

Differentiation of Competitive vs. Non-competitive Mechanisms Mediating Disruption of Moth Sexual Communication by Point Sources of Sex Pheromone (Part I): Theory¹

J. R. Miller · L. J. Gut · F. M. de Lame · L. L. Stelinski

Received: 1 November 2005 / Revised: 9 March 2006 /
Accepted: 7 May 2006 / Published online: 4 October 2006
© Springer Science + Business Media, Inc. 2006

Abstract This study establishes a theoretical framework for differentiating among possible behavioral mechanisms whereby sexual communication of moths is disrupted in crops treated with point sources of pheromone. The major mechanisms recognized in the mating disruption literature fall into two main categories: competitive (competitive attraction = false-plume-following) and non-competitive (camouflage, desensitization, and sensory imbalance). Each disruption mechanism has been precisely defined verbally, and then the distinguishing characteristics of the two categories were defined mathematically. The sets of predictions associated with each category were visualized by graphical plots of mathematical simulations. Profiles of simulated male visitation rates to pheromone-baited traps deployed in pheromone-treated crops were graphed against density of pheromone dispensers by using various types of axes. Key traits of non-competitive attraction are as follows: concave profiles on untransformed axes, with an asymptotic approach to zero catch of male moths in traps; a straight line with positive slope when $1/\text{catch}$ is plotted against dispenser density (Miller-Gut plot); and a straight line with negative slope when catch is plotted against dispenser density * catch (Miller-de Lame plot). Key traits of non-competitive disruption profiles include: an initial linear disruption profile on untransformed axes; a concave Miller-Gut plot; and a recurving Miller-de Lame plot. These differences in profiles provide a basis for distinguishing competitive from non-competitive mechanisms when analyzing disruption profiles from field experiments. Slopes and intercepts of these secondary plots can also reveal both male and female moth densities, if the relative

¹As this study progressed, striking similarities were noted between the kinetics of mating disruption by competitive attraction and enzyme kinetics. Because of space limitations, this congruence will be addressed in a future report.

J. R. Miller (✉) · L. J. Gut · L. L. Stelinski
Department of Entomology, Michigan State University, East Lansing, MI 48824, USA
e-mail: miller20@msu.edu

Present address:

F. M. de Lame
Henkel Consumer Goods Inc, Dial Center for Innovation,
15101 North Scottsdale Rd., Scottsdale, AZ 85254, USA

attractiveness of traps, females, and dispensers is known. The absolute value of the slope of the Miller-de Lame plot is a measure of each dispenser's activity (D_a) for suppressing catch of male moths in traps. An application activity ($D_{\bar{A}a}$) for a given dispenser can be calculated by multiplying D_a by the number of such dispensers applied per hectare of crop.

Keywords Mating disruption mechanisms · Disruption kinetics · Mathematical modeling · Percent disruption · Dispenser activity

Introduction

Mating disruption as currently applied to insects is the practice of continuously dispensing synthetic sex attractants into a crop for extended periods so as to suppress pest reproduction by interfering with mate finding. This pest management tactic holds considerable promise for management of moths and other pests that rely on long-distance chemical communication. In the United States, the demands for pest control by behavioral modification are rising as availability of conventional insecticides dwindles in the face of increasingly stringent regulatory policies. However, protocols for pheromone disruption of many important moth pests have not been optimized. In some cases, this tactic works robustly (e.g., redbanded leafroller, Novak and Roelofs, 1985; also in oriental fruit moth, Rice and Kirsch, 1990; Trimble et al., 2004, and other examples in Cardé and Minks, 1995), whereas in other cases results are mixed (e.g., obliquebanded leafroller, Agnello et al., 1996; Lawson et al., 1996; spruce budworm, Seabrook and Kipp, 1986).

General agreement has not been reached as to whether it is better to broadcast pheromone uniformly throughout a crop (e.g., microencapsulated formulations, Balkan, 1980; Vickers and Rothschild, 1991; Waldstein and Gut, 2003), or whether pheromone dispensers should be discrete sources spaced regularly throughout. In orchards, a spacing of 1–2 dispensers per tree is recommended for long-lasting, hand-applied pheromone dispensers like polyethylene tubes (ropes) (Rothschild, 1975; Nagata, 1989; Knight et al., 1998). The disruptive products used in some other crops favor an intermediate density of small and highly distributed point sources (e.g., hollow fibers, Doane and Brooks, 1981; Swenson and Weatherston, 1989; or laminated flakes, Tcheslavskaja et al., 2005). Likewise, there is divergence of opinion regarding the quantity of pheromone necessary for high-performance disruption and whether it is better to use the complete natural blend or just one or two of the major pheromone components (Knight et al., 1998; Minks and Cardé, 1988; Evenden et al., 1999). Different release devices, spacings, and chemistries may be called for (Gut et al., 2004) depending on the mechanism(s) of disruption to which a particular pest species is thought to be vulnerable.

It has often been pointed out that optimizing mating disruption will be aided by understanding the actual behaviors evoked or suppressed when insects are exposed to particular formulations of synthetic pheromones (e.g., Valeur and Löfstedt, 1996; Cardé et al., 1998; Evenden et al., 2000; Gut et al., 2004). The major mechanisms postulated to explain communicational disruption (Rothschild, 1981; Bartell, 1982; Cardé, 1990) include (formal definitions below): (1) false-plume-following; (2) camouflage; (3) desensitization—including adaptation and habituation; (4) sensory imbalance; and (5) combinations thereof. However, the evidence for which mechanism is mainly responsible for communicational disruption for particular pests under particular regimes of disruption remains largely circumstantial. We are aware of no example where a particular mechanism has been definitively proven to be the leading cause of mating disruption for any insect under actual field conditions.

Some might argue that biological phenomena like mating disruption are too complex to be usefully represented by simplistic explanatory models. Complications in interpretation are easy to envision if several disruption mechanisms operate simultaneously. However, we see value in attempting to break this seemingly complicated phenomenon into defined component causes, and assessing how each could shape overall outcomes. Recognizing and understanding patterns in disruption outcomes associated with individual explanatory models should facilitate recognizing and understanding outcomes from mixed models.

This analysis emphasizes competitive attraction as a primary contributor to mating disruption of moths by pheromone point sources. Competitive attraction has been variously referred to as: confusion (Knipling, 1979 *et ante*; Bartell, 1982), false-trail-following (Maini and Schwaller, 1992), and false-plume-following (Cardé, 1990; Stelinski et al., 2004a). Our attention was drawn to this mechanism when direct behavioral observations (Stelinski et al., 2004a, 2005a,b) revealed that oriental fruit moth (*Grapholita molesta*), obliquebanded leafroller (*Choristoneura rosaceana*), redbanded leafroller (*Argyrotaenia velutinana*), and codling moth (*Cydia pomonella*) all approached their respective polyethylene tube dispensers of pheromones at frequencies rivaling catches of moths occurring simultaneously in monitoring traps. Combined with earlier reports of attractiveness of dispensers used in mating disruption (e.g., Bartell, 1982; Barrett, 1995; Cardé et al., 1998; Witzgall et al., 1999; Maini and Accinelli, 2000), there is mounting evidence that competitive attraction is involved in communicational disruption of various moth species. In this paper, we: (1) explicitly define and formalize the competitive attraction explanatory model; (2) detail its predictions; and (3) determine where these predictions do or do not overlap with non-competitive explanatory models. This work sets the stage for a companion paper (Miller et al., 2006) that analyzes case studies from the literature for fit to competitive vs. noncompetitive disruption.

Definition, Assumptions, and Predictions of the Competitive-Attraction Explanatory Model for Communicational Disruption

Definition

We take *competitive attraction* to mean that the frequency with which male moths find calling females or monitoring traps (proxy for calling females) in a crop under disruption is reduced because males are diverted from orienting to females or traps due to preoccupation with nearby attractive or arrestive plumes from dispensers of synthetic pheromone. Accordingly, communicational disruption by sex attractant pheromones utilizes the same behavioral mechanisms normally enabling the responder to *find* (*sensu* Miller and Strickler, 1984) a calling female. These mate-finding mechanisms are mainly positive, plume-following anemotaxis combined with arrestment. Female moths under pheromone disruption by competitive attraction are envisioned to compete with sources of synthetic pheromone for responses from males.

Mating System in Which Pheromone Disruption by Competitive Attraction Operates

The mating system of moths using sex attractants for long-distance mate finding has been labeled *scramble polygyny* (Thornhill and Alcock, 1983) to describe the situation in which males compete heavily during limited windows of time for a share of calling females whose individual availability is fleeting. The sex ratio in a moth population is usually approximately one, but this does not mean that every male succeeds in mating. Individual males are rewarded for proficiency in detecting pheromone plumes and arriving at their sources.

Provided he is not physically or behaviorally defective, the first-arriving male usually mates with the calling female. Moreover, some males may mate numerous times, whereas others may never mate. When females mate infrequently, intrasexual competition among male moths is high, whereas that among females is comparatively low. This is because mated females cease calling (at least for a time), whereas all able-bodied males continue competing sexually throughout their lives. Under a regime of pheromone disruption by competitive attraction, scramble competition would be intensified for males by the addition of “false females” that make it more difficult for males to find authentic females. In addition, intrasexual competition would be intensified for females by deployment of many false females into the system. The effect is analogous to diminishing male density, or lowering the ratio of males to females. In the natural situation and with appreciable moth populations, any calling female is expected to be quickly found and mated. However, the signals of females could go unheeded under mating disruption operating by competitive attraction because males would be preoccupied by visits to the more abundant false females.

In the several cases where it has been quantified, fecundity of both male and female moths diminishes substantially with age (Knight, 1997; Jones and Aihara-Sasaki, 2001; Torres-Vila et al., 2002). Thus, delaying mating can contribute to pest control. However, when each mated female produces 100 or more viable eggs and mortality of larvae is low, efficacy in mating disruption must exceed ca. 98% for the pest population to decline (Knipling, 1979).

Assumptions of a Probability Model for Competitive Attraction

Figure 1 provides the spatial and numerical context in which we envision moth mating disruption to occur in one small portion of an orchard crop. This figure depicts a 0.3-ha plot of fruit trees infested with a tortricid moth pest. Active spaces of pheromone plumes generated by hand-applied pheromone dispensers in such an orchard vary from ca. 5–30 m in length, as estimated by portable electroantennogram devices (EAGs) (Suckling et al., 2006). For ease in viewing and interpreting Fig. 1, the density of dispensers (D) (Table 1 provides a key to abbreviations) is reduced from the usual 1–2 dispensers per tree. Instead, 24 dispensers of pheromone are spaced regularly throughout the 72-tree plot, which also contains 20 male (M) and 20 female (F) moths. One monitoring trap (T) baited with an optimized pheromone lure is deployed centrally in this plot, as is usual for assessing the effectiveness of communicational disruption, measured as inhibition of catch of males in traps relative to catch in an equivalent control plot not treated with pheromone. Wind, currently from the top left of the orchard, generates a pheromone plume from each dispenser and the trap. Active spaces are approximated by the light-gray ellipsoids snaking across tree rows. Shifts in wind direction over time would shift the direction and shape of plumes such that pheromone from individual sources would waft over varying sets of trees and moths through time. As females begin calling, their plumes mingle and compete with those from pheromone dispensers and the trap. Over a moth's lifetime, the encounters of males with pheromone sources (T , F , and D) are envisioned to occur in proportions approximating the relative densities and strengths of pheromone sources of each type in this orchard. The densities of male and female moths in this orchard would shift across time in accordance with their respective curves for entrance into and exit from the local reproductive pool. Variation in nightly reproductive activity would be influenced by abiotic factors like weather. However, orientational outcomes averaged across a full moth generation are envisioned to stabilize sufficiently to permit meaningful contrasts among different disruptive treatments sharing common conditions.

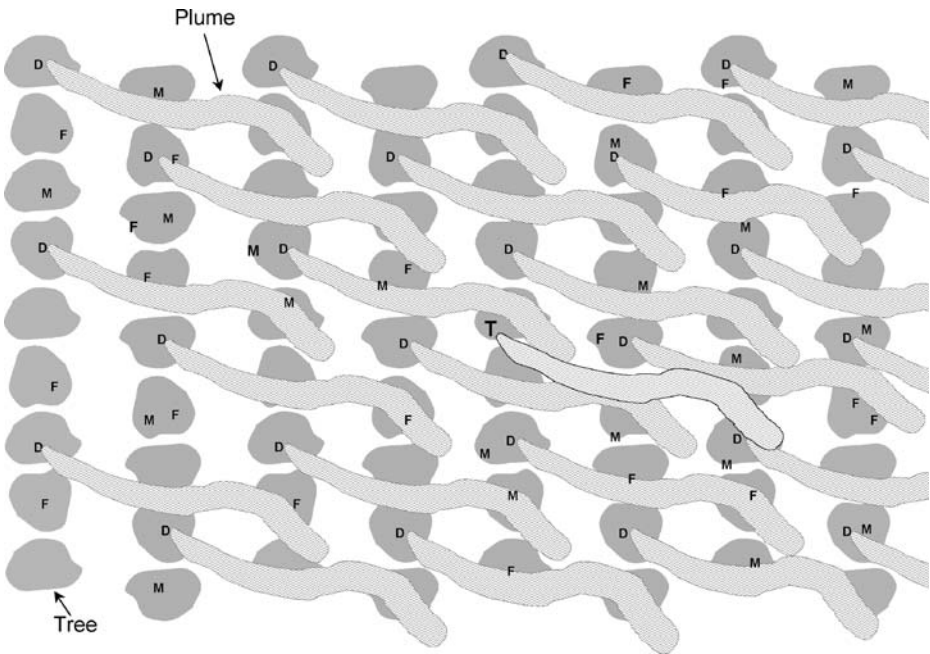


Fig. 1 Diagram of a 0.3-ha orchard plot of 72 trees containing 24 evenly distributed pheromone dispensers (D), 20 randomly distributed male moths (M), 20 randomly distributed female moths (F), and one centrally located monitoring trap (T). Wind originates from the top left.

Predictions of time-averaged outcomes from orientational events of male moths under disruption by competitive attraction are easiest to understand for the simplified, hypothetical situation where: (1) attractiveness is equal for *F*, *D*, and *T*; (2) each male engages in one attraction event per night; (3) the number of males removed by the one sticky trap has negligible impact on the male population; and (4) all females call and remain attractive through most of a several-hour reproductive period. Complexity will be systematically added once predicted outcomes of the simpler case are described.

Mathematically, this problem corresponds to that of loading a bag with 20 white spheres [= density of moth females (F_D) in Fig. 1], 24 green spheres [= density of dispensers (D_D)], and one red sphere [= density of traps (T_D)] and thoroughly mixing these spheres of equal size and mass. One male orientational event corresponds to reaching into the bag, randomly withdrawing one sphere, and then replacing it. The probability one draw will yield a white sphere is: $20/45 = 0.44$. Likewise, the probability one draw will yield a green or red sphere is: $24/45 = 0.53$, or $1/45 = 0.022$, respectively. With sufficient replication, the number of spheres of a given color drawn per set of draws equals the probability of drawing the given color at each draw multiplied by the number of draws per set, which equals the number of males in the plot when each male is allotted only one attraction event per night.

Translating the probability principles of the scenario described above to Fig. 1, the theoretically predicted male visitation rate per night to the trap is taken as synonymous with catch (*C*) to yield:

$$C = T_D M_D / (T_D + F_D + D_D) \tag{1}$$

Catch in this case = $1 * 20 / (1 + 20 + 24) = 0.44$ males/trap/night. Similarly, the predicted male visitation rate per night to the 20 females and 24 dispensers of Fig. 1 = 8.9 and 10.7, respectively.

There is ample precedent for applying standard probability theory to predict time-averaged male catches when females call in competition with attractive traps. Knippling (1979) and coworkers did so when exploring the possibilities of annihilating insect populations using a trap-out tactic. Other researchers (e.g., Mertins et al., 1967; Hardee et al., 1969; Roelofs et al., 1970; Nakasuji and Fujita, 1980) built on this approach to modeling competitive attraction and found its predictions realistic in field tests.

Predictions of Competitive Attraction Models

1. General predictions from the mass trapping literature.

Key predictions already validated in literature (above references) taking this probabilistic approach to competitive attraction are as follows: (1) efficacy is strongly and positively correlated with the density of traps baited with artificial pheromone; (2) efficacy of competitive attraction is strongly and negatively correlated with pest density; and (3) the density of traps required to control a substantial population of pest moths is prohibitively high due to material costs.

Table 1 Key to abbreviations

Term	Definition
A	Total area of crop (ha)
A_c	Area of crop covered by camouflaging pheromone plumes
A_{uc}	Area of crop not camouflaged by pheromone plumes
$C = V_{Tt}$	Catch (males/trap/time)
C_{max}	Male catch in traps placed into crop not receiving pheromone dispensers
D	Dispenser of synthetic pheromone deployed for disrupting sexual communication
D_a	Dispenser activity = suppressive effect of a dispenser on ability of males to find females or monitoring traps; the units are area (ha) over which one dispenser can theoretically reduce C_{max} by 50%
$D_{\bar{a}a}$	Dispenser application activity = $D_a * D_D$ = potency of a given pheromone formulation as applied to one ha
D_D	Dispenser density (dispensers/ha)
D_{sa}	Dispenser specific activity = $D_a/\mu\text{g}$ pheromone released by 1 dispenser/hr; the units are $\text{ha} * \text{hr}/\mu\text{g}$
F	Female moth
F_D	Female moth density (females/ha)
k_D	Attractiveness of a pheromone dispenser relative to that of a trap or female moth
k_F	Attractiveness of a female moth relative to that of a trap or dispenser
k_T	Attractiveness of a trap relative to that of a female or dispenser
M	Male moth
M_D	Male moth density (males/ha)
T	Trap baited with a pheromone lure; attracts and captures male moths
T_D	Trap density (traps/ha)
$V_{/D}$	Visitation rate of male moths to a dispenser (male visits/dispenser/time)
$V_{/F}$	Visitation rate of male moths to a female moth (male visits/female/time)
$V_{/T} = C$	Visitation rate of male moths to a trap (males/trap/time)

2. Predictions of mating disruption outcomes from our competitive-attraction model as applied to Fig. 1.

According to Equation (1), the nightly probability that a male will visit a given trap or a given female under the competitive-attraction assumptions of Fig. 1 is 0.44. If each visit to a female resulted in mating, 8.9 out of the 20 total females would mate on night 1. The comparable number of male visits to a given female in a control plot equivalent to that of Fig. 1, but without pheromone dispensers can also be calculated using Equation (1) as: $1T * 20M / (1T + 20F) = 20/21 = 0.95$. Mating disruption outcomes are typically scored by % inhibition of male catch in traps, calculated as: $[1 - (\text{mean catch per trap in the pheromone-treated plot} / \text{mean catch per trap in the check plot})] \times 100\%$ (Roelofs and Novak, 1981). That value for the current example is: $[1 - (0.44/0.95)] 100\% = 54\%$.

From the perspective of pest control, a 54% mating disruption efficacy per night for the 24 pheromone dispensers per 72 fruit trees is inadequate. Moreover, having nine of the 20 females mate on the first night lowers the total density of attractant sources for the second night: 11F, 24D, and 1T = 36 total. The calculated male catch on the second night for one trap or male visitation rate to a given female is: $1 * 20/36 = 0.56$, a value slightly higher than 0.44 male visits per female for night 1. It follows that 6.1 females of the 11 remaining virgins would mate on night 2, leaving only 4.9 of the original 20 virgin females after two nights. After night 3, the preponderance of females would have mated. The number of pheromone dispensers in Fig. 1 is clearly too low to control the pest under competitive attraction operating within the above assumptions.

A key prediction of competitive attraction is that moth catch per trap will be negatively correlated with density of competing attractant sources. This relationship is specified in Fig. 2a for the conditions of Fig. 1. However, densities of dispensers, moths, and traps are now scaled per hectare. An identical profile would result if male visitation rate per 3.3 virgin females per night were plotted on the *y*-axis of Fig. 2a. The effect of increasing dispenser density is nonlinear for competitive attraction. Initially, the impact of small increases in dispenser density is great; however, the return for a given increment in dispenser density progressively diminishes. Unfortunately for pest management, complete cessation of male visits per female or trap under a regime of competitive attraction is approached only asymptotically and never reached. The shape of this response profile is an inherent property of inverse functions, where a swelling D_D in the denominator of Equation (1) initially overwhelms but never completely negates T_D and M_D in the numerator.

Inverse functions lend themselves well to graphical analyses after an inverse transformation. Indeed, the simulated competitive attraction data from Fig. 2a when plotted as the inverse of male catch/trap/night ($1/C$) on the *y*-axis vs. D_D on the *x*-axis (designated hereafter as a Miller-Gut plot) yield a straight line. Equation (1) rearranged into the $y = mx + b$ format yields:

$$1/C = 1/T_D M_D * D_D + (T_D + F_D) / T_D M_D \quad (2)$$

For a given moth and trap density, the greater the slope of a Miller-Gut plot, the greater is the disruption per dispenser. Moreover, when attractiveness of $T = F = D$, the inverse of this slope equals $T_D M_D$ and hence reveals M_D , when T_D is known. Furthermore, the absolute value of the *x*-intercept of a Miller-Gut plot of competitive-attraction data equals $T_D + F_D$, when attractiveness of $T = F = D$. Even more importantly, this value also equals the number of dispensers D per hectare (D/ha) required to reduce male catch by $1/2C_{\text{max}}$, under these specified conditions. Larger absolute values for *x*-intercepts equate to lower disruptive

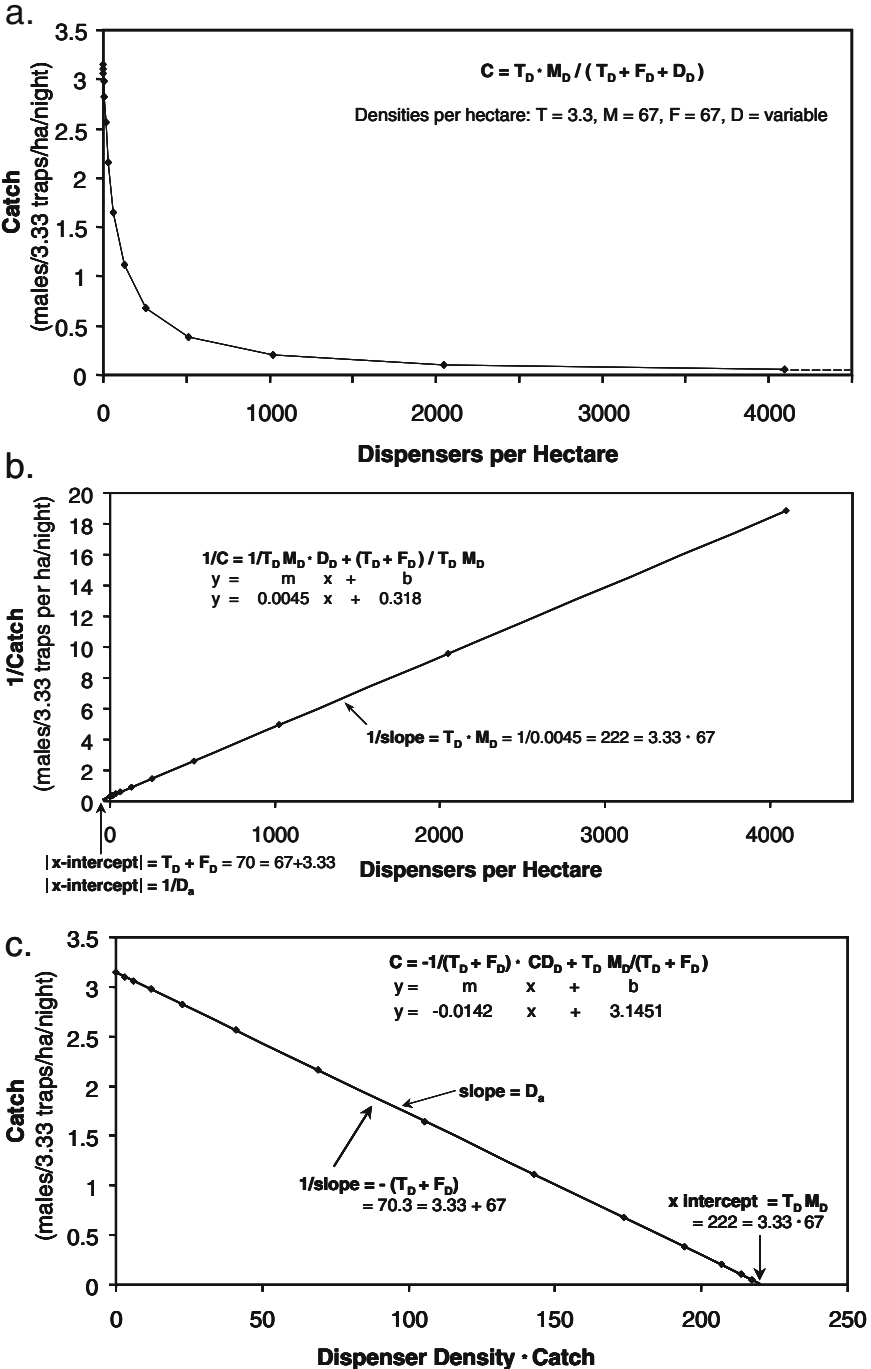


Fig. 2 Plots of a simulated communicational disruption profile for competitive attraction operating under the conditions of Fig. 1 and the assumptions given in text. (a) Untransformed plot; (b) Miller–Gut plot; (c) Miller–de Lame plot. See Table 1 for definition of abbreviations. Mathematical simulations were performed in Microsoft Excel.

potency per dispenser. The reciprocal of the absolute value of the x -intercept offers the most useful measure of disruptive activity per dispenser (D_a) expressed as the fraction of one ha over which a given dispenser would be capable of reducing catch by $1/2C_{\max}$. In Fig. 2b, $D_a = 1/70 = 0.0142$. Theoretically, each dispenser would be capable of suppressing catch in 0.042 ha (420 m²) by 50%. An increase in D_a for a given T_D and F_D reflects an increase in a dispenser's competitive attractiveness relative to the traps and females against which it was competing. D_a can be calculated variously:

$$\text{absolute value of the Miller – Gut } x\text{-intercept} = D_D \text{ yielding } 1/2 C_{\max} = 1/D_a \quad (3)$$

The x -intercept is calculated from the $y = mx + b$ equation by setting $y = 0$ and solving for x , which yields $x = y\text{-intercept}/\text{slope} = 1/D_a$. Rearrangement yields

$$D_a = \text{Miller – Gut slope} / \text{Miller – Gut } y\text{-intercept} \quad (4)$$

Substituting terms from Equation (2) yields, for the special case when attractiveness of $T = F = D$:

$$D_a = (1/T_D M_D) * T_D M_D / (T_D + F_D) = 1 / (T_D + F_D) \quad (5)$$

Under competitive attraction, we suggest that $D_{\bar{A}a}$ (dispenser application activity) become the designation for the disruptive activity of a given number of dispensers per designated area of treated crop and with each dispenser sharing a common D_a ; thus:

$$D_{\bar{A}a} = D_a * D_D \quad (6)$$

$D_{\bar{A}a}$ is unitless, since it results from multiplying ha/dispenser by dispensers/ha. Use of standard units of measure (i.e., hectare) will facilitate comparisons of disruption potencies across experiments and pest species. Substitution of $1/T_D + F_D$ from Equation (5) for D_a in Equation (6) yields:

$$D_{\bar{A}a} = D_D / (T_D + F_D) \quad (7)$$

In what we designate as a Miller-de Lame plot, male catch (C) is plotted on the y -axis against dispenser density * male catch ($D_D C$) on the x -axis. The resultant graph (Fig. 2c) yields a straight line; C_{\max} is the y -intercept, $T_D * M_D$ is the x -intercept, and the absolute value of the slope directly reveals D_a . Equation (1) can be rearranged into the $y = mx + b$ format as:

$$C = -1 / (T_D + F_D) * C D_D + T_D M_D / (T_D + F_D) \quad (8)$$

We suggest that the Miller-de Lame plot will be the more stringent test of whether actual experimental results from the field fit the theoretical predictions of competitive attraction. However, before that fit can be judged, assurance will be needed that deviation from the linear profile indicative of competitive attraction is not primarily attributable to sampling error inherent in low male catches. In field experiments, sampling error will rise as catch of males drops to tiny values because many dispensers are present. Moreover, this error will be compounded as increasingly imprecise values of C are multiplied by a swelling D_D . Thus, adherence of actual field data to a Miller-de Lame function like that of Fig. 2c is expected to deteriorate when moving from left to right on such a graph.

The principle that competitive attraction outcomes vary strongly with density of the target pest is demonstrated in Fig. 3a, as calculated under the conditions of Fig. 1 and its stated assumptions. Application of attractive pheromone sources at 50 dispensers per 72 trees of Fig. 1 predicts ca. 95% trap catch suppression for a moth population of 5 males and

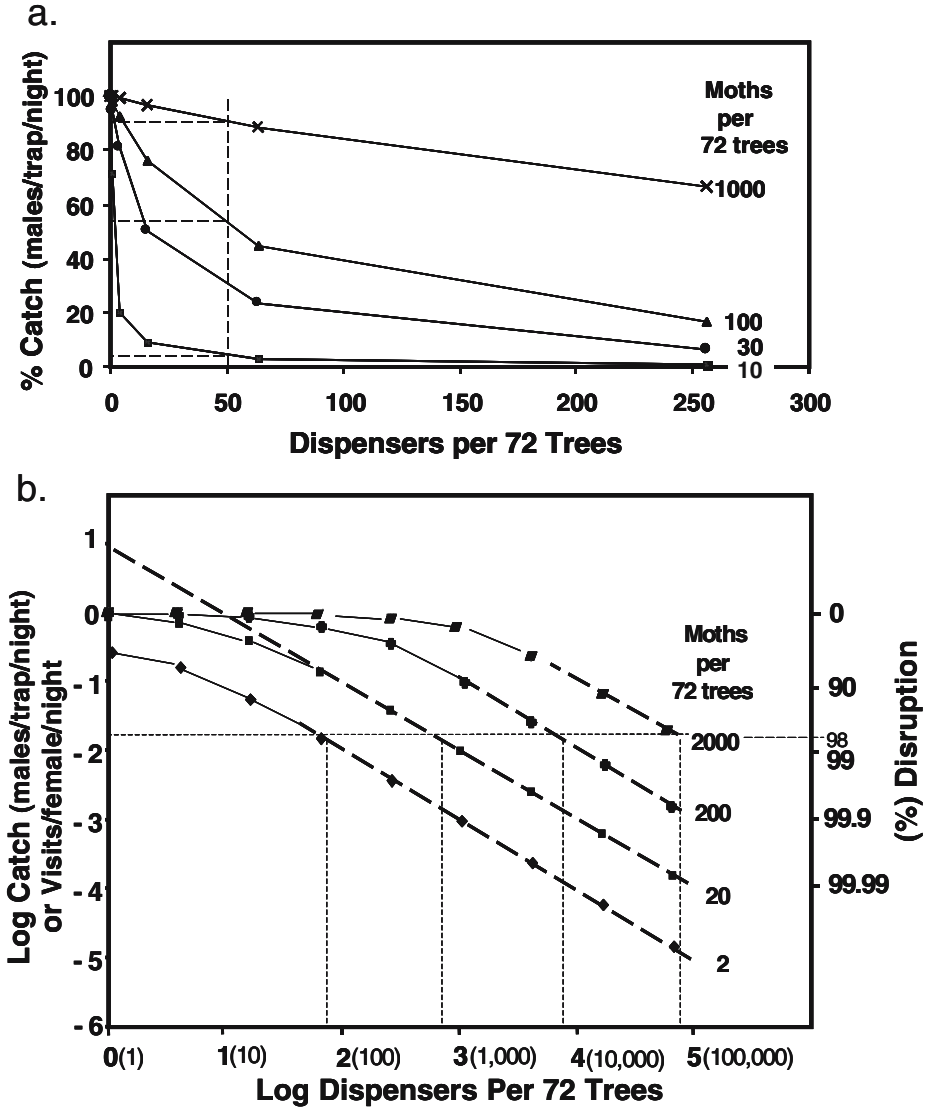


Fig. 3 Efficacy of simulated communicational disruption by competitive attraction as influenced by moth density under the conditions of Fig. 1 and its assumptions and a 1:1 sex ratio. Percent catch is expressed relative to catch in an equivalent plot not receiving pheromone dispensers. (a) Plot on untransformed axes; (b) plot on $\log_{10} \times \log_{10}$ axes; numbers within parentheses along the x -axis are the untransformed densities of pheromone dispensers.

5 females per 72 trees (Fig. 3a). However, the predicted disruption efficacy for 100 and 1000 moths per 72 trees is only ca. 45% and 10%, respectively.

A $\log_{10} \times \log_{10}$ plot of communicational disruption as a function of pheromone dispenser density displays this relationship across a wide range of pest and dispenser densities (Fig. 3b). Under competitive attraction, $\log \times \log$ plots for all pest densities become linear with a slope of negative 1 when the numbers of female moths become

inconsequential relative to the total number of attractant sources. Furthermore, the elevation (projected y -intercept) of each linear portion (bold) of the various profiles graphed in Fig. 3b reveals the density of males in the system. Conveniently, Fig. 3b also prescribes the number of dispensers required for a desired percent reduction in male visits (mating) across the various pest densities. This is accomplished by projecting a horizontal line across the graph at the desired value of percent disruption and reading out values of x at the intersections. For example, the horizontal dashed line in Fig. 3b indicates a 98% suppression of nightly male catch of males or visits per female. Values of x at the intersections along the dashed horizontal line prescribe that ca. 90, 900, and 9000 dispensers per 72 trees would be required to achieve 98% communicational disruption for moth densities of 2, 20, and 200 per 72 trees. This equates to 1.3, 12.5, and 125 dispensers per tree. These numbers are strikingly high but they are similar to the densities of traps Knipling (1979) and Roelofs et al. (1970) concluded from experimental data would be required for competitive trapping to control moth populations actually encountered in the field. Effective densities of traps proved cost-prohibitive. Fortunately, technologies are available (e.g., Miller et al., 2006) for deploying attractive pheromone dispensers at costs of materials and labor much less than required for a sticky trap.

A subset of data from Fig. 3b is displayed as a Miller-Gut plot in Fig. 4a This plot is not as immediately useful as the $\log \times \log$ plot (Fig. 3b) in prescribing dispenser densities needed for desired levels of disruption for particular pest densities. However, a distinct advantage of Miller-Gut and Miller-de Lame plots is that all data contribute to shaping a straight line, including the zero-pheromone treatment, where numbers of males caught are maximal (C_{\max}). Considering all data simultaneously maximizes precision when deriving secondary measures from each data set, such as D_a .

Inspection of Equation (5) and Fig. 4a reveals that D_a will rise as the density of calling females declines during a given moth generation. However, D_a is independent of male density. We suggest that sufficiently stable measures of D_a to permit efficacy comparisons of different disruption formulations can be obtained from tests averaging results across a full moth generation. Initial low D_a values obtained when the density of calling females is maximal will be averaged with more abundant higher D_a values from later in that generation. However, the best direct comparisons of disruption efficacy under competitive attraction will be those made with comparable moth populations, confirmed by reliable direct measurements of both male and female densities.

Simulations varying T_D , F_D , and D_D and theoretical calculations established that the x -coordinate of the point of convergence for Miller-Gut plots of varying moth densities (Fig. 4a) equals T_D (Fig. 4b), whereas the y -coordinate of the point of convergence equals $(F_D/T_D M_D)$ when $M_D = F_D$. Moreover, in simulations including no traps and where females and dispensers competed only with one another, Miller-Gut plots for male visitation rate to females under differing moth densities converged on the y -axis.

A final and the most obvious prediction of the competitive attraction model of pheromone disruption is that males approach pheromone dispensers in the field. It should be possible to document such attraction by direct visual observations, or indirectly, by trapping. The relative attractiveness of dispensers, lures, and females can be ascertained by deploying and observing them simultaneously under equivalent male populations and for equivalent times. For most experiments reported in the literature, traps collecting males operate continuously whereas females are thought to call for only part of the time that males are responsive. Such tests reveal time-averaged rather than instantaneous attraction of traps relative to females. Full understanding of attractiveness of traps vs. females will be necessary for a full interpretation of competitive-attraction data.

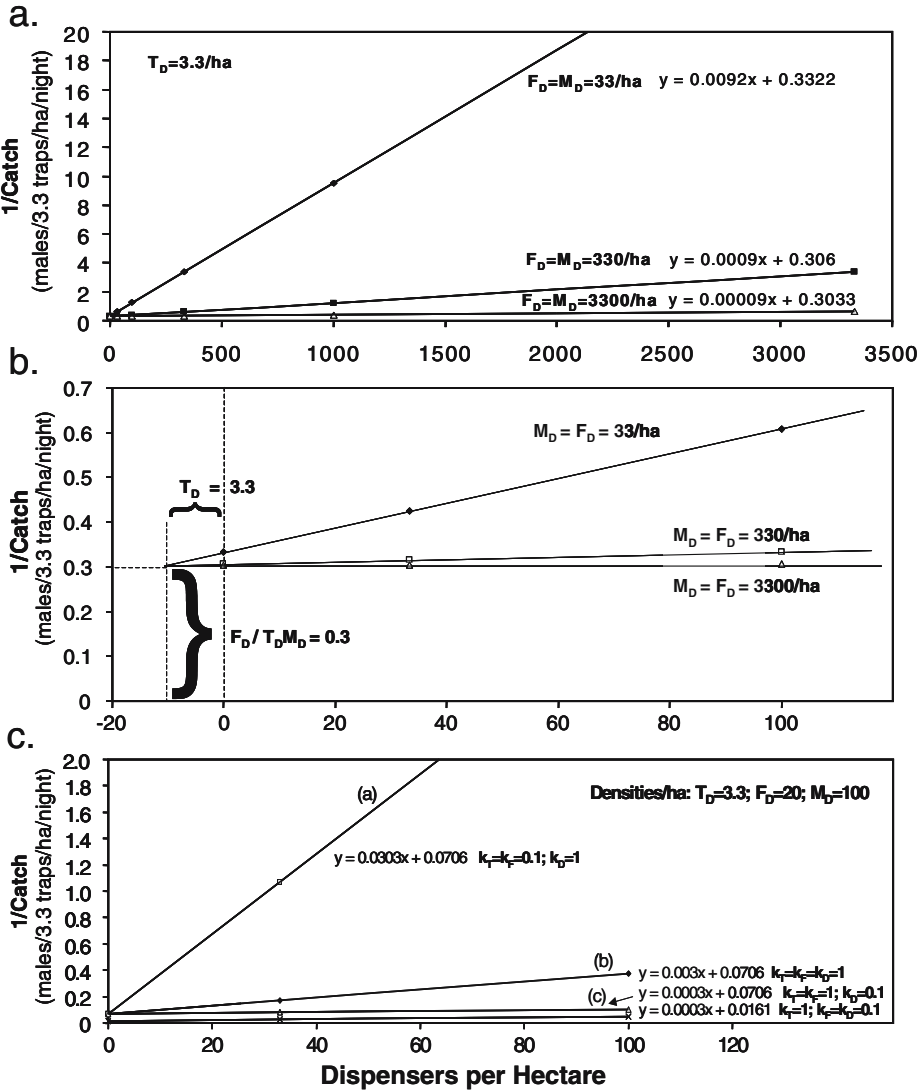


Fig. 4 Miller-Gut plots of simulated outcomes of communicational disruption by competitive attraction. (a) Influence of moth density; (b) expansion of the x - y intersection of (a); (c) influence of varying values of k_T , k_F , and k_D . See Table 1 for definition of abbreviations.

Variations from Initial Assumptions

Inequality of T , F , and D Attractiveness

Accommodating inequalities in attractiveness of pheromone point sources requires insertion of factors adjusting attraction strength into Equation (1). The expanded equation is:

$$C = k_T T_D M_D / (k_T T_D + k_F F_D + k_D D_D) \tag{9}$$

where k_T , k_F , and k_D are positive numbers representing the attractiveness of T , F , and D , respectively, relative to the most attractive of the trio, whose value is taken here as 1.0. When attractiveness of $T = F = D$, all k values equal one and drop out of the equation.

Changes in outcomes of competitive attraction due to shifts in relative attractiveness of D , F , and T can be calculated as follows. If attractiveness of D is 10-fold less than that for F and T , then $k_F = k_T = 1$, but $k_D = 0.1$. When all k values are expressed in terms of k_T , the equation becomes $C = k_T T_D M_D / (k_T T_D + k_T F_D + k_T D_D / 10) = k_T T_D M_D / k_T (T_D + F_D + 0.1 D_D) = T_D M_D / (T_D + F_D + 0.1 D_D)$. On the other hand, if attractiveness of D is 10 times greater than that of T or F , the k_T -substituted equation reduces to $C = T_D M_D / (T_D + F_D + 10 D_D)$. Effects of other changes in relative attractiveness of T , F , and D on male catch or visitation rate per female can likewise be calculated. In all cases, the graphical shape of the output remains unaltered, i.e., Miller-Gut (Fig. 4b) and Miller-de Lame plots yield straight lines (Fig. 4c). However, slopes and intercepts are shifted by alterations in k values (Fig. 4c). Values of k need to be considered when deriving values of $T_D M_D$ or $T_D + F_D$ from Miller-Gut or Miller-de Lame plots as per Fig. 2b and 2c. The following rules apply when $k_T = 1$:

$$1/\text{Miller-Gut slope} = \text{Miller-de Lame } x\text{-intercept} = T_D M_D / k_D \quad (10)$$

$$\text{Miller-Gut } x\text{-intercept} = 1/\text{Miller-de Lame slope} = -(T_D + k_F F_D) / k_D, \quad (11)$$

or when $k_T < 1$:

$$1/\text{Miller-Gut slope} = \text{Miller-de Lame } x\text{-intercept} = k_T T_D M_D k_D \quad (12)$$

$$\text{Miller-Gut } x\text{-intercept} = 1/\text{Miller-de Lame slope} = -(k_T T_D + k_F F_D) k_D \quad (13)$$

For example, the equation for graph (c) in Fig. 4c is: $y = 0.0003x + 0.0706$. It was generated from a relationship where $k_T = k_F = 1$, and $k_D = 0.1$; thus, attraction of $T = F = 10D$. Applying Equation (10), $1/\text{Miller-Gut slope} = 1/0.0003 = 3333 = T_D M_D / k_D$. This value matches (within rounding error) the expected value of 3300, where $T_D = 3.3$, $M_D = 100$, and $k_D = 0.1$, as per Fig. 4c. Applying Equation (11) to this same equation of Fig. 4c (c) yields: $\text{Miller-Gut } x\text{-intercept} = -0.0706/0.0003 = -235 = (T_D + k_F F_D) / k_D$. This value matches (within rounding error) the expected value of -233, where $T_D = 3.3$, $M_D = 100$, and $k_D = 0.1$, as per Fig. 4c. Thus, in addition to sensitivity to densities of moths and traps, slopes of transformed plots for competitive attraction data and x -intercepts are affected by the relative attractiveness of T , F , and D . When this experimentally accessible relationship is measured, densities of male and female moths can be computed with confidence from Miller-Gut or Miller-de Lame plots of experimental data.

The density of traps (T_D) in disruption protocols is usually low relative to F_D and D_D . Under this condition, altering attractiveness of T relative to F and D has negligible effect on mating disruption of female moths. However, varying the potency of the lure in a monitoring trap relative to that of F and D can markedly shift male catch. If nightly attractiveness of traps monitoring disruption efficacy exactly equaled nightly attractiveness of the average female, inhibition of male catch would be an exact proxy measure of mating disruption. When traps are more attractive than females, actual mating disruption will be under-estimated, but sampling will be more sensitive. Conversely, using monitoring traps that are less attractive than females could over-estimate the efficacy of mating disruption. Thus, knowledge of the relative attractiveness of T , F , and D is essential in order to accurately predict disruption efficacy via catch of males in traps under competitive attraction.

Raising the density of monitoring traps in a crop under disruption by competitive attraction will increase sample size and thus accuracy of the measured value for disruption.

However, mating disruption as measured by suppression of catches of males in traps deployed in disruption plots relative to control plots is not independent of trap density under competitive attraction. This is demonstrated in Fig. 5. Variation in relative inhibition of catch with varying trap density is greatest (albeit never extreme) for low moth densities and low densities of pheromone point sources. Percent disruption values shift with trap density because of inequalities in the total number of attractant sources in the control vs. treated crop. As was acknowledged above for D_a , the percent disruption measure will vary with T_D and F_D under competitive attraction. Thus, under disruption by competitive attraction, it is not surprising that discrepancies in disruption efficacy are reported for the same pest by different investigations by using a common disruption formulation but operating under different pest densities.

Multiple Attraction Events by Males per Diel Cycle

Assuming that most male moths engage in only one bout of orientation to a source of pheromone per day is an over-simplification leading to a liberal assessment of disruption efficacy in the above simulations. The effect of multiple orientations of males to pheromone sources per night can be accounted for by multiplying the above-calculated outcomes by the mean number of orientations/male/d. For example, if the average male successfully found four different pheromone sources per day, that disruption outcome is approximated by calculations as described above, but using four times the original density of males. In this example, the resultant diminution in disruption efficacy due to repeated male orientations could be offset by quadrupling the density of pheromone dispensers assuming that disruption occurs primarily by competitive attraction.

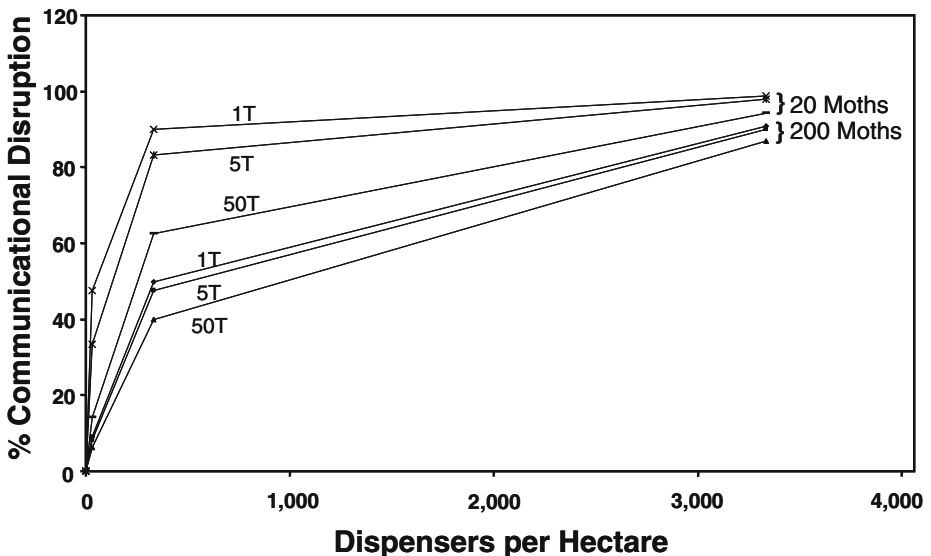


Fig. 5 Influence of trap and moth densities per hectare on simulated outcomes of communicational disruption by competitive attraction. Percent disruption in treated plots is expressed as male catch relative to that in equivalent control plots not receiving pheromone dispensers.

Variation in the Density of Females Calling

Increasing the density of calling females decreases simulated male visitation rates to a given female (Fig. 6). A similar pattern would emerge for catch of males per monitoring trap. This effect is pronounced only at low dispenser densities. During early emergence of adult moths of a given generation, the proportion of females in the population that call would be maximal and then drop as females exit the reproductive pool. A large number of females competing with traps could suppress male catch markedly in the beginning of the adult generation. The simulations in Fig. 3b suggest that, early in a moth generation, male catch could be slightly less than 1 male/trap/night for moth densities varying across 3 orders of magnitude at low pheromone dispenser densities. On a night when many females call, a catch of 1 male/trap/night indicates that every calling female would mate that night. However, as the majority of females became mated and few or none were left to call, male catch/trap/night could increase by orders of magnitude. This would result in the disruption profiles of Fig. 3b becoming increasingly linear and their actual y-intercepts would more nearly match their projected y-intercepts, i.e., the female depressive effect on male catch would be removed (Fig. 3b).

The idea that calling females can depress catch of male moths in pheromone-baited traps has been documented in the field. For example, Kehat et al. (1985) recorded a strong depressive effect of abundant virgin females on catch of *Spodoptera littoralis* males in pheromone-baited traps deployed in cotton. Catch of males was initially very low when males and virgin females began eclosing simultaneously in the crop and abundant mating pairs were directly observed. Catch in pheromone-baited traps began increasing and peaked

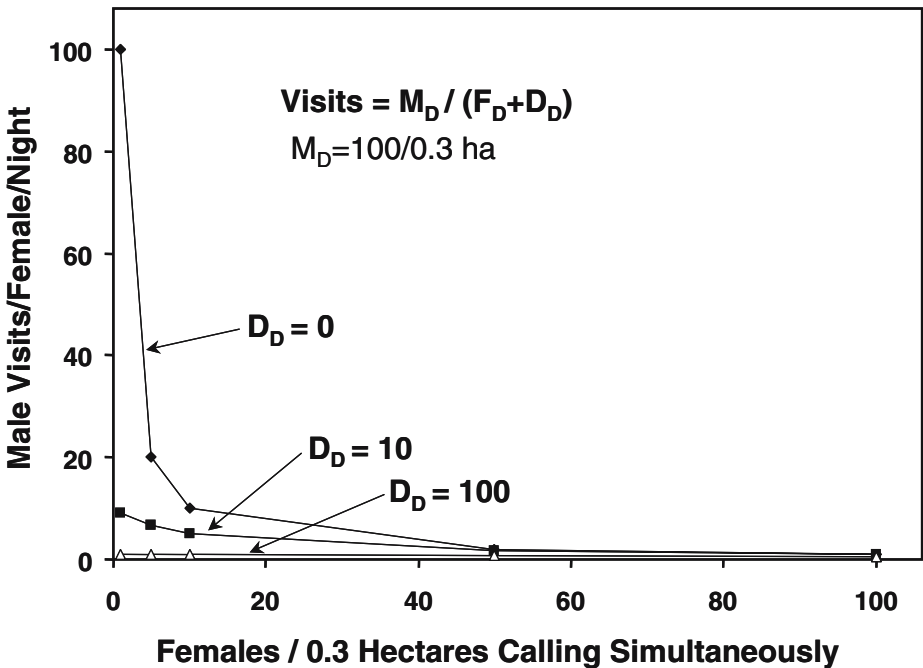


Fig. 6 Influence of dispenser and female moth densities on male visitation rates per female in simulated outcomes of disruption by competitive attraction.

5–6 after peak abundance of visible mating pairs. These authors cite similar findings for other moth species, where temporal patterns in appearance and abundance of virgin and mating moths were compared with highly resolved trapping data.

Shifting female competition for males over time may explain why catch of male moths in monitoring traps has proven to be poorly or indirectly correlated with crop damage (Knight, 1995; Gut et al., 2004). A catch of 1 male/trap/night can be obtained from the same moth population that later yields e.g., 30 males/trap/night, depending on how many females are unmated. However, the number of females mating on nights yielding catches of one or fewer males per night could have been many times higher than on nights yielding catches of 30 males/trap/night. Inconsistency between catches in pheromone monitoring traps and actual moth mating frequencies is an explicit prediction of competitive-attraction phenomena. A poor or offset relationship between male catch and crop damage can follow.

Variation in Moth Spatial Distribution

Barclay (1992) and Barclay and Judd (1995) pointed out that outcomes of competitive attraction vary depending on whether senders and receivers are regularly dispersed or clumped. Translated to the context of Fig. 1, it follows that mating would be more likely if multiple males and females were found on a given tree than when randomly distributed as in Fig. 1. Barclay (1992) explored the magnitude of this effect through simulation modeling and “found that control [by competitive attraction] would be about four times as difficult for a population that is highly clumped (k of the negative binomial distribution = 0.25) as for a regularly dispersed population.” Thus, where pests clump, the density of pheromone dispensers operating by competitive attraction will need to be increased at least several fold over the value suggested by our simulations that assumed a regular or random distribution.

Predictions of Alternative, Non-Competitive Models

The tradition of *strong inference* (Platt, 1964; Giere, 1984) recommends that researchers detail the predictions of all the alternative models potentially explaining a phenomenon and determine where the sets of predictions for explanatory models do or do not overlap. Strong tests aim at non-overlapping predictions. Although it is not feasible here to detail the predictions from all explanatory models and their combinations that might possibly contribute to pheromone disruption, we address those for which overlap in predictions is critical to valid interpretation of field data to be analyzed in the following paper (Miller et al., 2006).

Camouflage (Signal Jamming) and Its Predictions

Camouflage is proposed as the explanation for mating disruption where a calling female cannot be recognized and located by males encountering her pheromone plume because its guiding boundaries are obscured by ubiquitously present synthetic pheromone. Such a mechanism of communicational disruption seems better explained as *jamming* of the female’s signal—making it unintelligible by broadcasting signal of the same type—rather than blending it into a natural, heterogeneous background, as the term *camouflage* usually implies. Nevertheless, *camouflage* is entrenched in the literature and useful if defined. Under a pure camouflage model of pheromone disruption, males would not be attracted to pheromone dispensers. However, they would always retain the ability to orient to females

and traps that happen to emit pheromone into air not already containing a camouflaging background dosage.

It follows that each camouflaging plume released from a dispenser precludes males from finding females in that plume. If plumes from camouflaging dispensers were of average area (x) and not so dense as to overlap, then the total area of crop camouflaged (A_C) would be approximated by the linear function:

$$A_C = D_D * x. \quad (14)$$

If moths did not exit camouflaging plumes, efficacy of disruption by camouflage could be calculated as:

$$\% \text{ Disruption} = (1 - P_{\text{Auc}})100 = P_{\text{Ac}} * 100 \quad (15)$$

where P_{Auc} is defined as the proportion of total crop area that is uncamouflaged and P_{Ac} is defined as proportion of total crop area that is camouflaged. Assuming an even distribution of male and female moths, an average of 16 females and 16 males would not mate if 80% of the crop shown in Fig. 1 containing 20 male and 20 female moths were camouflaged. Assuming that the four uncamouflaged females mated with the four available males, this would yield a disruption of 80%. Female visitation rate would decrease linearly with dispenser density and disruption would be independent of moth density. Both of these predictions differ strikingly from those of competitive attraction.

Movement of female and male moths without regard to the distribution of pheromone from camouflaging dispensers is likely to diminish rather than enhance mating disruption over the situation where moths do not exit camouflaging plumes. If even brief periods in clean air resulted in successful calling, any receptive female spending a portion of her diel reproductive period outside a camouflaging plume could potentially mate. If so, the probability of remaining unmated would mirror the probability of never exiting a camouflaging plume upon successive flights. Under this scenario, efficacy of mating disruption would initially increase slowly as a function of dispenser density and then increase dramatically as plume coverage approached 100%. Such a disruption profile differs dramatically from that predicted for competitive attraction (Fig. 2a).

Temporarily invoking mixed explanatory models, disruption efficacy could be dramatically inferior to that predicted by Equation (15) if virgin females were repelled or deterred from calling by plumes from camouflaging dispensers. On the other hand, disruption efficacy would be enhanced if males were attracted into and remained within camouflaging plumes, while females aggregated outside camouflaging plumes. Here, competitive attraction would again be a major component of that overall phenomenon.

Quantitative Contrast of Predictions of Competitive Attraction vs. Camouflage

The above discussion suggests that mating disruption by camouflage generates a set of predictions different from that of competitive attraction. Explanations involving moth movement (but not attraction) diverge even further from the predictions of competitive attraction than does Equation (15). Thus, Equation (15) was selected for further contrast with competitive-attraction predictions of Equation (9), so as to differentiate among them quantitatively.

Adding traps into crops disrupted by camouflage so as to measure mating disruption injects a small element of competitive attraction. This causes a male-catch measure of disruption to vary somewhat with moth density. Males not camouflaged can respond either to females or to traps that are not camouflaged. Thus, for trapping data, the camouflage

equation needs to be modified to reduce male visitation rate to females by a proportion attributable to that absorbed on average by the trap used to measure the experimental outcome. This adjustment can be made as follows where $V_{/F}$ represents male visits/female/night and A the total crop area:

$$V_{/F} = M_D / (F_D + T_D) (A - A_c) \quad (16)$$

We simulated camouflage outcomes by two methods applied to Fig. 1. First, Equation (16) was employed after the proportion of Fig. 1 that was camouflaged was calculated by multiplying the measured area of one dispenser plume by the number of plumes to be overlaid and then subtracting the product from total crop area. Second, the proportion of area not covered in Fig. 1 by the various densities of plumes was measured experimentally, before invoking Equation (16). Using Microsoft PowerPoint™, varying densities of dispenser plumes were overlaid in a regular pattern onto the 72-tree orchard plot of Fig. 1, while minimizing plume overlaps. Areas covered by plumes from dispensers were blackened, whereas uncovered areas remained white. The percentage of total area that was white vs. black in each treatment picture so generated was quantified by using Scion Image™ software (National Institute of Standards and Technology, Gaithersburg, MD, USA; <http://www.nist.gov/lispix/imlab/>).

Outcomes of our first approach to camouflage simulations are compared in Fig. 7 with those for competitive attraction when both moth and dispenser density were variables. Camouflage profiles fell linearly with increasing dispenser density (Fig. 7a); the reduced slopes with reduced moth densities reflect the competitive effect of the monitoring trap. A similar outcome resulted from the overlay simulations (hence data not shown). However, beyond the highest dispenser densities of Fig. 7a, appreciable overlap of plumes was unavoidable. The effect was that additional crop coverage per added dispenser progressively declined. It was difficult to blot out the last vestiges of white from Fig. 1 even when 200 plumes were overlaid with the restriction that they must originate from a tree and not the aisles between rows of trees. Thus, both camouflage and competitive attraction simulations approached 100% disruption asymptotically.

We caution that experimental proof of an asymptotic profile for camouflage is required before much weight can be placed upon pictorial over-lay simulations. We have little confidence that pheromone dispersal can be approximated by such elementary modeling. It seems likely that turbulence and diffusion would homogenize pheromone distribution within the crop over time, particularly if fields were large and dispenser densities were high. Moreover, the simulations were conducted in two- rather than three-dimensional space. To disappear from the crop, pheromone would need to rise above the treated crop, exit from field edges, or be irreversibly absorbed or degraded. Alternatively, pheromone molecules could reversibly become adsorbed on solid surfaces (Karg et al., 1994; Gut et al., 2004), allowing buildup of pheromone to some above-threshold steady-state. Thus, camouflage should result in total communicational disruption. So, where moth densities were high and sample sizes robust, a linear or near-linear descent of a disruption profile to zero male visits per trap or female can be taken as strong evidence for one of the noncompetitive disruption mechanisms, like camouflage. Such a profile is inconsistent with competitive attraction. However, until the ambiguity is removed as to whether or not plumes from point-source dispensers of pheromone do or do not become spatially homogenized over time, an asymptotic approach of disruption profiles toward an efficacy of 100% cannot be used as a criterion to unequivocally differentiate between competitive vs. noncompetitive disruption mechanisms.

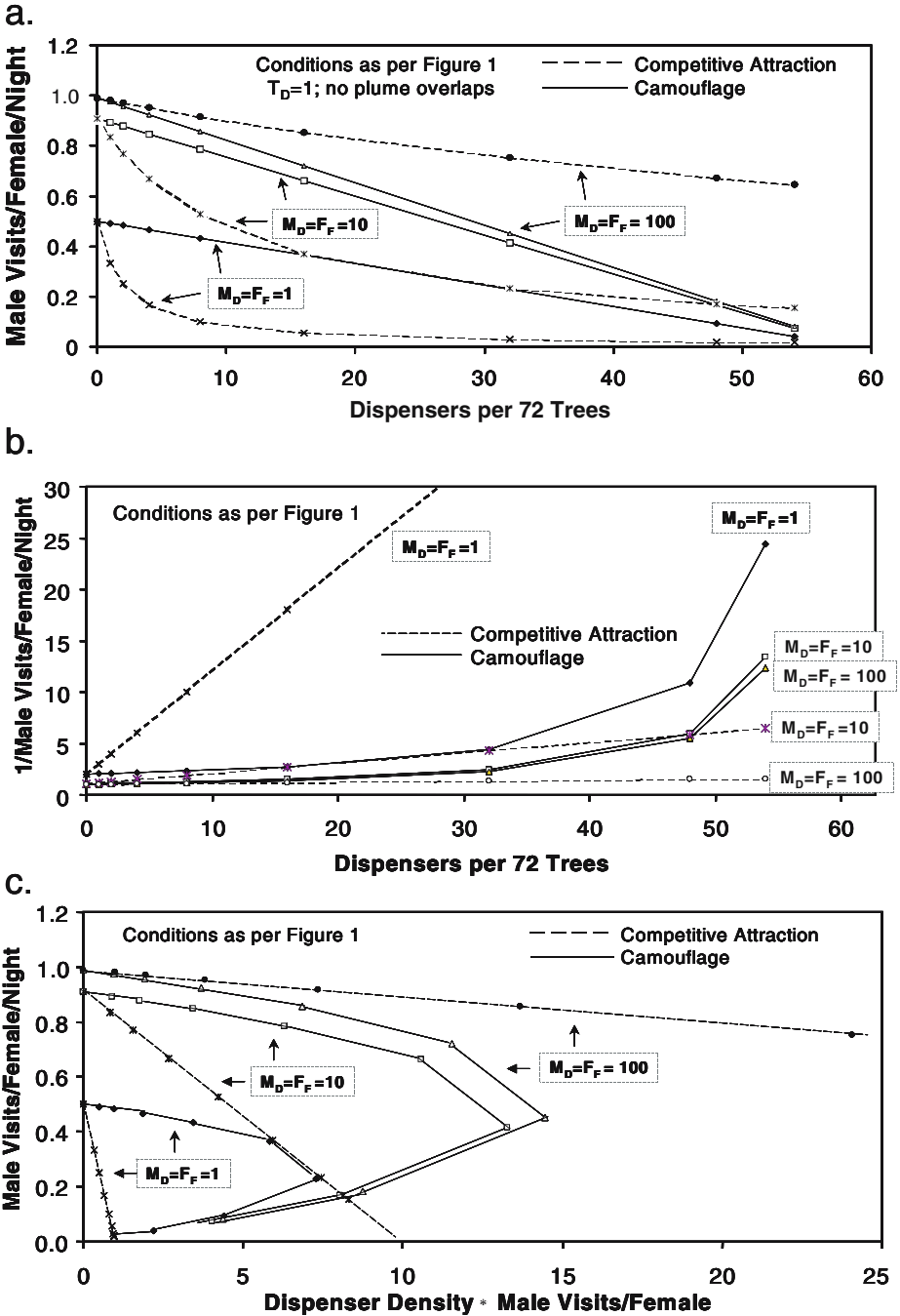


Fig. 7 Comparison of dosage–response profiles for simulated communicational disruption outcomes mediated by competitive attraction vs. camouflage. Plot types are (a) untransformed; (b) Miller–Gut; and (c) Miller–de Lame. In (b), outcomes for the lower two camouflage plots fall mostly on top of one another.

Nevertheless, Fig. 7 offers other distinctive predictions for such differentiation. The high sensitivity of competitive attraction outcomes to pest density has already been emphasized. With successive increases in moth density, disruption profiles become increasingly less concave on graphical plots (Figs. 3a and 7a). In contrast, the shape of camouflage profiles of catches of males in traps changes only slightly when moth densities are appreciable (Fig. 7a). The greatest influence of moth density on male visits/female/d in the Fig. 7a simulations occurred at the extreme of only one female competing with one trap. As the density of female moths increased, presence of a trap had progressively less influence on measured outcome. It is important to recognize that relative efficacy of communicational disruption operating by camouflage would not be influenced by pest density if pheromone dispensers were completely unattractive and no monitoring traps were inserted into the system. This is yet another case where applying an instrument (attractive trap) for measuring the performance of a system slightly alters the system.

Under extremely high pest densities, the predictions of competitive attraction and camouflage by large plumes become increasingly similar (Fig. 7a). Furthermore, simulations suggest camouflage would out-perform competitive attraction at high dispenser and pest densities. At very high pest densities, it is also possible that male and female moths may begin finding one another by non-chemical means (e.g., visual search; Levinson and Hoppe, 1983), further blurring interpretation of disruption mechanisms. If data analysis were limited only to untransformed plots like Fig. 7a, differentiation of camouflage vs. competitive attraction mechanisms would be best achieved at low pest and low dispenser densities.

Simulated camouflage and competitive-attraction outcomes were compared by using both Miller-Gut (Fig. 7b) and Miller-de Lame (Fig. 7c) plots in preparation for pattern recognition during comparisons of disruption data from the field (Miller et al., 2006) with data from simulations. A key distinction between mechanism classes is that competitive attraction yields straight lines on both types of secondary plots, whereas camouflage yields concave profiles on Miller-Gut plots (Fig. 7b) and distinctively recurved profiles on Miller-de Lame plots (Fig. 7c). Mathematical simulations confirmed a general rule that, when D_D causes a linear decrease in C , the maximum $D_D C$ for plots of C vs. $D_D C$ always equals $\frac{1}{2}C_{\max}$. This is because $D_D C$ values are being generated by the quadratic equation— $D_D C = -mD_D^2 + C_{\max}D_D$ —resulting from substituting $-mD_D + C_{\max}$ for C in the equation $y = CD_D$. Quadratic equations always yield symmetrical plots with their maximum midway between their intercepts, in this case 0 and C_{\max} .

Finally, the most direct way to differentiate whether camouflage or competitive-attraction mechanisms of disruption are operating under field conditions is to observe whether males orient to and closely approach pheromone sources. Such occurrences are inconsistent with pure camouflage, but are required by competitive attraction. However, experimenters would need to guard against false negatives. Under a high density of pheromone dispensers and a moderate pest density, the probability that males would be attracted to a dispenser under observation is low for competitive attraction. However, overall visitation rate to this type of source could be high when considering all such dispensers. Observational time required to acquire strong evidence either for or against competitive attraction or camouflage by directly observing occurrence or absence of orientations by male moths would be equally great.

Desensitization and Its Predictions

We take *desensitization* to mean that synthetic sex pheromone released from point sources in a crop causes male moths exposed to the pheromone to become less sensitive and/or less

responsive than they normally would be to female-produced pheromonal signals or their equivalents. Adaptation of olfactory receptor neurons of male moths can occur following continuous exposure of antennae to pheromone (Kuenen and Baker, 1981; Baker et al., 1988, 1989). This phenomenon is dosage-dependent, but reversible in pheromone-free air. A “long-lasting” adaptation has been described for several moth species (Kaisling, 1986; Stelinski et al., 2003a,b; Judd et al., 2005); it lasts for 10 to >60 min after the removal of moths from air containing high concentrations of pheromone. Pre-exposure to continuous or pulsed pheromone can decrease behavioral responsiveness to normal pheromone signals in many moth species (Bartell and Roelofs, 1973; Bartell and Lawrence, 1976; Sanders, 1985; Rumbo and Vickers, 1997; Daly and Figueredo, 2000). These behavioral modifications after exposure to volatilized pheromone last much longer than antennal adaptation, suggesting habituation (Bartell and Roelofs, 1973; Figueredo and Baker, 1992; Rumbo and Vickers, 1997; Stelinski et al., 2003a,b; Judd et al., 2005).

Despite the considerable attention desensitization has received as a candidate for explaining mating disruption, there is substantial evidence in the literature against it. The major inconsistency is that effective mating disruption occurs in crops at pheromone concentrations much lower than those required for desensitizing moths by adaptation or habituation (Schmitz et al., 1997; Rumbo and Vickers, 1997; Judd et al., 2005). Such data suggest that desensitization is not a leading contributor to mating disruption. For example, male grapevine moths (*Lobesia botrana*) were able to find pheromone-baited traps in the field following 8 hr of confinement in vineyards treated with mating disruption dispensers (1 dispenser/5 m²; each dispenser contained 500 mg of (E7,Z9)-dodecadienyl acetate; Schmitz et al., 1997). Reduction in the numbers of males captured in optimized pheromone traps in the field was obtained only when males were pre-exposed in the laboratory to pheromone at 4 µg/l air. This concentration vastly exceeds the average airborne concentration of pheromone (1–2 ng/m³) achieved in a crop treated with hand-applied mating disruption dispensers (Koch et al., 1997, 2002). In another example, reduction of male oriental fruit moth (*Grapholita molesta*) captures in optimized monitoring traps in the field occurred only after 1 hr of laboratory exposure to pheromone at 65 µg/m³ (3200 female equivalents/m³) (Rumbo and Vickers, 1997). Again, this high atmospheric concentration of pheromone required to desensitize *G. molesta* males far exceeded that achieved under typical mating disruption conditions in the field plots.

Long-lasting peripheral desensitization in obliquebanded leafroller (*C. rosaceana*) occurred only after minutes-long confinement in the laboratory in containers with pheromone concentrations of at least 1 ng/ml, or in the field after 1 d of confinement a few centimeters from polyethylene tube dispensers (Stelinski et al., 2003b). Given that feral *C. rosaceana*, *A. velutinana*, *G. molesta*, and *C. pomonella* approach and remain near such pheromone dispensers for only ca. 30 sec in apple trees (Stelinski et al., 2004a, 2005a), it is unlikely that this level of pheromone exposure is sufficient to induce long-lasting adaptation.

Nevertheless, key predictions of the desensitization model of mating disruption are: (1) efficacy should increase with dosage of pheromone released and thoroughness of coverage; (2) compared to that for competitive attraction, efficacy for desensitization would be relatively independent of pest density at low to moderate pest populations for reasons identical to those presented above for camouflage; and (3) the overall frequency with which male moths are observed orienting toward pheromone point sources in disruption plots would be greatly reduced relative to responses to similar sources in plots not treated with pheromone. Under increasing dispenser densities, male moths would have commensurately less chance to find pheromone-free spaces where they could recover normal sensory and behavioral capability. Thus, at high dispenser densities, disruption profiles for desensiti-

Table 2 Distinguishing traits of the two major categories of mating-disruption mechanisms

Trait	Competitive ^a	Non-competitive ^b
Shape of disruption profiles	Concave profile on untransformed plot; straight line with positive slope on M–G ^c plot; straight line with negative slope on M–de L ^d plot	Straight line on untransformed plot; concave profile on M–G plot; recurved profile on M–de L plot ^e
Convergence of efficacy profiles	Converge at coordinates $-T_D$, $+(F_D/T_D)$ (M_D) on M–G plot when attractiveness of $T = F = D$	No regular pattern of convergence on M–G plots
Influence of pest population on disruption efficacy	Strong	Little to none except when pest density rises to where mate-finding is possible without long-range pheromone
Sensitivity to plume size	Efficacy not highly sensitive to plume size so long as plume size for $T = F = D$	Efficacy directly proportional to plume size

^a Competitive attraction.

^b Includes camouflage, desensitization (adaptation; habituation), and sensory imbalance.

^c Miller–Gut plot = 1/catch on y-axis vs. dispenser density on x-axis.

^d Miller–de Lame plot = male catch on y-axis vs. dispenser density * catch on x-axis.

^e Certain types of non-competitive disruption are possible that deviate from these given predictions in ways that make them more dissimilar to the predictions of competitive attraction.

zation could drop even faster than those for camouflage. Such profiles should reach 100% efficacy at high densities of pheromone point sources.

Sensory Imbalance and Its Predictions

Sensory imbalance (Bartell, 1982; Flint and Merkle, 1983) is defined here as *disrupting mate-finding not via adaptation or habituation but by interfering with the male's ability to perceive (as opposed to receive) the normal sensory inputs associated with their species' sex pheromone*. For example, dispensing only one of the major components of a pheromone blend from dispensers could adulterate the normal blend of a female's plume that commingles with the dispenser plume, rendering her plume unrecognizable to males. Sensory imbalance shares the above predictions for desensitization.

Combinations of Explanatory Models

Until now, this paper has emphasized non-overlapping explanatory models. However, we recognize that, for moths under field conditions, these mechanisms may come into play sequentially or in combinations. For example, competitive attraction may bring males close to dispensers where desensitization might occur for certain pests. Thus, in evaluating actual field data, care needs to be taken to recognize patterns in outcomes indicative of single mechanisms acting alone, as well as multiple mechanisms perhaps acting sequentially or concurrently.

Conclusions

This analysis revealed that mating disruption by competitive attraction operates predominantly by division; the attention of males is literally divided between a given

female and nearby dispensers. On the other hand, non-competitive disruption operates predominantly by subtraction; moths in effectively treated areas of crop are literally subtracted from the total pool. Key traits useful in differentiating between these mechanisms are summarized in Table 2. They will be used to judge which category of mechanism is supported by actual experimental disruption profiles from the pheromone literature (Miller et al., 2006).

Acknowledgments We thank Travis Reed for technical assistance during simulations of camouflage using pictorial overlays, checking many of the calculations in this manuscript, and for manuscript editing. Others who improved this and the following manuscript were: Michael Miller, George Rothschild, Julia Letoutchaia, Rufus Isaacs, Alex Il'ichev, Wendell Roelofs, Sonny Ramaswamy, Piera Giroux, Juan Huang, David Epstein, and Peter McGhee.

References

- AGNELLO, A. M., RESSIG, W. H., SPANGLER, S. M., CHARLTON, R. E., and KAIN, D. P. 1996. Trap response and fruit damage by obliquebanded leafroller (Lepidoptera: Tortricidae) in pheromone-treated apple orchards in New York. *Environ. Entomol.* 25:268–282.
- BAKER, T. C., HANSSON, B. S., LÖFSTEDT, C., and LÖFQVIST, J. 1988. Adaptation of antennal neurons in moths associated with cessation of pheromone mediated upwind flight. *Proc. Natl. Acad. Sci. USA* 85:9826–9830.
- BAKER, T. C., HANSSON, B. S., LÖFSTEDT, C., and LÖFQVIST, J. 1989. Adaptation of male moth antennal neurons in a pheromone plume is associated with cessation of pheromone-mediated flight. *Chem. Senses* 14:439–448.
- BALKAN, J. A. 1980. Microcapsulation using coacervation/phase separation techniques, pp. 83–105, in A. E. Kydonius (ed.). *Controlled Release Technologies: Methods and Applications*, Vol. II. CRC Press, Boca Raton, FL.
- BARCLAY, H. J. 1992. Modeling the effects of population aggregation on the efficiency of insect pest control. *Res. Popul. Ecol.* 34:131–141.
- BARCLAY, H. J. and JUDD, G. J. R. 1995. Models for mating disruption by means of pheromone for insect control. *Res. Popul. Ecol.* 37:239–247.
- BARRETT, B. 1995. Effect of synthetic pheromone permeation on captures of male codling moth (Lepidoptera: Tortricidae) in pheromone and virgin female moth-baited traps at different tree heights in small orchard blocks. *Environ. Entomol.* 24:1201–1206.
- BARTELL, R. J. 1982. Mechanisms of communication disruption by pheromones in control of Lepidoptera: A review. *Physiol. Entomol.* 7:353–364.
- BARTELL, R. J. and ROELOFS, W. L. 1973. Inhibition of sexual response in males of the moth *Argyrotaenia velutinana* by brief exposures to synthetic pheromone and its geometric isomer. *J. Insect Physiol.* 19:655–661.
- BARTELL, R. J. and LAWRENCE, L. A. 1976. Reduction in responsiveness of *Epiphyas postvittana* (Lepidoptera) to sex pheromone following pulsed pre-exposure to pheromone components. *Physiol. Entomol.* 2:89–95.
- CARDÉ, R. T. 1990. Principles of mating disruption, pp. 47–71, in R. L. Ridgway and R. M. Silverstein (eds.). *Behavior-Modifying Chemicals for Pest Management: Applications of Pheromones and Other Attractants*. Marcel Dekker, New York.
- CARDÉ, R. T. and MINKS, A. K. 1995. Control of moth pests by mating disruption: Successes and constraints. *Annu. Rev. Entomol.* 40:559–585.
- CARDÉ, R. T., STATEN, R. T., and MAFRA-NETO, A. 1998. Behavior of pink bollworm males near high-dose, point sources of pheromone in field wind tunnels: Insights into mechanisms of mating disruption. *Entomol. Exp. Appl.* 89:35–46.
- DALY, K. C. and FIGUEREDO, A. J. 2000. Habituation of sexual response in male *Heliothis* moths. *Physiol. Entomol.* 25:180–191.
- DOANE, C. C. and BROOKS, T. W. 1981. Research and development of pheromones for insect control with emphasis on the pink bollworm, pp. 285–303, in E. R. Mitchell (ed.). *Management of Insect Pests with Semiochemicals: Concepts and Practice*. Plenum, New York.

- EVENDEN, M. L., JUDD, G. J. R., and BORDEN, J. H. 1999. Mating disruption of two sympatric, orchard inhabiting tortricids, *Choristoneura rosaceana* and *Pandemis limitata* (Lepidoptera: Tortricidae), with pheromone components of both species' blends. *J. Econ. Entomol.* 92:380–390.
- EVENDEN, M. L., JUDD, G. J. R., and BORDEN, J. H. 2000. Investigations of mechanisms of pheromone communication disruption of *Choristoneura rosaceana* (Harris) in a wind tunnel. *J. Insect Behav.* 13:499–510.
- FIGUEREDO, A. J. and BAKER, T. C. 1992. Reduction of the response to sex pheromone in the oriental fruit moth, *Grapholita molesta* (Lepidoptera: Tortricidae) following successive pheromonal exposures. *J. Insect Behav.* 5:347–362.
- FLINT, H. M. and MERKLE, J. R. 1983. Pink bollworm (Lepidoptera : Gelechiidae) communication disruption by pheromone composition imbalance. *J. Econ. Entomol.* 76:40–46.
- GIERE, R. N. 1984. Understanding Scientific Reasoning. Holt, Reinhart, and Winston, New York.
- GUT, L. J., STELINSKI, L. L., THOMPSON, D. R., and MILLER, J. R. 2004. Behaviour-modifying chemicals: Prospects and constraints in IPM, pp. 73–121, in O. Koul, G. S. Dhaliwal, and G. W. Cuperus (eds.). Integrated Pest Management: Potential, Constraints, and Challenges. CABI Publishing, Cambridge, MA.
- HARDEE, D. D., CROSS, W. H., and MITCHELL, E. B. 1969. Biological factors influencing responses of the female boll weevil to the male sex pheromone in field and large-cage tests. *J. Econ. Entomol.* 62:161–165.
- JONES, V. P. and AIHARA-SASAKI, M. 2001. Demographic analysis of delayed mating in mating disruption: A case study with *Cryptophlebia illepidia* (Lepidoptera: Tortricidae). *J. Econ. Entomol.* 94:785–792.
- JUDD, G. J. R., GARDINER, M. G. T., DELURY, N. C., and KARG, G. 2005. Reduced sensitivity, behavioral response, and attraction of male codling moths, *Cydia pomonella*, to their pheromone (*E,E*)-8,10-dodecadien-1-ol following various pre-exposure regimes. *Entomol. Exp. Appl.* 114:65–78.
- KAISSLING, K. E. 1986. Temporal characteristics of pheromone receptor cell responses in relation to orientation behaviour of moths, pp. 193–200, in T. L. Payne, M. C. Birch, and C. E. J. Kennedy (eds.). Mechanisms in Insect Olfaction. Clarendon Press, Oxford.
- KARG, G., SUCKLING, M. D., and BRADLEY, S. J. 1994. Adsorption and release of pheromone of *Epiphyas postvittana* (Lepidoptera: Tortricidae) by apple leaves. *J. Chem. Ecol.* 20:1825–1841.
- KEHAT, M., GOTHILF, S., DUNKELBLUM, E., BAR-SHAVIT, N., and GORDON, D. 1985. Night observations on the cotton leafworm, *Spodoptera littoralis*: Reliability of pheromone traps for population assessment and efficacy of widely separated pheromone dispensers for mating disruption. *Phytoparasitica* 13:215–220.
- KNIGHT, A. L. 1995. The impact of codling moth (Lepidoptera : Tortricidae) mating disruption on apple management in Yakima Valley, Washington. *J. Entomol. Soc. B.C.* 92:29–38.
- KNIGHT, A. L. 1997. Delay of mating of codling moth in pheromone disrupted orchards. *IOBC/WPRS Bull.* 20:203–206.
- KNIGHT, A. L., THOMPSON, D. R., and COCKFIELD, S. D. 1998. Developing mating disruption of obliquebanded leafroller (Lepidoptera: Tortricidae) in Washington State. *Environ. Entomol.* 27:1080–1088.
- KNIPLING, E. F. 1979. The Basic Principles of Insect Population Suppression and Management. Agric. Handbook No. 512, USDA, Washington, DC.
- KOCH, U. T., LÜDER, W., CLEMENZ, S., and CICHON, L. I. 1997. Pheromone measurement by field EAG in apple orchards. *IOBC/WPRS Bull.* 20:181–190.
- KOCH, U. T., CARDÉ, A. M., and CARDÉ, R. T. 2002. Calibration of an EAG system to measure airborne concentration of pheromone formulated for mating disruption of the pink bollworm moth, *Pectinophora gossypiella* (Saunders (Lep., Gelechiidae)). *J. Appl. Entomol.* 126:431–435.
- KUENEN, L. P. S. and BAKER, T. C. 1981. Habituation versus sensory adaptation as the cause of reduced attraction following pulsed and constant sex pheromone pre-exposure in *Trichoplusia ni*. *J. Insect Physiol.* 27:721–726.
- LAWSON, D. S., REISSIG, W. H., AGNELLO, A. M., NYROP, J. P., and ROELOFS, W. L. 1996. Interference with the mate-finding communication system of the obliquebanded leafroller (Lepidoptera: Tortricidae) using synthetic sex pheromones. *Environ. Entomol.* 25:895–905.
- LEVINSON, H. Z. and HOPPE, T. 1983. Preferential flight of *Plodia interpunctella* and *Cadra cautella* (Phycitinae) toward definite shape and position with notes on the interaction between optical and pheromone stimuli. *Angew. Entomol.* 96:491–500.
- MAINI, S. and ACCINELLI, G. 2000. Mating disruption–confusion method and sexual distraction: Comparison among different dispenser types for *Cydia molesta* (Busck) (Lepidoptera: Tortricidae). *Boll. Ist. Ent. G. Grandi Univ. Bologna* 54:113–122.
- MAINI, E. and SCHWALLER, R. 1992. Results of 12 years experience to control codling moth, *Cydia pomonella* L. by mating disruption. *IOBC/WPRS Bull.* 15:76–80.
- MERTINS, J. W., COPPEL, H. C., and KARANDINOS, M. G. 1967. Potential for suppression of *Diprion similes* (Hymenoptera: Diprionidae) with pheromone trapping: A population model. *Res. Popul. Ecol.* 17:77–84.

- MILLER, J. R. and STRICKLER, K. L. 1984. Finding and accepting host plants, pp. 127–157, in W. J. Bell and R. T. Cardé (eds.). *Chemical Ecology of Insects*. Chapman and Hall, New York.
- MILLER, J. R., GUT, L. J., DE LAME, F. M., and STELINSKI, L. L. 2006. Differentiation of competitive vs. non-competitive mechanisms mediating disruption of moth sexual communication by point sources of sex pheromone: (Part 2) case studies. *J. Chem. Ecol.*, this issue.
- MINKS, A. K. and CARDÉ, R. T. 1988. Disruption of pheromone communication in moths: Is the natural blend really most efficacious? *Entomol. Exp. Appl.* 49:25–36.
- NAGATA, K. 1989. Review: Pest control by mating disruption in Japan. *Jpn. Pestic. Inf.* 54:3–6.
- NAKASUJI, F. and FUJITA, K. 1980. A population model to assess the effect of sex pheromones on population suppression. *Appl. Entomol. Zool.* 15:27–35.
- NOVAK, M. A. and ROELOFS, W. L. 1985. Behavior of male redbanded leafroller moth, *Argyrotaenia velutinana* (Lepidoptera: Tortricidae), in small disruption plots. *Environ. Entomol.* 14:12–16.
- PLATT, J. R. 1964. Strong inference. *Science* 146:347–353.
- RICE, R. E. and KIRSCH, P. 1990. Mating disruption of oriental fruit moth in the United States, pp. 193–211, in R. L. Ridgeway, R. M. Silverstein, and M. N. Inscoe (eds.). *Behavior-Modifying Chemicals for Insect Management*. Marcel Dekker, New York.
- ROELOFS, W. L. and NOVAK, M. 1981. Small-plot disorientation tests for screening potential mating disruptants, pp. 229–242, in E. R. Mitchell (ed.). *Management of Insect Pests with Semiochemicals: Concepts and Practice*. Plenum, New York.
- ROELOFS, W. L., GLASS, E. H., TETTE, J., and COMEAU, A. 1970. Sex pheromone trapping for red-banded leafroller control: Theoretical and actual. *J. Econ. Entomol.* 63:1162–1167.
- ROTHSCHILD, G. H. L. 1975. Control of oriental fruit moth (*Cydia molesta*) (Busck) (Lepidoptera: Tortricidae) with synthetic female pheromone. *Bull. Entomol. Res.* 65:473–490.
- ROTHSCHILD, G. H. L. 1981. Mating disruption of lepidopterous pests: Current status and future prospects, pp. 201–228, in E. R. Mitchell (ed.). *Management of Insect Pests with Semiochemicals: Concepts and Practice*. Plenum, New York.
- RUMBO, E. R. and VICKERS, R. A. 1997. Prolonged adaptation as possible mating disruption mechanism in Oriental fruit moth, *Cydia* (= *Grapholita*) *molesta*. *J. Chem. Ecol.* 23:445–457.
- SANDERS, C. J. 1985. Disruption of spruce budworm (Lepidoptera: Tortricidae) mating in a wind tunnel by synthetic pheromone; role of habituation. *Can. Entomol.* 117:391–393.
- SCHMITZ, V., RENOU, M., ROEHRICH, R., STOCKEL, J., and LECHARPENTIER, P. 1997. Disruption mechanisms in the European grape moth *Lobesia botrana* Den & Schiff. III. Sensory adaptation and habituation. *J. Chem. Ecol.* 23:83–95.
- SEABROOK, W. D. and KIPP, L. R. 1986. The use of a two component blend of the spruce budworm sex pheromone for mating suppression, pp. 128–129, in I. A. Chaudry and C. Thies (eds.). *Proceedings, 13th International Symposium on Controlled Release of Biorational Materials*. Norfolk, Virginia.
- STELINSKI, L. L., MILLER, J. R., and GUT, L. J. 2003a. Presence of long-lasting peripheral adaptation in the obliquebanded leafroller, *Choristoneura rosaceana* and absence of such adaptation in the redbanded leafroller, *Argyrotaenia velutinana*. *J. Chem. Ecol.* 29:405–423.
- STELINSKI, L. L., GUT, L. J., and MILLER, J. R. 2003b. Concentration of air-borne pheromone required for long-lasting peripheral adaptation in the obliquebanded leafroller, *Choristoneura rosaceana*. *Physiol. Entomol.* 28:97–107.
- STELINSKI, L. L., GUT, L. J., PIERZCHALA, A. V., and MILLER, J. R. 2004a. Field observations quantifying attraction of four tortricid moth species to high-dosage pheromone rope dispensers in untreated and pheromone-treated apple orchards. *Entomol. Exp. Appl.* 113:187–196.
- STELINSKI, L. L., VOGEL, K. J., GUT, L. J., and MILLER, J. R. 2004b. Behaviors of naïve and pheromone pre-exposed leafroller moths in plumes of high-dose pheromone dispensers in a sustained-flight wind tunnel: Implications for pheromone-based mating disruption of these species. *J. Insect Behav.* 17:533–554.
- STELINSKI, L. L., MILLER, J. R., and GUT, L. J. 2005a. Captures of two leafroller moth species in traps baited with varying dosages of pheromone lures or commercial mating-disruption dispensers in untreated and pheromone-treated orchard plots. *Can. Entomol.* 137:98–109.
- STELINSKI, L. L., GUT, L. J., EPSTEIN, D., and MILLER, J. R. 2005b. Attraction of four tortricid moth species to high dosage pheromone rope dispensers: Observations implicating false plume following as an important factor in mating disruption. *IOBC/WPRS Bull.* 28:313–317.
- SUCKLING, D. M., DALY, J. M., CHEN, X., and KARG, G. 2006. Plume size and efficacy of aerosol pheromone dispensers against lightbrown apple moth. *J. Appl. Entomol.* (in press).
- SWENSON, D. W. and WEATHERSTON, I. 1989. Hollow-fiber controlled-release systems, pp. 173–197, in A. R. Jutsum and R. F. S. Gordon (eds.). *Insect Pheromones in Plant Protection*. Wiley, Chichester, U.K.

- TCHESLAVSKAIA, K. S., THORPE, K. W., SHAROV, A. A., LEONARD, D. S., REARDON, R. C., MASTRO, V. C., SELLERS, P., BREWSTER, C. C., and ROBERTS, E. A. 2005. Optimization of pheromone dose for gypsy moth (*Lymantria*: *Lymantriidae*) mating disruption. *Entomol. Exp. Appl.* 115:355–361.
- THORNHILL, R. and ALCOCK, J. 1983. *The Evolution of Insect Mating Systems*. Harvard University Press, Cambridge, MA.
- TORRES-VILA, L. M., RODRIGUEZ-MOLINA, M. C., and STOCKEL, J. 2002. Delayed mating reduces reproductive output of female European grapevine moth, *Lobesia botrana* (Lepidoptera: Tortricidae). *Bull. Entomol. Res.* 92:241–249.
- TRIMBLE, R. M., PREE, D. J., and CARTER, N. J. 2004. Comparison of a sprayable pheromone formulation and two hand-applied pheromone dispensers for use in the integrated control of Oriental fruit moth (Lepidoptera: Tortricidae). *J. Econ. Entomol.* 97:482–489.
- VALEUR, P. G. and LÖFSTEDT, C. 1996. Behaviour of male oriental fruit moth, *Grapholita molesta*, in overlapping sex pheromone plumes in a wind tunnel. *Entomol. Exp. Appl.* 79:51–59.
- VICKERS, R. A. and ROTHSCHILD, G. H. L. 1991. Use of sex pheromones for control of codling moth, pp. 339–354, in L. P. S. van der Geest and H. H. Evenhuis (eds.). *World Crop Pests*, Vol. 5. *Tortricid Pests: Their Biology, Natural Enemies, and Control*. Elsevier, Amsterdam.
- WALDSTEIN, D. E. and GUT, L. J. 2003. Comparison of microcapsule density with various apple tissues and formulations of oriental fruit moth (Lepidoptera: Tortricidae) sprayable pheromones. *J. Econ. Entomol.* 96:58–63.
- WITZGALL, P., BÄCKMAN, A. C., SVENSSON, M., KOCH, U., RAMA, F., EL-SAYED, A., BRAUCHLI, J., ARN, H., BENGTTSSON, J., and LÖFQVIST, J. 1999. Behavioral observations of codling moth, *Cydia pomonella*, in orchards permeated with synthetic pheromone. *Biocontrol* 44:211–237.