

# Encounters between aphids and their predators: the relative frequencies of disturbance and consumption

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## Abstract

Ecologists may wish to evaluate the potential for predators to suppress prey populations through the costs of induced defensive behaviors as well as through consumption. In this paper, we measure the ratio of non-consumptive, defense-inducing encounters relative to consumptive encounters (henceforth the 'disturbed : consumed ratio') for two species of aphids and propose that these disturbed : consumed ratios can help evaluate the potential for behaviorally mediated prey suppression. For the pea aphid, *Acyrtosiphon pisum* (Harris) (Homoptera: Aphididae), the ratio of induced disturbances to consumption events was high, 30 : 1. For the cotton aphid, *Aphis gossypii* (Glover) (Homoptera: Aphididae), the ratio of induced disturbances to consumption events was low, approximately 1 : 14. These results indicate that the potential for predators to suppress pea aphid populations through induction of defensive behaviors is high, whereas the potential for predators to suppress cotton aphid populations through induced behaviors is low. In measuring the disturbed : consumed ratios of two prey species, this paper makes two novel points: it highlights the variability of the disturbed : consumed ratio, and it offers a simple statistic to help ecologists draw connections between predator-prey behaviors and predator-prey population dynamics.

## Introduction

Animals attacked by predators experience one of two fates: they may be killed or not. Of course, death eliminates all opportunities for future reproduction and is therefore costly. To a lesser degree, however, animals that avoid consumption may also suffer costs. When animals successfully defend themselves by repelling or escaping from the predator, or when they are captured but rejected by the predator, they have been disturbed. Disturbed prey may lose feeding time, they may be wounded, or they may become exposed to other predators, and therefore suffer losses in their reproduction or survival (Karban & Baldwin, 1997; Lima, 1998b; Sih et al., 1998; Tollrian & Harvell, 1999). Because survival and reproduction contribute to population growth, predators have the potential to reduce

prey population growth by two mechanisms: through the consumption of prey individuals and through the induction of disruptive, costly defensive strategies (Sih et al., 1985; Anholt, 1997; Lima, 1998a; Beckerman et al., 2002).

Given that predator-induced defenses and their associated costs have the potential to suppress prey-population growth (Tamaki et al., 1970; Spitze, 1992 and references therein; McPeck & Peckarsky, 1998; Kuhlmann et al., 1999; Nelson et al., 2004), how can ecologists assess the potential contribution of behaviorally mediated effects in various predator-prey systems? In this paper, we propose a method for making such an assessment.

The relative strengths of the two mechanisms – consumption and induction – should depend on the outcomes of predator-prey encounters: encounters that kill prey individuals have a maximum impact on prey survival and reproduction; encounters that induce prey defenses necessarily have a smaller impact. Therefore, if induction of prey defense is to contribute substantially to prey suppression, encounters that induce prey defenses must be

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relatively common, compared to encounters that result in prey consumption. That is, because the costs of induced defense are relatively low, the rate of defense-inducing encounters must be relatively high before induction can be responsible for significant prey suppression. Thus, we propose that ecologists compare the relative rates of disturbance and consumption by measuring the disturbed : consumed ratio. The disturbed : consumed ratio is measured by observing the outcomes of predator–prey interactions, counting the number of predator–prey encounters resulting in predator-induced disturbance and the number resulting in consumption, and calculating the ratio of prey disturbance to consumption. A high ratio of disturbance to consumption indicates that the prey population might be influenced by behaviorally mediated effects, and a low ratio of disturbance to consumption indicates that the prey population probably is not influenced by behaviorally mediated effects. Although a disturbed : consumed ratio is not a definitive test for strong behaviorally mediated effects, it is a simple statistic that tests whether strong behaviorally mediated effects are likely or unlikely to be present.

We applied this diagnostic tool to two species of insect prey, the pea aphid, *Acyrtosiphon pisum* (Harris), and the cotton aphid, *Aphis gossypii* (Glover) (Homoptera: Aphididae). The results show that predators disturb many more pea aphids than they consume and that predators disturb far fewer cotton aphids than they consume. We hypothesize that predator-induced defensive behaviors have the potential to reduce population growth in the pea aphid but not in the cotton aphid. The goals of this paper are (1) to demonstrate that disturbed : consumed ratios are highly variable among species of prey and (2) to introduce the hypothesis that disturbed : consumed ratios are useful tools for evaluating the strength of behaviorally mediated effects in predator–prey systems. We do not test this hypothesis here, but we discuss our predictions for the pea aphid in light of field experiments published elsewhere. We also discuss disturbed : consumed ratios in terms of their utility and their limitations.

## Materials and methods

### Pea aphids, cotton aphids, and predator-induced feeding interruptions

The pea aphid is an herbivore of alfalfa and other legumes, and the cotton aphid feeds on cotton and on a broad array of other host plants. Both aphids are attacked by a suite of natural enemies, including coccinellids, heteropterans, lacewings, syrphids, and parasitoid wasps. Natural enemies have the potential to suppress the population growth of both pea aphids (Evans & England, 1996; Losey & Denno,

1998c; Snyder & Ives, 2003) and cotton aphids (Rosenheim et al., 1993; Slosser et al., 1998; Rosenheim, 2001). The pea and cotton aphids we studied were not tended by ants.

Aphids possess a range of defenses against predators, including morphological, social, chemical, and behavioral defenses (see Losey & Denno, 1998a for a brief review). Escape responses, in which aphids respond to predators by withdrawing their mouthparts from the plant and leaving the feeding site by walking or dropping, are relatively common among aphids. Pea aphids are well known for their escape response (see Losey & Denno, 1998a and Villagra et al., 2002 for references), which is triggered by predators 0.3–4.6 times per day in some alfalfa fields (Nelson, 2003). In contrast, cotton aphids typically do not express escape responses to predators (JA Rosenheim, pers. obs.; M Eubanks, pers. obs.).

In our studies of escape responses in pea and cotton aphids, encounters were defined as interactions between aphids and predators that resulted either in an aphid escape response or in consumption. Each encounter was then classified as disturbed or consumed based on its outcome for the aphid. Almost all observed encounters involved physical contact between predator and aphid. Incidental contacts, in which neither insect responded to the other, and other contacts in which the aphid's feeding activity was not interrupted were not counted as encounters. We counted the number of disturbance-inducing encounters and the number of consumptive encounters, and assessed their relative frequency using the disturbed : consumed ratio.

### The disturbed : consumed ratio for pea aphids in field arenas

Interactions of predators with pea aphids were observed in open-air arenas in alfalfa fields on the University of California – Davis campus in California, USA, between 19 October and 2 November, 2000. Each arena consisted of a stand of four alfalfa plants (*Medicago sativa*) in the center of a 30-cm-diameter polyvinyl chloride (PVC) ring. The ring's interior wall was coated with aqueous polytetrafluoroethylene (Fluon AD 1, Asahi Glass Fluoropolymers, Lancashire, UK) and stood 4 cm above the soil surface, which was covered with light sand. Each arena received 12 late-instar nymphal and 12 non-winged adult pea aphids that were collected from the field immediately prior to the observation period, and one predator, either a fifth-instar damsel bug nymph (*Nabis americanoferus* or *Nabis alternatus*) or an adult lady beetle (*Hippodamia convergens*). Predators were collected from the field 1–4 days in advance, held without food for 12 h before the observation period, and added to arenas 1 h after the aphids. Lady beetle adults' elytra were held shut with dental wax to prevent them from flying out of the arenas; they foraged actively on the alfalfa plants.

Predators were watched continuously for 1 h after introduction. Encounters with aphids were counted and their outcomes were recorded as disturbed [when the encounter resulted in a change in aphid behavior from feeding to not feeding (resting, walking, or dropping)] or consumed (when the encounter resulted in aphid consumption). Predators that walked to the arena wall were returned to the stand of alfalfa a maximum of two times before they were replaced with a different individual (two damsel bugs were replaced). A total of 20 arena observations were conducted in 10 temporal blocks, each block containing one damsel bug observation and one lady beetle observation. A G-test was used to compare the disturbed : consumed ratios of the two predators. We used t-tests to compare the rate of consumption encounters and the rate of disturbance-inducing encounters for the two types of predators.

#### **The disturbed : consumed ratio for pea aphids foraging freely in the field**

Video cameras were used to record the feeding activity of pea aphids in five fields of alfalfa during August and September 2001. Feeding aphids were located by a haphazard search, and their activity was recorded on videotape using camcorders mounted on tripods approximately 1 m from the aphids. Aphids were observed as mid-instar and late-instar nymphs and as winged and non-winged adults; the youngest nymphs were not observed because they were too small to be seen when the videotape was reviewed. At night, aphids were illuminated using the camera-mounted infrared light. Aphids were checked periodically during the videotaping process. Observations ended (1) when aphids spontaneously stopped feeding, (2) when aphids were disturbed or consumed in encounters with other insects, (3) when cameras ran out of videotape, or (4) at the cut-off times that ended a 12-h day or night. Videotapes were viewed to reveal the times and reasons that aphids stopped feeding. Three observations in which the view became obscured and the time and reason for stopping feeding could not be determined were discarded.

#### **The disturbed : consumed ratio for cotton aphids foraging freely in the field**

We directly observed the outcomes of encounters between cotton aphids (*Ap. gossypii*) and two classes of predatory insects: larval lacewings (*Chrysoperla* spp.) and predatory heteropterans (juvenile and adult *Nabis* spp., *Zelus renardii*, *Orius tristicolor*, and *Geocoris* spp.). Adult lacewings were collected from the field and housed with food in the laboratory for oviposition. Eggs were held singly in vials to await the hatching of larvae. Neonate larvae were released onto cotton plants (*Gossypium hirsutum*) in cotton fields within 6 h of hatching. One hundred and sixty-two

observations, each 4 h in duration, were made of neonate first-instar lacewings between July and September in 1995 and 1996 in 10 cotton fields in California, USA; further details appeared in Rosenheim et al. (1999).

Predatory heteropterans were located by searching plants in cotton fields and were observed for 2-h periods. The four genera and two life stages of predatory heteropterans were observed in approximately equal numbers; in total, 152 observations of predatory heteropterans were conducted between July and September in 1997 and 1998 in four cotton fields in California, USA.

All encounters between the focal predators and cotton aphids were recorded and sorted into two categories: disturbed (when the aphid responded to predator presence by interrupting its feeding or when the predator captured and released the aphid) and consumed (when the predator captured and fed on the aphid, killing it). A G-test was used to compare the disturbed : consumed ratios of the two classes of predators. Disturbance effects in nearby, non-contacted aphids were observed only rarely. Because encounters were observed by following a focal predator and focusing primarily on aphids that it physically contacted, some non-contact encounters may have occurred unobserved. If so, their exclusion is expected to have only a small effect on the reported results.

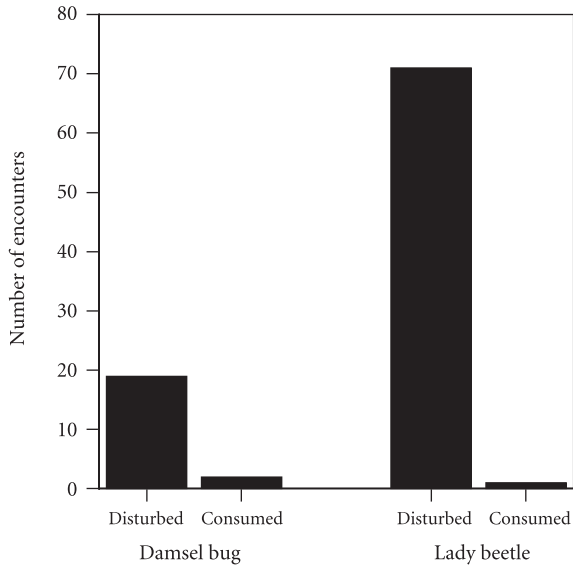
## **Results**

#### **The disturbed : consumed ratio for pea aphids in field arenas**

In the 10 arenas with damsel bugs, 21 encounters were observed, of which 19 led to aphid disturbance and two led to consumption; thus, for damsel bugs, the ratio of aphids disturbed : consumed = 19 : 2. In the 10 arenas with lady beetles, 72 encounters were observed and the ratio of aphids disturbed : consumed = 71 : 1 (Figure 1). Clearly, both predators disturbed many more aphids than they consumed. The relative frequencies of disturbance and consumption were not significantly different between damsel bugs and lady beetles ( $G = 2.18, P = 0.14$ ). However, the disturbance rates of the predators were significantly different: lady beetles disturbed more than three times as many aphids per hour as damsel bugs [mean number of disturbances per hour ( $\pm$  SE) for damsel bugs was 1.9 ( $\pm$  0.4) and for lady beetles 7.1 ( $\pm$  1.4);  $t = 3.5, P < 0.01$ ]. Consumption rates were not significantly different between the predator types [mean number of consumptions per hour ( $\pm$  SE) for damsel bugs was 0.2 ( $\pm$  0.1) and for lady beetles 0.1 ( $\pm$  0.1);  $t = -0.6, P = 0.56$ ].

#### **The disturbed : consumed ratio for pea aphids foraging freely in the field**

Observation durations ranged from 1 min to 10 h and 29 min. In total, 101 pea aphids were observed for 178.1 h



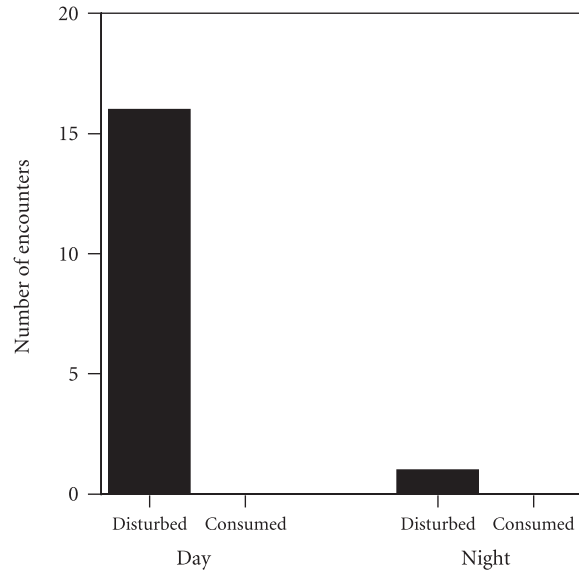
**Figure 1** Number of encounters between pea aphids (*Acyrtosiphon pisum*) and damsel bugs or lady beetles, resulting in disturbance or consumption. Encounters were observed in arenas in alfalfa fields.

(the aphids were 34 nymphs, 19 winged adults, and 48 non-winged adults.) Ninety-seven aphids were observed for 132.9 h during daytime, 08:00–20:00 hours. Ten aphids were observed for 45.2 h during nighttime, 20:00–08:00 hours. (Six aphids provided both day and night observations.) For aphids whose feeding was interrupted by a predator, the outcome of the interaction was recorded as disturbed or consumed.

Aphids were disturbed more frequently than they were consumed (Figure 2). Of the 97 pea aphids observed during daytime, 16 had their feeding interrupted by a predator. All 16 were disturbed; none were captured or consumed. Ten aphids were observed during night hours: one was disturbed and none were consumed. Thus, in total, we observed 17 predator-induced disturbances and zero consumption (Table 1). (Aphids expressed escape behaviors in eight additional observations: six in response to non-enemies and two in response to arthropods that could not be clearly distinguished as enemies or non-enemies; see Table 1.) Thus, members of the full, unmanipulated community of predators naturally present in alfalfa clearly disturb substantially more pea aphids than they consume.

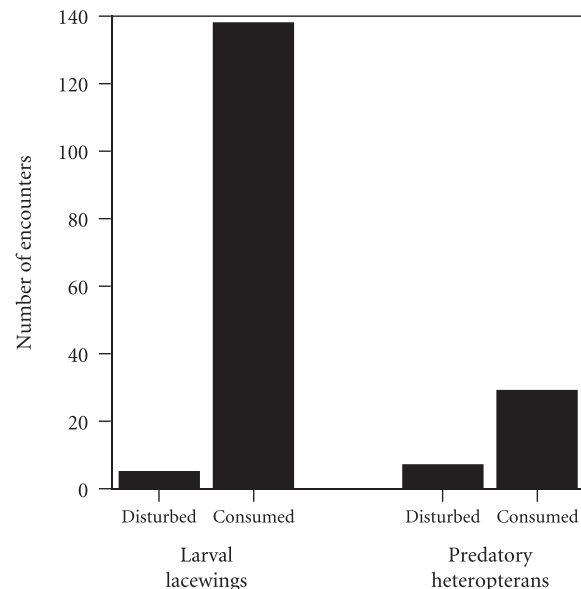
**The disturbed : consumed ratio for cotton aphids foraging freely in the field**

We observed 143 encounters between larval lacewings and cotton aphids: five encounters resulted in disturbance of the aphid and 138 encounters resulted in capture and consumption of the aphid (Figure 3). Thus, for lacewings,



**Figure 2** Outcomes of encounters between feeding pea aphids (*Acyrtosiphon pisum*) and foraging predatory insects observed in video recordings in alfalfa fields. No encounters resulted in consumption.

the ratio disturbed : consumed = 5 : 138. Thirty-six encounters were observed between predatory heteropterans and cotton aphids, and they yielded the ratio disturbed : consumed = 7 : 29. The disturbed : consumed ratios of lacewings and heteropterans are significantly different



**Figure 3** Outcomes of encounters between foraging predators, either lacewings or heteropterans, and cotton aphids (*Aphis gossypii*) feeding on cotton in the field.

**Table 1** Insects observed disturbing pea aphids during 132.9 h of daytime and 45.2 h of nighttime video-recorded field observation. No pea aphids were observed being captured or consumed

Insect inducing disturbance	Number of aphid disturbances observed
<i>Nabis</i> spp.	4
<i>Orius tristicolor</i>	3
<i>Collops</i> spec.	3
<i>Hippodamia convergens</i>	1
Parasitoids of aphids	2
Ants	3
Syrphid larvae <sup>a</sup>	1
Enemy subtotal	17
Parasitoids of hosts other than aphids	1
Leafhopper adults	1
Pea aphids	2
<i>Lygus</i> nymphs	1
Unidentified <sup>b</sup>	1
Non-enemy subtotal	6
Undetermined	2
Undetermined subtotal	2
Grand total	25

<sup>a</sup>The syrphid-induced disturbance was observed at night; all others occurred in daytime.

<sup>b</sup>The unidentified disturbing agent was classified as non-enemy based on its minute size and lack of orientation toward the aphid.

( $G = 8.6$ ,  $P < 0.01$ ), implying that lacewing larvae convert relatively more encounters into consumptions, whereas heteropterans convert relatively more encounters into disturbances. This comparison between lacewings and heteropterans is presented with a note of caution because the two classes of predators were studied in different years; however, we believe the comparison is biologically meaningful for two reasons: all observations were of unmanipulated insects foraging freely in the field, and each data set integrates observations made throughout the growing seasons of two consecutive years.

Observations in this study were conducted with newly hatched lacewing larvae. In a separate study (data not published), similar observations of older lacewing larvae, instars 1–3, were conducted, and 145 encounters between larval lacewings and cotton aphids were recorded. All 145 encounters resulted in capture and consumption of the target aphid. Here also, it is possible that some induced disturbances may have gone unrecorded in a small number of non-contacted aphids. However, given that none of the contacted aphids managed to escape, these data indicate that the extremely low disturbed : consumed ratios

of neonate lacewings are substantially similar to those of older lacewing larvae.

## Discussion

Given an encounter with a predator, a pea aphid is likely to leave its feeding location and suffer an interruption in its feeding activity; a cotton aphid is likely to remain at its feeding site and suffer consumption. When pea aphids were observed in open-air field arenas, 97% of their encounters with predators resulted in aphid escape and 3% resulted in aphid consumption. In observations of pea aphids under natural field conditions, 100% of encounters with predators induced aphid predator-avoidance behavior and none led to prey capture or consumption. Cotton aphids showed the reverse pattern: 4% of encounters with foraging lacewings resulted in disturbance and 96% in consumption. When heteropterans were the predator, 19% of encounters induced disturbance and 81% resulted in consumption of the cotton aphid.

Table 2 summarizes disturbed : consumed ratios measured in several species of aphids. Some aphids express disturbed : consumed ratios greater than 1 : 1, reflecting escape responses nearly as effective as that of the pea aphid, whereas others are less responsive to predator presence and express disturbed : consumed ratios smaller than 1 : 1, similar to that of the cotton aphid. The variation in patterns of encounter outcomes among aphid species shows that the disturbed : consumed ratio can range widely, even within one family of insects. What do disturbed : consumed ratios tell us about the ecologies of these aphids? We hypothesize that the differences among aphid species in their disturbed : consumed ratios indicate differences in the mechanisms by which these aphids may be suppressed by their predators: low disturbed : consumed ratios probably reflect predator–prey dynamics dominated by consumption, and high disturbed : consumed ratios reflect predator–prey dynamics that have the potential to be governed partly by induction as well. By indicating the frequency of disturbance relative to consumption, disturbed : consumed ratios serve to describe the potential contribution that predator-induced disturbances could make to prey population suppression. This is a valuable point of information. Ecologists have recently expanded their recognition that predator–prey systems operate through behavioral as well as consumptive interactions (Preisser et al., 2005). However, it can be difficult to distinguish behavioral from consumptive mechanisms of prey population suppression. In many systems, it may be easier to measure disturbed : consumed ratios than to measure the population-level impact of predator-induced defenses. We propose that disturbed : consumed ratios can provide an

**Table 2** Outcomes of encounters between aphids and their predators – a review of the literature. Predator–aphid pairs are ranked by percent disturbed

Aphid	Predator	Experimental plant and venue	Percent disturbed	Percent consumed	Number of encounters observed	Reference
<i>Acyrtosiphon pisum</i>	Various (see Table 1)	Alfalfa in the field	100	0	17	Present study
<i>Acyrtosiphon pisum</i>	<i>Hippodamia convergens</i> adults	Alfalfa in field arenas	99	1	72	Present study
<i>Acyrtosiphon pisum</i>	<i>Coccinella septempunctata</i> adults	Broad bean in the laboratory	94	6	155	Braendle & Weisser (2001)
<i>Acyrtosiphon pisum</i>	<i>Nabis</i> spp. nymphs	Alfalfa in field arenas	90	10	21	Present study
<i>Microlophium evansi</i>	<i>Adalia decempunctata</i> larvae	Nettle leaves in the laboratory	90	10	2715	Dixon (1958)
<i>Microlophium evansi</i>	<i>Adalia decempunctata</i> adults	Nettle leaves in the laboratory	86	14	594	Dixon (1958)
<i>Schizaphis graminum</i>	<i>Coccinella septempunctata</i> adults	Grain sorghum in field cages	82	18	Data not reported	McConnell & Kring (1990)
<i>Schizolachnus pineti</i>	<i>Syrphus vitripennis</i> larvae	Pine saplings in the field	80	20	61	Kidd (1982)
<i>Acyrtosiphon pisum</i>	<i>Adalia bipunctata</i> larvae	Bean leaves in the laboratory	70	30	451	Klingauf (1967)
<i>Acyrtosiphon pisum</i>	<i>Syrphus</i> spec. larvae	Bean leaves in the laboratory	64	36	235	Klingauf (1967)
<i>Acyrtosiphon pisum</i>	<i>Chrysopa vulgaris</i> larvae	Bean leaves in the laboratory	62	38	115	Klingauf (1967)
<i>Neomyzus circumflexus</i>	<i>Adalia bipunctata</i> larvae	Bean leaves in the laboratory	28	72	137	Klingauf (1967)
<i>Aphis gossypii</i>	Adult and nymphal heteropterans ( <i>Nabis</i> spp., <i>Zelus renardii</i> , <i>Orius tristicolor</i> , and <i>Geocoris</i> spec.)	Cotton in the field	19	81	36	Present study
<i>Myzus persicae</i>	<i>Adalia bipunctata</i> larvae	Various plant leaves in the laboratory	19	81	272	Klingauf (1967)
<i>Myzus persicae</i>	<i>Syrphus</i> spec. larvae	Various plant leaves in the laboratory	5	95	112	Klingauf (1967)
<i>Aphis gossypii</i>	<i>Chrysoperla</i> spp. larvae	Cotton in the field	4	96	143	Present study

initial assessment of the role of induced defenses relative to the role of consumption in prey suppression.

Testing this hypothesis will require (1) measuring disturbed : consumed ratios for a number of predator–prey systems, (2) measuring the population-level costs of disturbance for each prey, and then, for each study system, (3) comparing the predicted strength of behaviorally mediated effects to their observed strength. The two measurements necessary for a test of our hypothesis have been made for one species of insect prey, the pea aphid. In studies published elsewhere, we used two methods to estimate the suppressive effect of predator-induced disturbance on pea aphid population growth. First, we exposed pea aphids to predators whose mouthparts had been surgically blunted and, therefore, transmitted only disturbance effects. These non-consumptive predators retained 39–80% of the suppressive effect of normal predators; presumably

this occurred because many of a normal predator's encounters with pea aphids result not in consumption but in disturbance (Nelson et al., 2004). Second, we measured the frequency and the reproductive cost of disturbance under field conditions and found that predator-induced disturbances reduce pea aphid population growth by 2–35% (Nelson, 2003). Thus, two independent methods of quantifying the population-level costs of disturbance for the pea aphid support the conclusion that the costs of disturbance are indeed substantial, as suggested by the very high disturbed : consumed ratios reported in this study. Although similar studies in other systems are needed, studies of the pea aphid provide some initial support for our hypothesis that the relative frequencies of disturbance and consumption correspond to the mechanisms underlying the suppression of a prey population by predators.

The information provided by disturbed : consumed ratios may be useful, but it is also limited. Disturbed : consumed ratios tell us only about the potential for disturbance-mediated prey suppression, whereas the actual contribution of predator-induced disturbances will depend on their associated costs. Disturbances will impact prey population growth only if they are costly. If they are not costly – if disturbances are experienced only by prey individuals that have little to lose in terms of future survival and reproduction (senescing individuals, for example), or if disturbances impose no costs (due to physiological compensation, for example) – then their impact on prey population growth will be limited, even if they are common. However, the costs of disturbance need not be large, because a disturbance that is induced frequently can impact population growth even if its costs are small (Nelson, 2003).

A second limitation of disturbed : consumed ratios is that they focus exclusively on behavioral escape responses. However, induced defenses include morphological and physiological responses as well as behavioral responses, all of which can impose costs. An example of predators inducing morphological changes in aphids occurs when the exposure to predator cues induces aphids to produce more winged offspring and fewer non-winged offspring (pea aphids: Dixon & Agarwala, 1999; Weisser et al., 1999; Sloggett & Weisser, 2002; Kunert & Weisser, 2003; cotton aphids: Mondor et al., 2005). This response is costly because winged aphids are less fecund than non-winged aphids (Campbell & Mackauer, 1977; Dixon, 1998, p. 113). An example of predators inducing physiological changes occurs when aphids defend themselves against parasitoids through encapsulation of the parasitoid egg (Carver & Sullivan, 1988; Godfray, 1994, p. 232; Henter & Via, 1995). This response is costly because immune responses can divert resources away from reproduction (Frost, 1999). Thus, escape behaviors represent only one of several pathways by which induced responses to predators may lead to prey suppression. Although disturbed : consumed ratios may help gauge the potential impact that predators can have by inducing defensive behaviors, ecologists will need to rely on additional metrics to assess induction-mediated effects more broadly.

A third limitation of disturbed : consumed ratios is that they are unlikely to be fixed in any given system; rather, they may depend on an array of conditions. Factors affecting disturbance rates of aphids include aphid clone (Braendle & Weisser, 2001), aphid density (Kidd, 1982; McConnell & Kring, 1990, but see Losey & Denno, 1998a), aphid stage (Dixon, 1958; Klingauf, 1967; McConnell & Kring, 1990; Losey & Denno, 1998a), plant type (McConnell & Kring, 1990; Grevstad & Klepetka, 1992; Clark &

Messina, 1998), ant attendance (Stadler et al., 2003), and predator type (Klingauf, 1967; Losey & Denno, 1998a,b) [see Losey & Denno (1998a) for a review]. Consumption rates are also likely to vary (van den Meiracker & Sabelis, 1999; Villagra et al., 2002). Thus, disturbed : consumed ratios should be based on observations made over a range of ecological conditions.

Despite their limitations, disturbed : consumed ratios may lead to useful insights and new questions about the nature of predator–prey systems. In the arena observations of pea aphids, lady beetles disturbed more than three times as many aphids per hour as damsel bugs. Losey & Denno (1998a) observed interactions between pea aphids and predators in 1-h trials in laboratory arenas and obtained similar results: the proportion of pea aphids dropping off the plant was more than three times greater for lady beetles than for damsel bugs. In a related study, damsel bugs suppressed pea aphid populations partly through non-consumptive effects, presumably by inducing costly disturbances in their prey even while their consumptive abilities were blocked (Nelson et al., 2004). Thus, the still greater disturbance effect of lady beetles shown in this paper suggests that the often observed suppressive effect of lady beetles on pea aphid populations (Evans & England, 1996; Losey & Denno, 1998c; Harmon et al., 2000) may in large part be mediated by the effects of adult lady beetles on aphid behavior. For predator–prey systems that exhibit high degrees of predator-induced defensive responses, it may be useful to account for the consequences of defense-inducing encounters, as well as the consequences of consumptive encounters when interpreting the population-dynamical effects of predators.

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