants, wasps, bugs,** parasitoids
Diet breadth	specialist, **generalist**	ants, wasps, bugs, **parasitoids**
Feeding niche	exposed, **concealed**	**parasitoids**
Foraging behavior	solitary, **gregarious**	**parasitoids**
Morphology	**hairs,** spines, smooth	**ants,** wasps, **bugs,** parasitoids
Ontogeny	early instar, **late instar**	**ants**
Size	**large,** medium, small	ants, **wasps, bugs,** parasitoids

Notes: The boldface categories of defensive characteristics are attributes of larvae that received either high levels of rejection by predators or low levels of parasitism. Defenses were tested against the enemies listed in each row and were effective against the boldface enemies.

† None of these characteristics is assumed to have evolved as a defense mechanism; rather, associations have been noted between these characteristics and enemy response.

‡ See *Methods: Assigning defensive characteristics to prey species* for explanations of how categories were determined.

§ Ants were *Paraponera clavata* (Formicidae), bugs were *Apiomerus pictipes* (Reduviidae), wasps were *Polistes instabilis* (Vespidae), and parasitoids were 73 identified and 6 unidentified ichneumonoid species, 5 unidentified chalcidoid species, and 13 unidentified tachinid species.

Mackauer et al. 1990) as variables to identify potentially useful biological control agents, we make use of the refuge model and use antipredator and antiparasitoid mechanisms as variables in our models. If quantitative models based on specific prey defenses in natural systems could successfully predict the outcome of specific biological control efforts, such an approach would be attractive because of its simplicity.

A prey-based approach assumes that effective antipredator and antiparasitoid mechanisms found in pests are good predictors of the likelihood that particular enemies will successfully eliminate pest species. Insects have many effective defenses against natural enemies, including behavioral, chemical, morphological, and physiological traits (reviewed by Eisner [1970], Edmunds [1974], DeVries [1987], Witz [1990], Evans and Schmidt [1991], Gross [1993], Godfray [1994], Dyer [1995]; Table 1). However, a common fallacy is that defenses are assumed to be equally effective against the entire suite of natural enemies (or the differences in the efficacies of various defensive mechanisms are ignored) (Witz 1990, Dyer 1997). Under this assumption antipredator and antiparasitoid mechanisms might not be useful predictors of the success of a new biological control agent. However, Dyer (1997) found that this assumption about defenses against natural enemies is not valid; many defensive mechanisms were not equally effective against three different predator species (Table 1). L. Dyer and G. Gentry (*unpublished data*) also found that parasitoids may be deterred by a different suite of defenses than those that deter predators (Table 1).

In this paper, we use data from published studies of natural enemy–prey interactions (Sheehan 1991, Dyer 1995, 1997) to predict probability of success of biological control programs. We then use data from the BIOCAT biological control database (Greathead and Greathead 1992; also see the BIOCAT web page)[2] to evaluate the reliability of these predictions. In doing so, we address the following general questions: (1) Can biological control success be predicted from specific pest defenses (i.e., characteristics that are associated with lower levels of enemy attack)? and (2) Do natural enemies respond to larval defenses similarly in natural and managed systems?

METHODS

Study systems

In the natural systems, the prey species studied were all lepidopteran larvae (132 species). Enemies included an ant, *Paraponera clavata* (Formicidae); a bug, *Apiomerus pictipes* (Reduviidae); a wasp, *Polistes instabilis* (Vespidae); and 73 species of ichneumonoids (Sheehan 1991, Dyer 1997). The prey studied from biocontrol programs were mostly lepidopteran larvae (110 species) and some coleopteran larvae (40 species) against which biological control efforts had been directed and recorded on BIOCAT. The biological control agents included 39 species of hymenopteran and dipteran parasitoids, and 28 species of hemipteran, coleopteran, and hymenopteran predators.

Assigning defensive characteristics to prey species

Table 1 summarizes defensive characteristics and how they were categorized for this and previous studies. Defenses were categorized utilizing the same methods found in Dyer (1995, 1997). Two additional antiparasitoid mechanisms (not included in Dyer 1995, 1997) that we examined were foraging behavior and feeding niche. We classified larvae known to feed in

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[2] URL = 〈http://www.bdt.org.br/bdt/irro/biocat〉

groups of three or more as gregarious, otherwise they were classified as solitary. For feeding niche, we classified leaf rollers, folders, tiers, and web makers as ‘‘concealed feeders’’ while larvae known to feed on exposed surfaces of leaves were classified as ‘‘exposed feeders.’’ This classification is different from other feeding-niche classification schemes (Hawkins and Lawton 1987, Gross 1991, Sheehan 1991, Hawkins and Gross 1992, Hawkins 1993, Cornell and Hawkins 1995) that compare external and internal feeders (e.g., borers) or that usually have many more levels of feeding niche that vary from very concealed to completely exposed. Nevertheless, this is a reasonable ecological definition of exposed vs. concealed (and semi-concealed) feeders that is useful for providing balanced statistical models with fewer cells.

To assign defensive categories to species with which we have not worked, we used information in keys and the primary literature cited in BIOCAT (Baker 1972, Covell 1984, Scott 1986, DeVries 1987, Sheehan 1991, Stehr 1993). Because of a paucity of published data, we were unable to include a chemistry variable for the parasitoid models in natural systems or for the biological control models.

Models for natural predators and parasitoids

We used data from Dyer (1997) to predict success of predators as biological control agents against pests with specific defensive characteristics. Briefly, Dyer (1997) compared a bug (*Apiomerus pictipes*), a wasp (*Polistes instabilis*), and an ant (*Paraponera clavata*), as predators of 34 species of lepidopteran larvae. Logit models (Agresti 1984) were used to examine associations between larval antipredator mechanisms and rejections by the three predators (Table 1). The response variable for the predator models was categorical with two levels: rejected vs. not rejected.

To predict success of parasitoids as biological control agents against pests with specific defensive characteristics, we used data from Sheehan (1991; the data were originally collected by Schaffner and Griswold 1934). We only included species for which we could find reliable information on their defensive characteristics; this reduced the 135 species used by Sheehan (1991) to 98 species in our analyses. After we examined frequency histograms for levels of parasitism (Fig. 1), we categorized parasitism levels into high (>30%), medium (from 15% to 30%), and low (<15%). Categorization of parasitism was necessary to allow for comparisons with results from the predator models and the biological control success models. The number of categories (three) was chosen to mirror the three categories used for success of biological control (success, establishment, and failure), and the cutoffs for particular categories were chosen to reflect abrupt breaks in the frequency histogram. In addition, the upper cutoff value of 30% is appropriate since it is close to the parasitism rate at which biocontrol becomes successful (Hawkins et al. 1993, Hawkins and Cornell 1994).

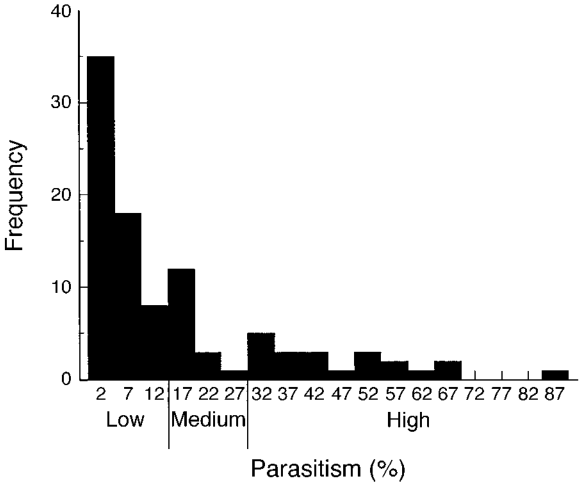

FIG. 1. Frequency histogram for levels of parasitism found in 98 species of lepidopteran larvae (data collected by Schaffner and Griswold [1934]). Numbers on the *x* axis are the midpoint of each interval, and vertical lines below the *x* axis separate the three levels of parasitism (low, medium, and high) used for the parasitoid response variable in logit models. Each level of parasitism is represented by a distribution that is skewed to the left and is surrounded by breaks (visible with a narrower interval) in the data. The cutoff for ‘‘high’’ levels of parasitism is also appropriate since it is close to the parasitism rate at which biocontrol becomes successful (Hawkins et al. 1993).

We used two-dimensional contingency tables to examine associations between parasitism and defensive characteristics. Those variables that were significantly associated with parasitism were included in a logit model, with levels of parasitism (high, medium, and low) as the dependent variable. Variables in this and all other logit models were screened for multicollinearity. All parsimonious logit models in this and the previous paper (Dyer 1997) were tested for goodness of fit using the χ^2 statistic (methods described by Tabachnick and Fidell 1996) with alpha > 0.05 indicating a model that fits the data. This test is analogous to measures of dispersion (described by Haberman 1982) that indicate how much variation in the data is accounted for by the model.

We calculated odds ratios (along with 95% confidence intervals) from the predator and parasitoid models to predict the percentage of prey with given defensive characteristics that should have high levels of parasitism or predation. We made the assumption that ‘‘high levels of parasitism or predation’’ is a good indicator of success of a biological control program (Hawkins et al. 1993, Hawkins and Cornell 1994).

Models for biological control success

We used BIOCAT to search all incidences of biological control on lepidopteran and coleopteran larvae that are pests on various crop systems, plantations, pastures, and forests. We only included species for which we could obtain sufficient information to classify their defensive characteristics. We used data from a total of 116 biological control efforts with parasitoids and 44 biological control efforts with predators. Because of small sample sizes, we collapsed categories of success into a variable with three levels for the parasitoids: success, establishment, and failure. BIOCAT rates the outcome of releases as failed, unknown, temporarily established, established, partial success, substantial success, and complete success. We categorized everything from partial success to complete success as a ‘‘success,’’ while we classified failed and temporarily established as a ‘‘failure.’’ We did not use data with unknown outcomes. For the predator models, there were two categories of success (to mirror the two levels of the response variable in the natural-systems models), so the ‘‘established’’ category was collapsed into the ‘‘failed’’ category. All biological-control practitioners may not accept including partial success in the ‘‘success’’ category, but this approach allowed for balanced models, and the results from these models can be interpreted with this definition of success in mind.

As with the natural systems, we used contingency tables to examine associations between biocontrol-program success and pest defensive characteristics. The categories for predictor variables were the same as in the models for natural systems with the exception of morphology, which only included hairy and smooth larvae because of a lack of data for spiny larvae. For parasitoids, all characteristics that were significantly associated with the success variable ($P < 0.05$ in contingency tables) were included as independent variables in a nonhierarchical logit model with success/establishment/failure as the dependent variable. For the predators, there were too many structural zeroes and other logistical problems, so a logit model was not possible. Interactions were therefore not tested for predators, and all results reported for biocontrol with predators are from two-dimensional contingency tables. To test the predictive power of our models from natural systems, we used linear regression with observed percentages of biocontrol success as a dependent variable and the predicted percentages from the natural-system logit models as an independent variable.

Results

Predators in natural systems

Detailed results from the work with predators are found in Dyer (1997). Briefly, chemistry and diet breadth were the most important predictors of rejection by predators (Table 1), with chemically defended specialist herbivores being better protected than generalist herbivores without chemical defenses. There was also a significant association between type of predator and rejections; ants were least likely to reject prey, bugs were intermediate in their responses, and wasps frequently rejected prey. Other important larval defenses included size, morphology, and coloration. Large prey were less acceptable than smaller prey for the wasps and bugs but not for the ants; hairs deterred predation by the ants and bugs but not by the wasps; and brightly colored larvae were frequently rejected by the wasps but not by the ants and bugs. All of the predators rarely rejected small, cryptic, and smooth larvae.

TABLE 2. Parsimonious logit models used for parasitoids in natural and biocontrol systems (interactions with the dependent variable are analogous to ‘‘main effects’’ in linear models).

Natural systems	Biocontrol systems
Overall fit	
$\chi^2 = 8.7$, df = 11, $P = 0.7$	$\chi^2 = 8.9$, df = 5, $P = 0.1$
Variables and interactions included in the model	
Parasitism levels Foraging behavior Feeding niche Diet breadth × Parasitism levels Foraging behavior × Parasitism levels Feeding niche × Parasitism levels	Foraging behavior Diet breadth × Level of success Foraging behavior × Level of success
Significant predictors of the response variable	
Diet breadth ($\chi^2 = 10.9$, df = 2, $P = 0.004$) Foraging behavior ($\chi^2 = 8.9$, df = 2, $P = 0.01$) Feeding niche ($\chi^2 = 8.7$, df = 2, $P = 0.01$)	Diet breadth ($\chi^2 = 8.6$, df = 1, $P = 0.01$) Foraging behavior ($\chi^2 = 16.7$, df = 1, $P = 0.0002$)

Notes: The ‘‘overall fit’’ is analogous to a measure of strength of association between the model and the observed data; $P > 0.05$ indicates a model that fits the data. Logit models for predators are reported elsewhere (Dyer 1997).

Parasitoids in natural systems

The saturated model for parasitoids in natural systems included levels of parasitism as the response variable and diet breadth, foraging behavior, feeding niche, and all interactions as predictors. No other defenses were significantly associated with levels of parasitism in two-dimensional tables (morphology, $\chi^2 = 4.2$, df = 4, $P = 0.4$; coloration, $\chi^2 = 1.8$, df = 4, $P = 0.8$; and size, $\chi^2 = 5.3$, df = 4, $P = 0.3$). In the parsimonious, unsaturated model, the best predictors of levels of parasitism were diet breadth, foraging behavior, and feeding niche (Table 2). Specialists, gregarious feeders, and concealed feeders were more likely to have high levels of parasitism than generalists, solitary feeders, and exposed feeders. There were no significant interactions between predictors (from comparisons with the saturated model: diet breadth × foraging behavior, $\chi^2 = 1.1$, df = 2, $P = 0.6$; feeding niche × foraging behavior, $\chi^2 = 0.2$, df = 2, $P = 0.9$; feeding niche × diet breadth, $\chi^2 = 1.8$, df = 2, $P = 0.4$; three-way interaction, $\chi^2 = 0.3$, df = 2, $P = 0.8$).

TABLE 3. Predicted levels of parasitism, predicted levels of attack by predators, and observed levels of successful biological control for larvae with the given characteristics.

Defensive characteristics	Categories	Predicted levels of parasitism or predator attack (%)†		Observed levels of successful biocontrol‡	
		Mean	CI	%	*N*
Parasitoids					
Diet breadth	Specialist	34.1	13.1	24.6	17/69
	Generalist	12.9	5.3	8.5	4/47
Foraging behavior	Gregarious	27.8	10.5	26.5	9/34
	Solitary	17.1	6.8	14.6	12/82
Feeding niche	Concealed	35.3	16.5	18.8	12/64
	Exposed	18.5	6.6	17.3	9/52
Predators					
Morphology	Hairy	22.6	11.4	0	0/8
	Smooth	42.8	15.3	38.5	10/26
Coloration	Bright	16.1	5.7	11.1	2/18
	Cryptic	49.3	17.1	50	8/16
Diet breadth	Specialist	27.0	18.1	28.6	6/21
	Generalist	65.2	20.4	30.8	4/13
Chemistry	Palatable	96.3	11.6	no available data	
	Neutral	92.9	26.1	no available data	
	Unpalatable	7.4	3	no available data	

† Predictions (means and 95% confidence intervals) were made using log-odds from the logit models described in the text; the values indicate the percentage of species with given characteristics that should have high levels (>30%) of parasitism or predation. Models were constructed from data collected in natural systems.

‡ Values are percentages of successful biological control programs for pest species with the given characteristics. Sample sizes (*N*) are presented with the denominator indicating the number of biocontrol programs attempted against pests with the given characteristic and the numerator indicating the number of successful programs.

Success of biological control

When predators were used as biological control agents, the variables significantly associated with success or failure were coloration ($\chi^2 = 6.7$, df = 2, $P = 0.04$) and morphology ($\chi^2 = 4.4$, df = 1, $P = 0.04$). Predation failed as a biocontrol measure when the pests were brightly colored or hairy, and was successful when the pests had any other color pattern and morphology. Diet breadth ($\chi^2 = 0.02$, df = 1, $P = 0.9$), foraging behavior ($\chi^2 = 0.1$, df = 1, $P = 0.8$), feeding niche ($\chi^2 = 0$, df = 1, $P = 1$), and size ($\chi^2 = 3.3$, df = 2, $P = 0.2$) were not significantly associated with success or failure of biological control.

The saturated model for parasitoids in biocontrol systems included success, establishment, or failure as the response variable and diet breadth, foraging behavior, and the two-way interaction as predictors. No other defenses were significantly associated with success in two-dimensional tables (morphology, $\chi^2 = 0.3$, df = 2, $P = 0.9$; coloration, $\chi^2 = 4.9$, df = 4, $P = 0.3$; feeding niche, $\chi^2 = 0.2$, df = 2, $P = 0.9$; and size, $\chi^2 = 0.5$, df = 4, $P = 0.9$). In the parsimonious, unsaturated model, diet breadth and foraging behavior were significant predictors of success (Table 2), but there was no diet breadth × foraging behavior interaction (from the saturated model, $\chi^2 = 5.2$, df = 2, $P = 0.08$). Parasitoids were more effective at controlling specialists as opposed to generalists and were more successful when the pests were gregarious as opposed to solitary feeders.

There was incomplete congruence in significant predictors for natural and biocontrol systems, but predictors in the biocontrol systems (for which smaller sample sizes were available) comprised a subset of predictors in the natural systems. In addition, the structure of the association was always the same between natural and biocontrol systems. For example, gregarious larvae were more likely to have high levels of parasitism than solitary larvae, and biological control with parasitoids was more successful against gregarious larvae (Table 3). The linear regression revealed that predicted percentages of high levels of parasitism from natural systems explained 53% of the variation in biocontrol success ($F_{1,10} = 11.2$, $P = 0.007$, $r^2 = 0.53$).

DISCUSSION

Defensive characteristics of pests were good predictors of success of biological control, and predictability varied depending on the natural enemy used. Morphology and coloration were significant predictors of success when predators were used, while diet breadth and foraging behavior were significant predictors of success for parasitoids. This general result corroborates aspects of the refuge theory (Hawkins et al. 1993) and similar studies that have uncovered associations between specific insect defenses and success of biocontrol (Stiling 1990, Gross 1991, Hawkins and Gross 1992). Our present study differs from previous work because we used independent data from natural systems to predict success of biocontrol and we predicted success for other natural enemies (predators).

Our results suggest that knowledge of defensive characteristics could be used alone or in conjunction with natural-enemy attributes (e.g., host specificity, high reproductive capacity, high rate of successful search, enemy density dependence) to create selection criteria for the choice of appropriate biological control agents. For example, if a pest were a generalist herbivore, a predator would have a higher probability of success as a biocontrol agent than a parasitoid would because parasitoids are not very successful against such pests in either ecological studies or biological control programs (Table 3). Therefore, most biocontrol efforts using parasitoids against various generalist species of *Spodoptera* (Noctuidae) have not been successful (BIOCAT database), whereas predators, such as *Calosoma blaptoides* (Carabidae), might be more successful if used against these generalists. Potentially, specific orders or guilds of predators could be given particular consideration based on their preference for pests with certain defensive attributes (Table 1, Dyer 1997). In our study, parasitoid guilds (see Mills 1994*b*) were not differentiated, but given sufficient data, defensive attributes could be used to determine appropriate parasitoids to use for biocontrol.

The issue of how basic research on tritrophic interactions can help guide biological control programs is illuminated by the fact that natural-systems models significantly predicted the outcome of biological control, suggesting that prey defenses function similarly in natural and agricultural (or semi-natural) systems. Kogan (1986) points out that there is considerable theoretical and empirical overlap between basic research on plant–insect interactions and applied research on host–plant resistance, even though these have been disparate fields throughout most of their respective historical developments. Several other studies have illuminated this overlap between basic and applied systems (e.g., Gross 1991, Hawkins 1994). The results from our study further support Kogan's (1986) arguments that basic research on tritrophic interactions and the evolution of defensive characteristics could be useful to biological-control researchers (and vice versa). More ecological studies that include multiple-species comparisons from natural systems could therefore be helpful for biological control. Although guidelines could be formulated using only data from biological control programs (such as the models constructed from BIOCAT for this and other studies) these data are not very complete or reliable (Mills 1994*a*) because of different focuses, methods, and fiscal concerns.

The most notable problem with using defensive characteristics to predict biocontrol success is that the state of knowledge on efficacies of defenses in natural systems is incomplete. Large multiple-species comparisons using data collected by the same investigator or using similar methods (such as those used for analyses in this study) are rare. Furthermore, the comparisons that do exist have omissions, and it is these omissions that should be the focus of further research. Some defenses that we were unable to fully examine in our previous research were encapsulation and host plant/herbivore chemistry. Because chemistry may be one of the most effective larval defenses (Dyer and Floyd 1993, Dyer 1995, 1997; also, see Table 3), it would be worthwhile to collect data on the efficacies of herbivore chemical defenses in natural and managed systems. Simple bioassays for chemistry can be quickly and easily performed and would be useful for categorizing the palatability of pests (Dyer 1995, C. Dodson, L. Dyer, and G. Gentry, *unpublished data*). If a particular type of natural enemy was found to be less susceptible to chemical defenses (such as a koinobiont parasitoid [Gauld and Gaston 1994]), it could be chosen as a control agent against unpalatable pests. Other natural enemies found to be more susceptible to chemical defenses (such as some types of predators [Dyer 1997]) might be more appropriate enemies for control of palatable or neutral pests.

In conclusion, we have presented a limited, yet promising, approach to prey-based decision making for biological-control practitioners based on data from natural and agricultural systems. This approach consistently predicted probability of successful biological control and described 53% of the variation in success of biocontrol efforts. Although not all defenses were examined, studies can easily be expanded to include other prey characteristics such as encapsulation or host chemistry. This approach would greatly benefit from additional field studies on natural systems along with tests of its predictions in biocontrol systems.

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