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This contribution is dedicated to the memory of Prof. Dan Gerling, a scientist, a colleague and a friend

Whiteflies and white lies: Dan Gerling's speculation on deceptive communication in parasitoid-host interactions

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ABSTRACT

We used game theory to assess speculation from the late Dan Gerling that whitefly hosts might evolve to exploit the chemosensory system of their parasitoid natural enemies via fake (pseudo) marking pheromones. We considered three scenarios. Scenario 1 assumed parasitoid response to hosts was non-evolvable and hardwired. Here, we found that pseudo-marking was a viable strategy; values at fixation depended upon costs and benefits of marking. Scenario 2 assumed parasitoid host acceptance was non-evolvable and plastic. Here, we found that strong fake marking was common when parasitism was moderate, that is when the risk was high but parasitoids would tend to reject because good hosts were available. Scenario 3 assumed plastic parasitoids that could co-evolve with the host. Here, we found parasitoid sensitivity to host marks, at the population level, never stabilized. By contrast, fake host marking did stabilize but only at high signal strength when levels of parasitism were intermediate (i.e. 30–40%); when parasitism was more common, marks were ignored and hiding from enemies became more effective. We discuss the potential for evolution of pseudo-oviposition marks in the general sense with reference to sensory deception in non parasitoid-host systems.

KEYWORDS: Behavior, co-evolution, computer model, deception, game theory, host discrimination, marking pheromones, mimicry, oviposition, parasitoid.

INTRODUCTION

Over thirty years of cooperation, we were struck by the late Prof. Dan Gerling's passion, observational skills and his utmost perseverance. Many of our interactions with Dan started in a characteristic pattern. He would write, phone or email one of us (BDR) with an observation that seemingly did not make sense. Over the years, we and Dan began to refer to these apparent anomalies as 'Gerling questions': Why didn't parasitoids host discriminate when they should have, why did sex ratios depart from expected, why couldn't population dynamics explain local densities, *etc*.? Our job was and still is to explore these oddities that Dan had uncovered.

We want to stress that Dan Gerling did not seek anomalies but rather he was not limited by theoretical or common observational expectations. He developed clever methods to confirm his observations, he produced replicable results, and

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he challenged us to explain the sometimes-poor fit between theory and his observations. Our take on these observations was that they represented one of four possibilities: (i) they were exceptions that proved the rule, (ii) they were apparent anomalies only because they lacked the appropriate context, (iii) these observations disproved the basic theory, or (iv) they were novel phenomena that required new theory. Below, we discuss the fourth possibility and provide some novel theory.

GERLING'S SPECULATION ON 'FAKE NEWS'

Several years ago, Gerling described an observation that, on first blush, was not easy to explain. It was an observation that many parasitoid biologists had made before but largely disregarded. Gerling noted that despite his best attempts to maintain high quality (whitefly) host colonies, many of these healthy (unparasitized) hosts were rejected by their *Eretmocerus* spp. parasitoids, presenting a challenge for those investigating parasitism. Gerling found this phenomenon unsettling: theory suggests that parasitoids should always accept good quality, healthy hosts but may reject low quality hosts depending upon availability of healthy ones (Van Alphen & Visser 1990). There was no theory to explain why parasitoids should refuse healthy hosts. In Gerling's setup, none of the standard measures of host quality (e.g. age and size) varied in any systematic manner to explain the rejections. Of course, it is possible that the *Eretmocerus* spp. females were cueing in on some aspect of host quality that Gerling had not measured. He noted one further detail: during rejection, his parasitoids appeared to treat some of these healthy hosts as if they were already parasitized (Gerling *et al.* 1987). How might this be?

It is well known that many species of parasitic arthropods apply oviposition marks to their hosts during or subsequent to parasitism (van Lenteren 1981; Hoffmeister & Roitberg 2002). These species-specific marks function to help a female parasitoid avoid larval competition between her offspring, largely though rejection of parasitized hosts. Other members of the parasitoid population can read these marks and make decisions regarding non-sib competition, thus, such marks act as honest signals (Roitberg & Mangel 1988). In general, encounters with oviposition marks lead to rejection of hosts. *Eretmocerus* spp. are primary parasitoids that lay their eggs between whitefly nymphs and the leaf surface (Liu *et al.* 2015). There is evidence for deposition of cuticular hydrocarbon oviposition marks by *Eretmocerus* spp. (Buckner & Jones 2005). In closely related species of *Eretmocerus*, there is some cross-species recognition of parasitism (Ardeh *et al.* 2005), likely based upon these chemical cues. Adult parasitoids may also feed on whitefly hosts to obtain nutrients necessary to enhance fecundity. Such feeding is facilitated by penetrating the host cuticle via the ovipositor (Gerling *et al.* 1998).

Insect herbivores are under threat from parasitoids and may evolve a number of tactics as defense including exploitation of their enemy's host-exploitation behavior. One such parasitoid behavior might be host marking. Gerling speculated that some of his healthy hosts were perceived by the *Eretmocerus* spp. to be

already parasitized and the most likely culprit, as noted above, would be chemical cues (pseudo-oviposition marks) produced by the whiteflies. In other words, hosts might exploit the sensory apparatus of their enemies to avoid being parasitized (Stevens 2013). We are not aware of any previous literature that documented host arthropods producing compounds that mimic the oviposition marks of their natural enemies but the lack of evidence does not mean lack of occurrence. If 'fake marks' do exist, it behooves us to elucidate the circumstances under which they might evolve, the implications for parasitoid–host co-evolution and the observation that only some of the hosts appeared to be pseudo-marked.

The question that Dan Gerling raised falls under the more general rubric of deception (Mokkonen & Lindstedt 2016) more specifically, deceptive communication (Ruxton & Schaefer 2011). In nature, the strategy of deception takes many forms and is widespread throughout the biological kingdoms, including self-deceit (Trivers 2011). Deception confers safety to brightly colored, but otherwise palatable butterflies (Brower 1958), affords protection to poisonous-looking but otherwise harmless snakes (Rabosky *et al.* 2015), and provides fostering services to otherwise delinquent cuckoo parents (Krüger 2007) to name but a few examples. A good instance of cross kingdom deception can be found in orchid–bee systems, wherein orchid flowers exquisitely mimic the size, shape and odor of a female bee thereby attracting male bees to the flower (Johnson & Schiestl 2016). Subsequent attempts to mate with the pseudo female causes a transfer of pollen to the orchid with no reward to the deceived male (Gaskett 2011). The odor deception in this case is the mimicking of the pollinator's sex pheromone by the orchid. These tactics follow a common strategy: mimic a true threat or signal already established, i.e., a sex pheromone is the model that is selected for, in nature.

Many predators including birds, reptiles and mammals, have evolved to avoid easily detectable, unpalatable prey (Nishida 2002). A good example of such prey are the monarch butterflies, which evolved bright coloration to advertise their (honest) unpalatability (Brower 1958 but see Mallet 2001). Once this relationship was established, the honest signal (i.e., warning coloration) was open for exploitation by other species. In this case, the palatable viceroy butterfly gained protection from predators by evolving a warning coloration that mimicked the coloration of the monarch. This widely accepted explanation generally assumes that the predator's response to the warning coloration is fixed or out of step with respect to an arms race (but see Koch *et al.* 2005). However, theory has suggested, and studies corroborate the concept, that predators can act as dynamic mediators in the evolution of model–mimic systems. If predators learn the palatability of butterflies from their experience with both model and mimic, they may constrain the evolutionary success of the mimic. This would be the case when mimic frequency becomes too high, relative to the frequency of the model.

Note that while prey and their predators have been the focus of deceptive or Batesian mimicry, the same concepts should hold for hosts and their parasitoids.

Parasitoids fall into a special class of parasite that, by definition, kill their hosts during a close association with them (Godfray 1994). When a parasitoid rejects a host because that host is perceived to sit below some host quality criterion, such behavior is equivalent to a predator rejecting an unpalatable prey.

Predators are not the only brokers in systems of deception, however. We thus propose to use the more general term of "mediator" when discussing the evolution of deception. In the case of palatable and unpalatable butterflies, the mediator is a predator; in the case of fake marks, the parasitoid marks are the models, the fake marks the mimics and the parasitoid the mediator. For the brood-parasitizing cuckoos, the mediator is the host parent species (Lotem 1993). In sum, the mediator is the third player in the co-evolutionary game between model and mimic, acting as a selective agent on both model and mimic, and having its mediating behavior (e.g., signal discrimination or sensitivity to signal) selected for via interactions with model and mimic players.

We broaden the aforementioned base of theory on the evolutionary ecology of deception with the aforementioned pseudo-marking pheromone problem introduced to us by Dan Gerling. We specify the likelihood of this specific form of deception occurring in nature, and generalize our conclusions to other cases where such deception has been demonstrated. As noted by Stuart-Fox (2005) and Mokkonen and Lindstedt (2016), the evolutionary consequences of deception will depend upon the costs (e.g. production of specific compounds) and benefits to both receiver and sender, often in a frequency dependent manner (e.g. Chubaty *et al.* 2014). Our approach explicitly considers such costs in a game-theoretic context.

Here, we analyze the evolution of deceptive marking strategies in host populations, under different modes of parasitoid acceptance (e.g. hardwired, plastic, *etc*.) of marked hosts. Of course, as noted above, sensory exploitation of a parasitoid, by its host during assessment, need not be based on marking pheromones but rather on any chemical, visual or auditory cues that the parasitoid employs to assess hosts. Thus, the implications from this example are not specific to chemical deception.

The system we envision is analogous to other forms of mimicry, often described as Batesian: the true oviposition mark of a parasitoid would play the role of model, and the fake oviposition mark of the host plays the role of mimic. As noted above, the mediator in this model mimic system is the parasitoid itself, and like the host parent species in brood-parasite systems, must discriminate a signal originally evolved for use by the parasitoid to avoid self-parasitism. Additionally, the degree of sensitivity to the signal should evolve to reflect the accuracy of information conveyed by the mark. We assume that the fake mark is chemically identical to the original compound and that there is no way for parasitoids to evolve higher-level discrimination but note that perfect mimicry is not always necessary to function well so long as the are costs of discrimination (receptors, brain function, reduction in host exploitation rate) are high relative to benefits (avoidance of poor-quality hosts) (see Sherratt & Peet-Paré 2017).

Hosts may have more common strategies for minimizing risk of parasitism; we consider hiding as one such traditional strategy, and we examine the evolution of fake marking within the background of this more common response to parasitism. Because the payoffs for fake marking and hiding are frequency dependent (see below) we determine the success of fake-mark evolution at two stages in the evolutionary process (Maynard Smith 1982). We address two questions: first, can fake-marking strategies invade a population of hiding, but true marking strategies in hosts; and second, are fake-marking strategies evolutionarily stable, that is do they do well against themselves? To accomplish this, we use a simulation model to explore the evolution of pseudo (fake) mark signals under different modes of parasitoid response to the mark, hardwired and plastic, evolvable and non-evolvable, as described below. What are the outcomes of such interactions?

METHODS

In the parlance of game theory, we sought the evolutionary stable hiding and fake mark strategies (Maynard Smith 1982) for insect herbivores for defense against insect parasitoids. The benefit from hiding and fake marking is via increased survival through reduced encounters with parasitoids and increased rejections, respectively and the cost is reduced fecundity for those that survive to reproduce, thus the classic tradeoff while the costs are fixed, the probabilities of survival depend upon the aforementioned (flexible or non-flexible) parasitoid foraging tactics. Thus, herbivore fitness is not a simple summation. For parasitoids, fitness is accrued from parasitizing hosts. Parasitoids benefit from rejecting true marked hosts and thus avoiding offspring competition and by not wasting time parasitizing already-parasitized hosts. Those benefits depend upon availability of healthy hosts as well as lost opportunities from rejecting peudo-marked but otherwise healthy hosts. We considered three scenarios of increasing parasitoid oviposition-decision complexity, to assess their impact on evolutionary stable host pseudo-marking strategy.

We simulated evolutionary and co-evolutionary processes via genetic algorithm (GA's) computer simulations. GA's are numeric optimization techniques that operate by means analogous to natural selection; they are useful when studying systems that are analytically intractable (Goldberg 1989; Sumida *et al.* 1990; Axelrod 1997). Possible strategies are encoded in binary strings (called chromosomes or genes), and are translated into phenotypes that are subjected to a fitness function. A population of strategies is initiated and allowed to evolve for a fixed number of non-overlapping generations (usually long enough for a stable solution to emerge). In each generation, strategies replicate themselves with likelihood proportionate to their relative performance (i.e., fitness) at some objective criterion, and the new population of strategies is subjected to the fitness function. A mutation function is implemented each generation, whereby random, heritable, changes in strategies occur, to generate variation for the GA to appraise. This ensures that all regions

of solution space are explored. A cross-over function is included, whereby successful strategies exchange partial chromosomes; this enhances the efficiency of the optimization process. The simplest stability criterion is convergence to a single (or pure) strategy (an evolutionary stable strategy, or ESS, in the classical language of game theory (Maynard Smith 1982)). Other criteria for stability include mixed strategies (i.e., a distribution of pure strategies, sometimes referred to as an evolutionary stable state, or ESSt), or a cyclic or dynamic evolutionary state (i.e., a stable cycle of strategy displacement and replacement). While the lexicon and logic of GA's is analogous to processes of natural selection and genetic evolution, we emphasize that we use a GA here as an optimization engine; we are interested only in the evolution of the phenotypes, and we are not implying that the underlying genetics are accurately reflected by the "genetics" of the models (see Gomulkiewicz *et al.* 2000; Perry & Roitberg 2005), i.e. we employ the phenotypic gambit (Grafen 1982) in a game context. Also, note that mutation and cross-over rates that are employed in GA's are model tuning parameters and are not meant to take on values from natural biological systems.

The model – overview

As noted above, hosts employ two anti-parasitoid strategies, hiding and deception. We defined host hiding (*h*) as 1-(probability of detection), i.e. an outcome of host effort, assuming a constant search by parasitoids. We encoded *h* in a single gene, with 32 possible tactics ranging from 0 to 1.0. A cost for hiding was assumed in direct proportion to the tendency to hide, and ranged from 0.5 to 1.0 fitness units. Thus, hiding involved a tradeoff: high values conferred protection from parasitism, but decreased fitness, for example, via reduced opportunity to forage (e.g. Kraaijeveld & Godfray 2003). Pseudo (or mimicked) oviposition marking signal strength (γ) hereafter referred to as fake marking strength was also encoded by a single gene with 32 possible strategies ranging from 0 to 1.0, corresponding to the signal strength of the fake mark. Low γ values represented weak marks (i.e., low signal strength), and cost the least to produce, while high γ values represented strong marks and were most costly to produce. We assumed an asymmetry in the cost of hiding (reduced foraging) and fake marking (release of metabolic end products), such that marking costs proportionately less than hiding (Hoffmeister & Roitberg 2002). However, the benefits of both hiding and fake marking were frequency dependent, so predicting their performance was not always intuitive as a simple game because parasitoid response to marks need not be fixed nor non-evolvable. Success at hiding was only relative to the other hiding strategies in the host population (i.e., a frequency dependent game) however, success at marking also depended on non-linear host acceptance function by parasitoids (scenarios 2 and 3), which was in turn dependent on the amount of mark (true and fake) in the host population (i.e., host detection and acceptance by parasitoids was a fixed proportion of hosts in each generation, thus hosts were playing against themselves). (See Hochberg 1997 for an analogous study on hiding and antibiosis traits.) The

general model of parasitoid response took the form of a critical threshold function: a parasitoid rejected a host it had encountered only if the host mark strength (γ) was greater than a rejection threshold specific to the parasitoid, α_p, where:

$$\alpha_p=\alpha_0+(1-\alpha_0)\bar{\gamma}^{\chi} \quad (1)$$

Here, α_0 was the initial rejection threshold (i.e., mark level) that reflected the minimum mark level for rejection by the parasitoid, $\bar{\gamma}$ was the mean mark level (i.e., signal strength) in the population of hosts (whether due to mimic-mark strategies or model marks from actual parasitism events), and χ was a shape parameter that described the sensitivity of a parasitoid's response to the amount of mark in the host population.

We used three specific scenarios of the model of parasitoid response to host fake-mark signal, reflecting three biological possibilities of mediation between true and fake marks. The first scenario of parasitoid response was a hardwired, non-evolving response, whereby the threshold for rejecting a host was fixed and insensitive to the mean amount of mark in the environment. It was expressed by simplifying equation 1:

$$\alpha_p=\alpha_0 \quad (2)$$

We conducted a sensitivity analysis on the rejection threshold parameter, α_0 for different levels of parasitism.

Our second scenario of parasitoid response was a non-evolving plastic response described by equation 1. Here, the parasitoid's initial rejection threshold (α_0) was modified by the mean mark value in the population ($\bar{\gamma}$). This model reflected the idea that parasitoids require hosts to produce progeny, rendering them less choosy about host quality as perceived mean host quality declines (i.e., as the mean mark level in the population increases). Again, we treated α_0 and χ as parameters, and conducted sensitivity analyses on these terms for different levels of parasitism.

Our third scenario of parasitoid response treated parasitoid response parameters α_0 and χ as co-evolving, plastic strategies against a backdrop of co-evolving hide and fake-mark strategies in the host population. We encoded α_0 with 32 strategies, that varied from 0 to 1.0, and χ with 32 strategies, that ranged from 0.001 (i.e., essentially zero) to 64, giving us a very broad range of values to work from. Thus, we had a coupled GA: one population of host hide and fake mark strategies and one population of parasitoid α_0 and χ (i.e., response) strategies; each provided the ecological context for the other in a joint fitness function. Fitness, as discussed below depends upon survival and fecundity for the host and from successful parasitisms for the parasitoid. The variables of the model are summarized in Table 1, and we illustrate the three scenarios of the model reflecting the three modes of parasitoid response in Figure 1.

Simulation and fitness assessment

We initialized host populations with a uniform random distribution of hiding values and no fake marking tendency. Fake markers entered the population as

Table 1. A summary of the variables from the host fake mark genetic algorithm. Ranges or values given may be specific to versions I, II or III of the model (see text for details).

Variable or Parameter	Value or Range of values
Host Genetic Algorithm	
Number of generations	I, II: 200, III: 1000
Number of model runs per generation	1; II, III: 10
Size of host population	1000
Number of "Hide" alleles	32
Number of "Fake mark" alleles	32
Mutation rate	2%
Cross-over rate	10%
Parasitoid Genetic Algorithm (III)	
Number of generations	1000
Number of model runs per generation	10
Size of parasitoid population	100
Number of "Initial Accept" alleles	32
Number of "Shape Parameter" alleles	32
Mutation rate	2%
Cross-over rate	10%
Simulation	
Parasitism level	10–90%
Handling time (III)	3, 5, 7, 9 time units.

mutants. This approach allowed us to answer our question whether fake markers could invade a population of non-deceptive, hiding individuals. After initialization of host and parasitoid populations, hosts were subjected to a simulation and fitness calculation though, as noted above, parasitoid strategies were non-evolvable in scenarios 1 and 2 thus, parasitoid fitness was moot. A host was selected randomly (from a uniform distribution) to determine if it was detected by a parasitoid (based on the host's hide tendency). If undetected, a new host was selected and subjected to this same detection test, until a host was "found." Once detected, a random parasitoid was selected from the parasitoid population queue (see below) and it assessed host condition, as described above. If the parasitoid rejected the host, the process of host and parasitoid selection started again. If the parasitoid accepted the host, it parasitized and marked the host with a strong mark (level = 1.0), and incurred a handling time penalty for the acceptance; this is the time cost component. The genetic identity (ID) of the parasitoid was stored in the host. If a parasitoid accepted a host that had been previously parasitized (i.e., it superparasitized the host), then the subsequent parasitoid displaced the first parasitoid with some probability (0.05, 0.25). Here, we assumed that a host could bring forth a single, solitary parasitoid, with a strong advantage to parasitoids being the first to accept a host. After the encounter, the host was immediately available for further parasitism

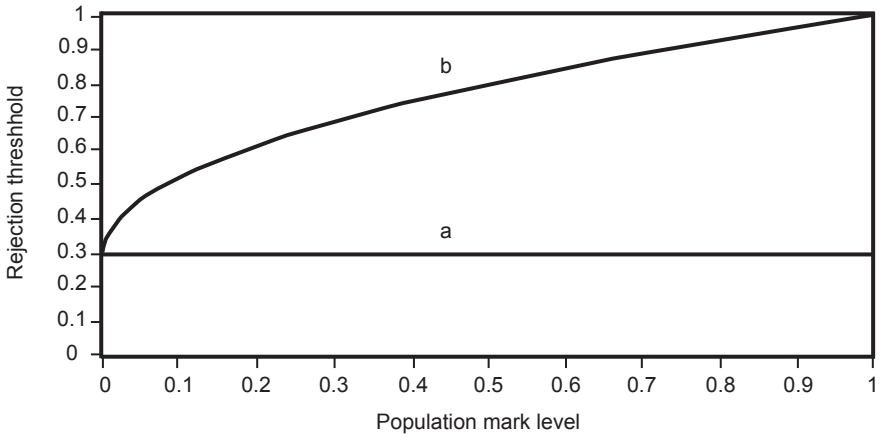

Fig. 1: Rejection responses of parasitoids in a theoretical host-parasitoid system, based upon parasitoid's response to oviposition marks: (a) the parasitoid's hardwired, non-evolvable rejection threshold for marked hosts (true or otherwise), α_p, with initial rejection threshold, α_0, set to 0.3. This response (scenario 1) is insensitive to the amount of mark (true or fake) in the environment (i.e., host population); (b) a plastic host rejection response (scenarios 2 (non-evolvable), 3 (evolvable)) where rejection threshold α_p, depends on the initial rejection threshold α_0 mean mark level in the population ($\bar{\gamma}$), and a sensitivity parameter χ (α_0=0.3, χ=0.3).

events. The parasitoid, however, did not join the queue of parasitoids encountering hosts, until its handling time penalty decreased to zero. All parasitoids with handling time penalties had their penalties decreased by one unit of time at the onset of each round of host-parasitoid encounter. The use of a handling time penalty was the cost that parasitoids paid for accepting a host though as noted above, was unimportant for the non-evolvable parasitoids in scenarios 1 and 2. This process continued until a fixed proportion of hosts had been accepted for parasitism (ranging from 10–90% of host population size). At the end of the simulation, the fitness of each host was determined. If a host was parasitized, it received a fitness score of zero. If a host was healthy at the end of the simulation, it received a fitness score of one reduced by the intrinsic costs of its hide and mark tendencies. The identification of each parasitoid offspring was recorded and used to determine fitness of the parasitoids. These fitness scores were then used in the reproduction procedure of the GA wherein each generation host and parasitoid populations were initiated at 1000 and 100 individuals, respectively (we did not accommodate population dynamics in this version of our model).

The above description describes the third scenario of our model (co-evolving hosts and parasitoids). In the first and second versions of our model, global parameters for the parasitoid responses to host mark were used rather than specific parasitoid players (i.e., only the host population was assessed, because the parasitoid population did not evolve).

Analysis

Our model was coded in C++ and run on a personal computer. Different starting conditions (by initialization with different random seeds) were used for each run of the model, and preliminary analyses provided us with an idea of a sufficient number of runs to conduct for each version of the model. In the first and second versions of the model, a single run of 200 generations was sufficient to produce a stable distribution of strategies.

In the second version, however, the outcome was somewhat dependent on starting conditions for some parameter settings, so ten runs for each combination of parameters were generated and analyzed. In the third version of the model, some evolving strategies did not settle down (even for model runs >10,000 generations). Thus, we show mean results for 10 runs of 500 generations, and discuss the uncertainty in other results. Where strategies did not stabilize to a single value, we used an autocorrelation function to determine if any periodicity in strategy was occurring (JMP In 4.0, student edition).

RESULTS

Scenario 1: Hardwired behavior that does not evolve

The results for the single run of version 1 of the model is illustrated in Figure 2. A starting population of non-marking, uniformly distributed hiding hosts (Fig. 2a) converged to strategies of low hide and high fake-marking tendencies after 200 generations (Fig. 2b). All parameter values for version 1 of the model stabilized in a similar fashion. The fitness of the host population initially declined but ultimately stabilized at a high level (Fig. 2c). The mean hide and mark tendencies in the host population are shown in Figure 2d for a typical run.

Scenario 2: Plastic behavior that does not evolve

At low levels of parasitism (10 %), fake marking stabilized at a moderate level (~0.6) as the primary defensive tactic employed by hosts against parasitoids, while the tendency by hosts to hide was very low. This pattern was similar for all parasitoid parameters of α_0 (initial rejection threshold) and χ (mark sensitivity shape parameter) (results not shown).

With the low risk of parasitism (~10 %), hosts did not need to invest in defense; when they did, they chose the less costly defense (i.e., fake marking). When parasitism was increased to 30 %, the pattern described above was essentially the same, except that the value of marking was ~0.9, dropping off slightly for low values of α_0 and high values of χ (Figs 3a, b). This region of parameter space corresponded to a parasitoid that had a very low threshold for rejecting hosts and was not sensitive to the amount of mark in the population. Under these circumstances, there was a lower payoff for investing in a fake mark. When parasitism increased to 60 % and beyond (not shown) the mean tendencies of hosts to hide and mark became sensitive to the parasitoid parameters α_0 and χ. Hiding was universally low except for when α_0 was high and χ was low. This region of parameter space

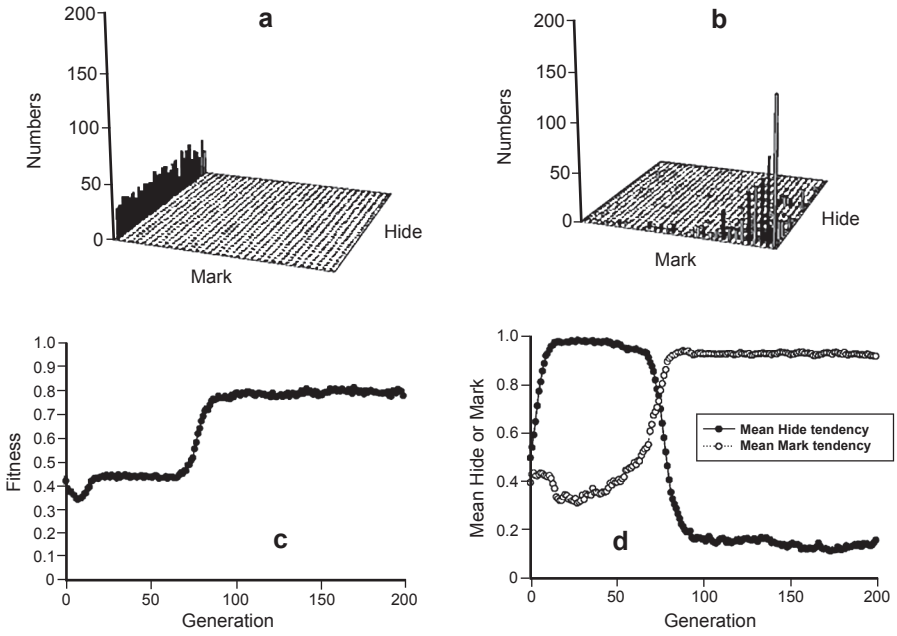

Fig. 2: Genetic algorithm simulations of host defense strategies in a theoretical host-parasitoid system. Distributions of host defense strategies (i.e., hide and fake-mark tendencies) at the outset (a) and end (b) of a typical run of scenario 1 (i.e., hardwired, non-evolvable parasitoid response to oviposition marks). Over time, the fitness (c) and hide and fake mark tendencies (d) of the host population stabilized.

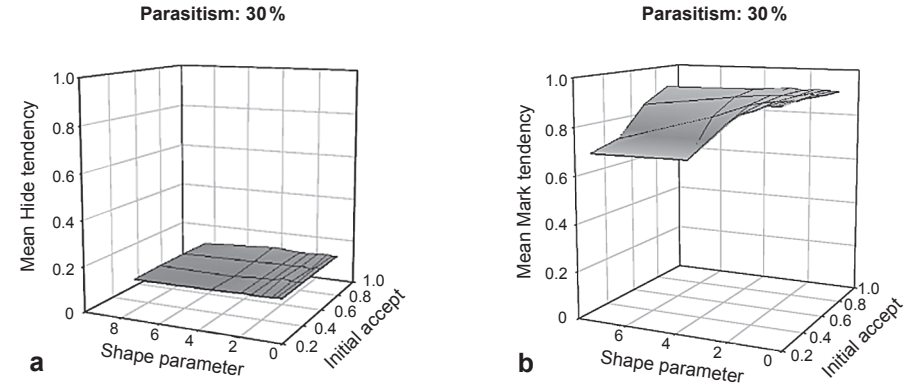

Fig. 3: Genetic algorithm simulations of host defense strategies in a theoretical host-parasitoid system with the parasitoid's non-evolvable, plastic response to oviposition marks (scenario 2). Evolutionarily stable host mean hide and mark tendencies for parasitism levels of 30% (a, b) for $\alpha_0 = 0.1, 0.3, 0.5, 0.7, 0.9$ and $\chi = 0.5, 0.75, 1.0, 1.5, 2.0, 2.5, 4.0, 8.0$.

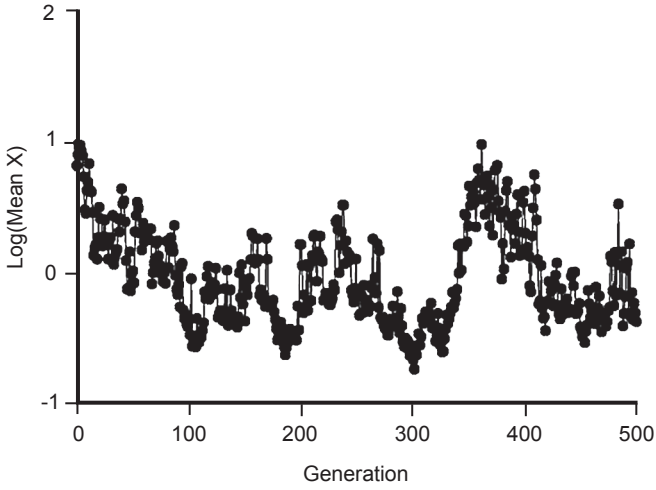

Fig. 4: Genetic algorithm simulations of host defense strategies in a theoretical host-parasitoid system with the parasitoid's evolvable, plastic response to oviposition marks (scenario 3). Chi (χ) was a shape parameter that described the sensitivity of a parasitoid's response to the amount of oviposition mark (true or otherwise) in the host population was not observed to stabilize in any runs of the fake mark. Depicted here are values from a typical run of 500 generations, with parasitism being 30%.

corresponded to a non-choosy parasitoid, i.e., one that was not sensitive to the amount of mark on a host or the amount of mark in the population. Concordant with this pattern, was a shift from a high mean tendency to mark to a modest mean tendency to mark. Again, if a parasitoid was not choosy, then hosts did not invest in the mark.

Scenario 3: Co-evolving behavior

While the host strategies of hiding and marking and the parasitoid strategy of rejection threshold (α_0) stabilized in most runs of the model, parasitoid sensitivity to host population (χ) rarely ever stabilized (Fig. 4). We evaluated the parasitoid sensitivity to host population mark level (χ) parameter for model runs of up to 10,000 generations. Upon visual inspection, no stable patterns were discernable and autocorrelation tests failed to detect a significant periodicity to the values of the parameter. Thus we looked to the joint fitness plot to assess the stability of the system (Fig. 5). After 500 generations, the joint fitness of hosts and parasitoids had essentially stabilized. (We confirmed our visual assessment of stability by continuing several runs for thousands of generations and observed no further change.) In almost all runs, mean host fitness increased while parasitoid fitness decreased. This reflected the fact that parasitoids were less able to exploit host populations as hosts evolved ways (i.e., hide and fake-mark strategies) to protect themselves from parasitism, even though parasitoids were evolving responses to those host strategies.

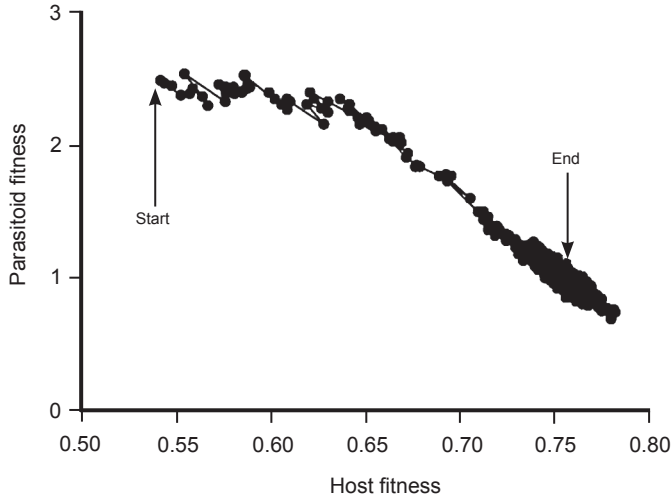

Fig. 5: Joint fitness phase plot of theoretical host and parasitoid populations when hosts defend themselves through hiding and fake oviposition making, from a typical run of the co-evolving, plastic parasitoid response (scenario 3) based upon genetic algorithm. The point marked 'Start' represents the joint fitness after the first generation of the genetic algorithm, and the point marked 'End' represents the joint fitness after the final generation of the genetic algorithm.

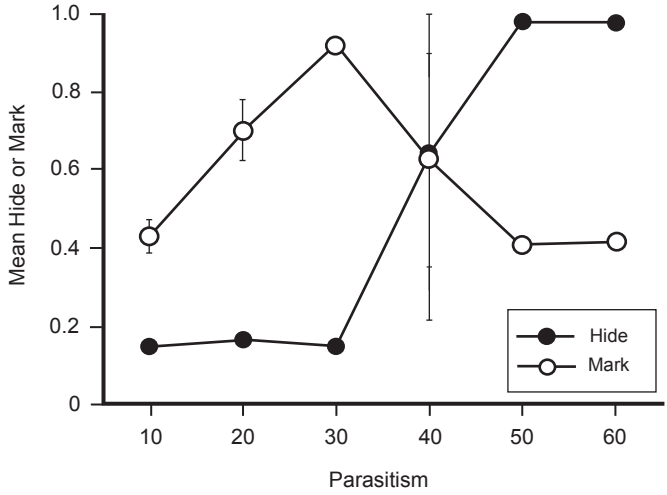

Fig. 6: Genetic algorithm simulations of host defense strategies in a theoretical host-parasitoid system with the parasitoid's evolvable, plastic response to oviposition marks (scenario 3). Mean hide and fake mark defense tendencies versus parasitism level (10%). Points represent the mean value for 10 runs of the model and error bars reflect the standard deviation of the means.

The mean hide and mark tendencies in host populations that co-evolved with their parasitoids are summarized in Figure 6. At low levels of parasitism (10%), hosts do not hide, but do use a moderate amount of fake marking to deter parasitoids. As parasitism level increased, hosts increased their tendency to fake mark. It appears that 30–40% parasitism rate represented a critical threshold whereby host strategy switched from high fake marking, non-hiding, to moderate fake marking and high hiding. At high levels of parasitism, regardless of host tendency to fake mark, there would have been high levels of mark (true) in the host population; this raised the rejection threshold for parasites to a point where marks (true or fake) became irrelevant. This would have had the effect of selecting against hosts that employed fake marks, and it was under these conditions that hiding became a viable tactic for avoiding parasitoids.

When we varied handling time penalty, no differences in parasitoid response were noted (results not shown). We also modified the probability of successful superparasitism events, and in general, the patterns we observed above held, although fake marking occurred at a lower level of parasitism (results not shown).

DISCUSSION

Fake news has become a popular topic in the mainstream press of late (Hunt 2016). Of course, deceptive communication where "(on average) the response of the perceiver benefits the informer but not the perceiver" (Ruxton & Schaefer 2011) has been documented for some time. Dan Gerling was, to our knowledge, the first to suggest that host arthropods might exploit the sensory systems of their parasitoids by employing fake oviposition marks. Predicting the prevalence of such a strategy requires a good understanding of the context of parasitoid–host interactions. We used game theoretic models to evaluate potential for fake marking to invade and stabilize in a population of hiding-strategy hosts under three possible parasitoid–host interaction scenarios with increasing complex parasitoid responses to host marking pheromones.

In Scenario 1, fake marking—but not hiding—evolved as the primary mode of defense by hosts against parasitoids. This result is not surprising given two of our assumptions: first, parasitoids had an evolutionarily static, hardwired response to the level of oviposition mark, and therefore were unable to counter (evolutionarily) the strategies of the host population; second, we assumed that fake marking was relatively less costly relative to hiding. This version of our model served as a base line for comparison to our other versions of the model. Interestingly, this simplification may reflect the underlying biology of other biological systems. Numerous authors have suggested sexually selected traits in males may have evolved to take advantage of a pre-existing sensory biases in females (Rand & Rand 1990, 1998; Rand & Keddy-Hector 1992; Ryan & Cummings 2013). As such, sensory exploitation is possible, because the putative pre-existing sensory bias in females is often portrayed as a hardwired, non-evolvable, or static condition in females

(but see Lynch *et al.* 2005; Pilakouta *et al.* 2017; Ida & Karino 2017, for exceptions). Because evidence for this static, hardwired bias has been found we do not dismiss such a possibility in the system we envisage here. One can imagine systems where the value of parasitized hosts is so low that parasitoids would never evolve plasticity in response to oviposition marks (Sherratt & Peet-Paré 2017).

In Scenarios 2 and 3 of our model, parasitoids had a plastic response to the level of marking in the population. These models might be considered to be more stringent as conditions for the evolution of host fake marking, and accordingly, we found the evolution of fake marking to be sensitive to the parasitoid strategies. Host fake-marking could evolve at intermediate levels of parasitism. With low levels of parasitism, the threat of parasitism simply was not high enough to warrant paying a cost to implementing a defense (whether it be hiding or fake-marking). With high levels of parasitism, hiding became the primary defense tactic employed by hosts. The shift from no defense to fake marking as a defense, at intermediate levels of parasitism, is understood to be due to fake marking costing less than hiding, and paying off because the overall level of marking in the host population (from fake and true marks) was not causing parasitoids to become insensitive to host mark levels. At high levels of parasitism, however, parasitoids encountered high levels of marking (whether from true or fake marks) and ignored the information in mark, rendering fake ones irrelevant. Thus, we saw a shift from fake marking to hiding.

In Scenario 3 of our model, parasitoid strategies were able to evolve in response to host strategies. Not surprisingly, complex dynamics ensued (Szolnoki & Perc 2014). It is clear from our analysis that some sort of arms race occurred under a variety of conditions and this race could continue indefinitely with parasitoids modifying and re-modifying their response to mark strength and frequency. In general, fake marking can evolve so long as parasitism rates are low or moderate. However, as in version 2, under conditions of high parasitism, fake marks are ignored thus providing little protection and as such do not evolve. Hochberg (1997) also found that the success of hiding versus antibiosis depended upon parasitoid attack rates.

We noted that while the threshold strategy (i.e., the acceptance threshold parameter) stabilized, the sensitivity to level of mark parameter did not. It appears that under most conditions, a high acceptance threshold evolved, and therefore there would be very little difference between fitness scores for alternative sensitivity parameters, and therefore not easy for the GA to establish a clear optimal value.

Finally, we noted that changing the handling time penalty for parasitoids had little effect on the strategies that evolved. This was likely because all parasitoids incurred the same time penalties, and parasitoid strategies were playing against themselves, not hosts. We also found that increasing the probability of successful superparasitism marginally reduced the likelihood of fake mark evolution in hosts. This is because higher levels of superparasitism allows for parasitoids to be more insensitive to mark levels on hosts.

Some caveats must be issued with regard to our assumptions. We assumed no cost to the host from being inspected and rejected. In fact, many parasitoids assess host quality after insertion of the ovipositor into the host's body (van Lenteren 1981) and such insertions could lead to host mutilation (Keinan *et al.* 2012) though, in this case, *Eretmocerus* lays its eggs under hosts. When there is injury from host assessments, it is likely to disfavor the evolution of fake marks. Further, we assumed no host feeding by parasitoids. In reality, post-assessment host feeding could play a significant role in performance of fake marks. We did not find any literature that showed that host feeding was enhanced or mitigated by oviposition marks but such effects could alter the evolutionary or co-evolutionary dynamics of fake marking. From a modeling perspective, this means that fake marks are less effective at increasing survival when parasitoids host feed.

In addition, within each model run, we assumed that the habitats in which fake marks evolved were highly stable and host population growth was density independent and aspatial (but see Wajnberg *et al.* 2012). Fluctuations in productivity can impact population densities and as a result, interaction rates (see above), supply of mutations and cost of mutations, all key elements of co-evolutionary dynamics (Hochberg & van Baalen 1998).

How common are fake marks in nature? To date, no surveys have been conducted and so it is impossible to estimate. Anecdotal information suggests that known healthy hosts are frequently rejected by parasitoids in the laboratory and in nature. Whether this is due to the presence of fake marks or deployment of other quality-masking defenses is not known but is well within the realm of possibility (e.g. Hoffmeister & Roitberg 1997). More specifically, cross species exploitation of species-specific pheromones has been documented and may be far more common than thought. Haynes *et al.* (2002) have shown how bolas spiders lure moths to their web sling by mimicking the sexual pheromones of their prey. Another interesting example exists in a system we study wherein a fly and wasp exploit one another's marking systems, the fly to avoid its enemy and the wasp to increase efficiency of exploitation of its host (Hoffmeister & Roitberg 1997). Further still, and highly pertinent here, a virus has recently been implicated that modifies host discrimination in a parasitoid (Gandon *et al.* 2006; Varaldi *et al.* 2006).

Professor Dan Gerling had great interest in biological control and so, the question must be asked as to whether fake marks could impact biological control of whitefly or other or arthropod pests. We envision two possible concerns. First, if fake marks reduce attacks on healthy hosts, efficacy of biocontrol will be reduced, *per se*. Second, expression of fake marks by some members of the host population could lead to either concentration of attacks on hosts that are not pseudo marked or spreading of attacks across the population, depending upon overall parasitism rates and concomitant response (see Results above). This could stabilize or destabilize dynamics, respectively (Mangel & Roitberg 1992; Hassell 2000).

Finally, we can ask what our paper says about co-option of signals in general. We caution against generalizing these sorts of scenarios as simple life-lunch asym-

metries wherein hosts face much more severe consequences, per interaction event, than their enemies (Dawkins & Krebs 1979). Resultant dynamics will dependent upon evolutionary and ecological constraints and context (Roitberg 2018).

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