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The evolution of locomotory behavior in profitable and unprofitable simulated prey

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Abstract Prey that are unprofitable to attack (for example, those containing noxious chemicals) frequently exhibit slower and more predictable movement than species that lack these defenses. Possible explanations for the phenomenon include a lack of selection pressure on unprofitable prey to avoid predators and active selection on unprofitable prey to advertise their noxiousness. We explicitly tested these and other hypotheses using a novel “artificial world” in which the locomotory characteristics (step size, waiting time, and angular direction) of artificial profitable and unprofitable computer-generated prey were subject to continued selection by humans over a number of generations. Unprofitable prey evolved significantly slower movement behavior than profitable prey when they were readily recognized as unprofitable, and also when they frequently survived predatory attacks. This difference arose primarily as a consequence of more intense selection on profitable prey to avoid capture. When unprofitable prey were very similar (but not identical) in morphological appearance to profitable prey, unprofitable prey evolved particularly slow movement behavior, presumably because when they were slow-moving they could be more readily recognized as being unprofitable. When unprofitable prey were constrained to move slowly, a morphologically identical profitable prey species evolved locomotor mimicry only when it had no more effective means of avoiding predation. Overall, our results provide some of the first empirical support for a number of earlier hypotheses for differences in movement between unprofitable and profitable prey and demonstrate that locomotor mimicry is not an inevitable outcome of selection even in morphologically similar prey.

Keywords Aposematism · Warning signals · Mimicry · Movement · Locomotion

Introduction

It has long been recognized that potential prey species that possess noxious qualities on attack by predators (e.g., unpalatability, stings, or venoms)—hereafter called “unprofitable” prey—tend to be conspicuous in some way (Wallace 1867; Darwin 1871; Poulton 1890). However, it is less well appreciated that such species also tend to exhibit slow and predictable movement (Pasteels et al. 1983; Whitman et al. 1985; Chai and Srygley 1990; Srygley and Chai 1990; Marden and Chai 1991; Pinheiro 1996; Hatle and Faragher 1998; Hatle et al. 2002). The slow movement reported in conspicuous unprofitable species is qualitatively different from the near motionlessness exhibited by many cryptic but otherwise profitable species (those lacking significant noxious qualities once attacked). Indeed at first, this combination of conspicuousness and slow movement appears maladaptive since it would render any prey item that possessed these traits both easily detectable and readily caught by naive predators (Hatle and Faragher 1998; Sherratt 2002). In his seminal work, Bates (1862) recognized the same general phenomenon, noting (p. 499) that unpalatable Heliconid and Ithomine butterflies “show every sign of flourishing existence, although of slow flight, feeble structure, unfurnished with apparent means of defense, and living in places which are incessantly haunted by swarms of insectivorous birds.”

Several theories have been proposed to explain why slow movement [variously referred to as “sluggish” in grasshoppers (Hatle et al. 2002) and “deliberate” in butterflies (Chai and Srygley 1990)] is more common in “unprofitable” than “profitable” species. Chai and Srygley (Chai and Srygley 1990; Srygley and Chai 1990a, 1990b) noted that unprofitable prey might be slow moving because there is no need to flee from predators, and therefore no selection for evasive behavior. Moreover,

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sluggishness may actually be selectively advantageous in unprofitable prey if rapid movement is energetically costly (Chai and Srygley 1990; Dudley 1991). Slow movement may also play a role in reducing recognition errors of predators (Guilford 1986; Srygley and Chai 1990b), particularly in cases where unprofitable prey have profitable (Batesian) mimics (Srygley 1994, 1999). Indeed, if profitable prey are not only more readily identified but also more readily caught when they move slowly, then slow movement might be selected as an honest signal of prey defense (Chai 1996; Sherratt and Beatty 2003). Finally, Hatle and coworkers (Hatle and Faragher 1998; Hatle et al. 2001, 2002; Hatle and Whitman 2001) have proposed a more mechanistic explanation for the phenomenon: slow movement may be beneficial because it does not as readily elicit attacks from motion-orientated predators. This hypothesis is based on direct observation and careful experiments, but it is important to note that the motion orientation of predators could just have plausibly arisen as a secondary consequence of the fact that unprofitable prey species tend to be slow. Furthermore, if sluggishness were selectively advantageous as an attack deterrent per se, then one might expect that profitable prey would also evolve such behavior.

To date, there has been very little experimental work to formally test, compare, and develop the above theories: movement behavior is difficult to manipulate, and most work on prey defense has focused on aspects other than motion (Edmunds 1974; Evans and Schmidt 1990; Srygley 1999). In this paper, we describe experiments that investigated the evolution of movement behavior in computer-generated profitable (predators gain points on attack) and unprofitable (predators lose points on attack) prey, when subject to continued selection by foraging humans. Human models have long been used to test and refine ideas relating to predation (e.g., Holling 1959; Dill 1975; Knill and Allen 1995; Glanville and Allen 1997)

and represent visual foragers with a high potential for learning and strategizing. Here their use was desirable not only because of the flexibility they allowed but also because participants would have relatively few preconceptions concerning the profitability of prey that moved in certain ways (a “novel world,” Alatalo and Mappes 1996).

In our experiments, individuals of a single unprofitable and a single profitable prey species exhibited heritable variation in their movement behavior. The two prey species were very different, very similar, or identical in morphological appearance (no mimicry, imperfect mimicry, and perfect mimicry). Unprofitable prey items survived attack with a fixed probability (see Järvi et al. 1981; Wiklund and Järvi 1982; Pinheiro 1996), whereas profitable prey items were always “killed” when attacked. By preventing those prey individuals that were killed by foragers from contributing to the next generation, we have, for the first time, simulated the evolution of movement characteristics in unprofitable and profitable species as a consequence of selective predation.

Materials and methods

We developed a computer program to simulate the evolution of locomotory traits in Microsoft Visual Basic 6. The human predators (55 subjects) used in the experiments (10 in total, see Table 1) had no knowledge of the experimental aims. Volunteers participated in only one replicate and in only one experiment (running for 20 generations, except experiment 1). Their virtual foraging environment consisted of a white area of computer screen, which was 29 cm long and 19 cm high. Prey items were square (15×15 mm) and were either uniform in color (experiments 1–3, red, unprofitable, blue, profitable) or composed of a 9×9 mm mosaic of colored cells (experiments 4–10, allowing varying degrees of mimicry). We chose not to make prey more realistic in morphology (for instance, by using pictures of butterflies or grasshoppers) because we did not want volunteers to have any expectations about how any particular species should behave.

Individual prey (selected at random from the total pool of available profitable and unprofitable survivors) were released by

Table 1 Outline of the experiments that were conducted ($n=5$ replicates per experiment except experiment 1 where $n=10$). Ticks refer to presence, crosses to absence. Profitable prey were present in all experiments and consistently had zero survivorship on attack

Experiment number	Unprofitable prey present	Morphological mimicry	Unprofitable prey survivorship on attack (q)	Notes
1	x	None	0	No evolution, 48 fixed forms of prey
2	x	None	0	
3	✓	None	0	
4	✓	Imperfect	0	Prey species distinguishable only when they move slowly
5	✓	Perfect	0	
6	✓	Perfect	0.8	
7	✓	Perfect	0	Unprofitable prey slow with no evolution (no restriction on profitable prey)
8	✓	Perfect	0	Unprofitable prey fast with no evolution (no restriction on profitable prey)
9	✓	Perfect	0	Unprofitable prey slow with no evolution (profitable prey cannot move quickly $minw > 300$ ms)
10	✓	Perfect	0	Unprofitable prey fast with no evolution (profitable prey cannot move quickly $minw > 300$ ms)

mouse clicking anywhere in the arena. No more than one prey item was ever visible at any one time; hence, movement rate per se did not change the frequency of contact between predators and prey. On release, the prey item moved across the screen either from left to right or from right to left (decided at random), starting from anywhere along the left or right vertical edge of the arena. The movement behavior of any individual prey was dictated by the allelic forms of its three artificial genes. The allelic form of an individual's first gene determined the distance the prey item moved in millimeters each time it made a "step" (parameter s , limits $mins$ to $maxs$). The allelic form of its second gene determined how long in milliseconds the prey item would wait before taking its next step (parameter w , limits $minw$ to $maxw$). The third gene dictated the angular range from which a movement direction was randomly selected. This angular range was expressed as a fraction a of the 180° plane (limits 0–1), symmetrical around the horizontal (for instance, for right-to-left movement, 0 = move along the 90° horizontal, 0.5 = angle between 45° and 135°). Any angle that would take a prey item beyond the upper or lower horizontal borders of the arena was not allowed (in which case, a new angle was again selected at random from within the permissible range).

Prey were attacked by moving the mouse cursor over the item. On attacking a profitable prey item, the human predator added b (=1) points to its total displayed score, while on attacking an unprofitable prey item the predator lost c (=1) points from its score. To enhance the stimulus (Rowe 2002), attacks on profitable and unprofitable prey generated distinct sounds. Prey that were successfully attacked disappeared from the screen. Profitable prey were always killed on attack, but unprofitable prey survived attack with a fixed probability q (=0, except where stated).

Generations came to an end when 50% of the total starting prey population (totals $N_U = 50$ unprofitable and $N_P = 50$ profitable prey except where stated) had moved past the predator. Surviving individuals of each species at the end of each generation were allowed to reproduce back to their starting densities by randomly selecting a parent for each of the individuals in the new generation from the total pool of parental survivors of each species. During reproduction there was a 5% chance, analogous to a mutation, that any given gene of an offspring would have a different allele from that of its parent. Following mutation, an offspring's step size differed from its parent by a randomly chosen real number between -50 and $+50$ mm, waiting time was increased or decreased by a randomly chosen real number between -500 and $+500$ ms, or the angular range was increased or decreased by a randomly chosen real number between -0.2 and $+0.2$ (all subject to aforementioned limits placed on these parameters).

Experiment 1

In experiment 1 we simply evaluated the catchability of profitable prey with different step sizes (10, 25, 50, and 100 mm), waiting times (50, 100, 500, and 1,000 ms), and angular ranges (0.1, 0.5, and 0.9 equivalent to 18° , 90° , and 162° range, respectively) by presenting these 48 forms in random order and asking volunteers to attempt to attack them. This same set of 48 prey phenotypes was presented 10 times in succession to a given volunteer (each time in random order, with no evolution), and we replicated this experiment for 10 different human predators.

Experiments 3–6

All other experiments were replicated 5 times, with each individual predator continuing to attack prey for 20 prey generations (individual replicates taking approximately 35–45 min each to complete). In the vast majority of these experiments, the initial values of s for each of the 50 prey items of each species were selected from a truncated normal distribution with mean 50 mm and standard deviation 50 mm ($mins=1$, $maxs=100$); the initial values of w were selected from a truncated normal distribution with mean

500 mm and standard deviation 500 ms ($minw=10$, $maxw=2,000$), while a was selected from an even distribution between 0 and 1 (unprofitable prey in experiments 7–10 were set rather differently). In experiment 2 we considered how step size, waiting times, and angular range tend to evolve when only 50 profitable prey were present ($N_D = 0$). Experiment 3 had very similar aims, but this time we also introduced readily identifiable unprofitable prey. In experiment 4 unprofitable and profitable species were both patterned in form, but they could be distinguished on careful inspection of their colors (imperfect mimicry). Our interest here was whether there would be selection for unprofitable prey species to move slowly, thereby rendering themselves more readily distinguishable from profitable prey. In experiment 5 the unprofitable and profitable prey species were morphologically identical, while in experiment 6 we ran an analogous set of experiments with perfect mimicry but this time allowing unprofitable prey to survive attacks with a relatively high probability ($q=0.8$). In this latter pair of experiments, we anticipated that the locomotory behavior of unprofitable prey would not be subject to such intense selection. A key question therefore was whether differential selection would give rise to differences in behavior and/or whether profitable prey would be selected to mimic them.

Experiments 7–10

In experiments 7–10 unprofitable and profitable species were identical in appearance, but only the movement characteristics of profitable prey species were allowed to evolve. Unprofitable prey were set to be either slow and predictable (experiments 7 and 9, $s=25$, $w=1,000$, $a=0.2$) or fast and unpredictable (experiment 8, $s=75$, $w=100$, $a=0.8$; experiment 10 $s=75$, $w=400$, $a=0.8$). In all cases, profitable prey began with mean s at 50, mean w at 500, and mean a at 0.5, as described earlier. Here we were interested to see whether profitable prey would evolve movement characteristics that resembled unprofitable prey and/or whether they would be selected to evolve rapid movement. In experiments 7 and 8, parameters s , w , and a were subject to the limits described earlier. However, we were also interested in seeing whether mimicry evolved in profitable prey when even the fastest and most erratic forms could be readily caught (as indicated by experiment 1). Therefore, in experiments 9 and 10 we limited w to a minimum of 300 milliseconds.

Controls

Finally, to evaluate how s , w , and a would evolve for 20 generations in the absence of predation (through genetic drift alone), we began with the same starting conditions as described for experiments 2–6 and ran 1,000 simulations in which no mortality occurred yet the same inheritance and mutation rules were applied. Because morphological similarity between profitable and unprofitable prey plays no role when there is no visual selection, these runs effectively represent general no-predation controls for all of these experiments.

Results

Evolution of movement characteristics in profitable prey

As expected, prey items that moved with long steps (s) and short waiting times (w) between steps were the least catchable of the phenotypes by the human predators (Fig. 1). A simple (no interaction terms) four-way analysis of variance on the proportion of a given phenotype caught by human predators indicated that the values of step size and waiting time both strongly influenced catchability

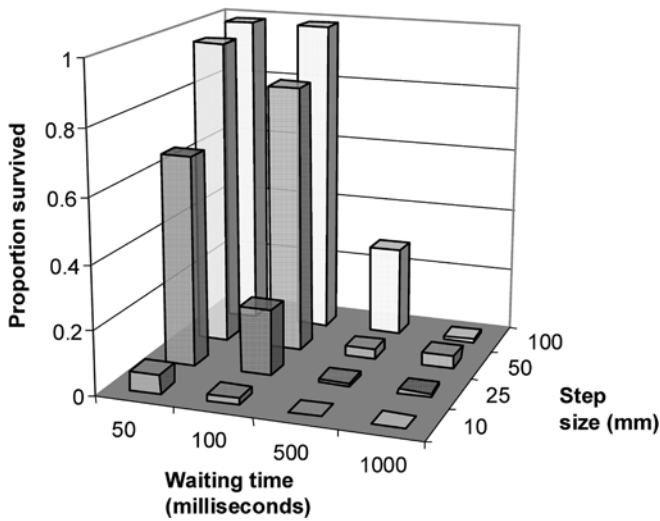


Fig. 1 A range of different locomotory phenotypes were released in random order in 10 consecutive batches, replicated for 10 different human subjects (100 releases per phenotype). Here we show the survival rates of phenotypes with 4 levels of step size and 4 levels of waiting time (angular range was held at 0.5). Short inter-step waiting times enhanced prey survival, particularly when step sizes were long

(speed $F_{3,462} = 157.56$, $P < 0.001$, time $F_{3,462} = 272.73$, $P < 0.001$). The proportion caught did not vary significantly with either the angular range ($F_{2,462} = 0.56$, $P > 0.05$) adopted by prey or the human subject ($F_{9,462} = 0.62$, $P > 0.05$).

In experiment 2 (and indeed in most other experiments) profitable prey items became much harder to catch over time (several orders of magnitude harder, Fig. 2a), primarily as a consequence of their much lower evolved waiting times (Fig. 2b). Comparison of the results of experiments 2 and the no-predation controls indicated that the final mean waiting times of profitable prey after 20 generations differed according to whether there was predation, but no other locomotory characteristics differed significantly [multivariate analysis of variance (MANOVA) on presence /absence of predation Pillai's trace = 0.032, $F_{3,1001} = 11.10$, $P < 0.001$; Wilks' lambda = 0.968, $F_{3,1001} = 11.10$, $P < 0.001$; step size $F_{1,1003} = 1.58$, $P > 0.05$; waiting time $F_{1,1003} = 30.94$, $P < 0.001$; angular range $F_{1,1003} = 1.14$, $P > 0.05$]. As expected from observing the actual trials, the final mean evolved waiting times of profitable prey with predation were significantly lower (more than 10 times so) than the waiting times of their respective controls without predation (45.5 and 674.1 ms, respectively, $t_{1003} = 5.562$, $P < 0.001$).

Differences in the evolved movement behavior of profitable and unprofitable species

The results of experiments 3–5 (as well as experiment 6 and controls) are summarized in Fig. 3a–c. Here we wished to compare the locomotory attributes that finally evolved in profitable and unprofitable prey after 20

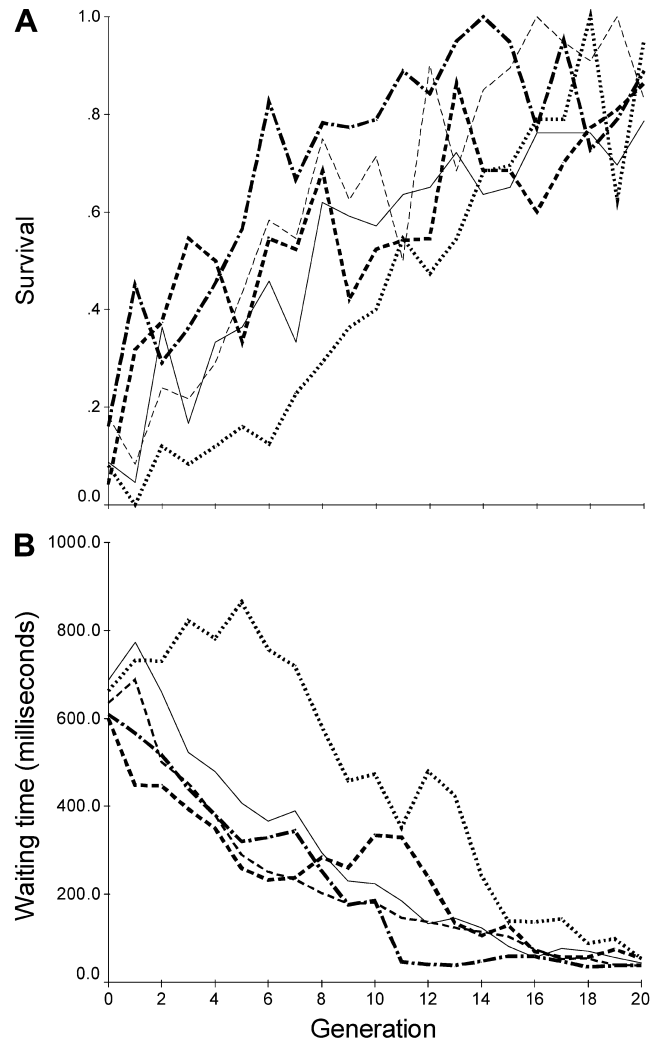


Fig. 2A, B Results of five simulations involving only profitable prey (lines show the separate replicates) in experiment 2 (no unprofitable prey present). **A** The proportion of prey items released into the arena that survive increased over 20 generations of selection. **B** This enhanced survivorship arose largely because profitable prey consistently evolved short inter-step waiting times

generations and to examine whether the degree of morphological mimicry between the two species influenced these differences (experiments 3–5). As both species were subject to selection by the same human predator in any given trial, their evolved responses may not be independent. There was little evidence for lack of independence (relatively few correlations between the attributes of profitable and unprofitable prey within individual experiments were statistically significant). However, to be conservative, we conducted a MANOVA on the *difference* in movement attributes between unprofitable and profitable prey per replicate in experiments 3–5. All multivariate tests of the effects of mimicry on the difference in attributes were highly significant (Pillai's trace = 0.904, $F_{6,22} = 3.03$, $P = 0.026$; Wilks' lambda = 0.207, $F_{6,20} = 3.99$, $P < 0.01$). Separate ANOVAs (Zar 1999) indicated that the difference in mean waiting times between profitable and unprofitable prey per

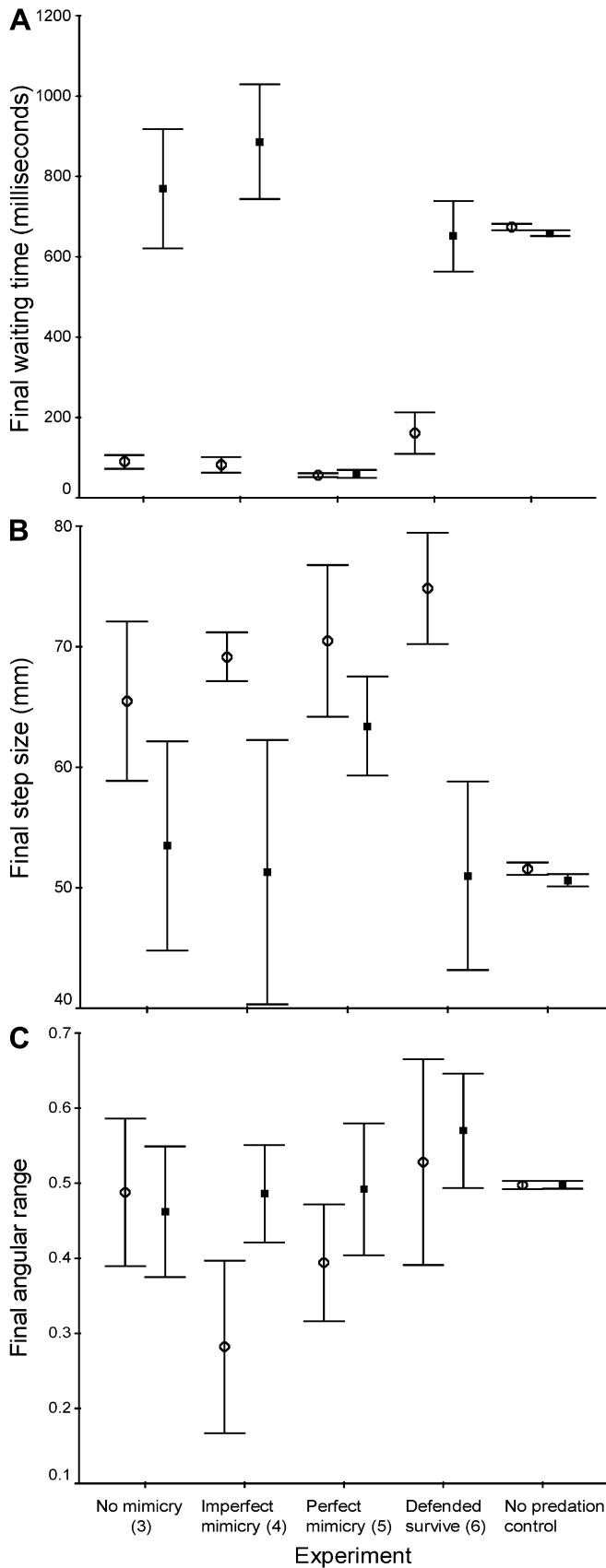


Fig. 3 Final evolved **A** mean waiting times, **B** step sizes, and **C** angular ranges in profitable (*open circles*) and unprofitable prey (*dark squares*) when the two species morphologically resembled one another to a varying extent (no mimicry, imperfect mimicry, and perfect mimicry) and when unprofitable prey survived the majority of attacks (experiments 3–6 respectively). Overall means are shown ± 1 SE, based on their respective within-treatment variances

replicate varied according to the extent of mimicry (difference in step size between profitable and unprofitable prey of the same replicate: $F_{2,12}=0.27$, $P>0.05$; difference in waiting time: $F_{2,12}=16.27$, $P<0.001$; difference in angular range: $F_{2,12}=1.10$, $P>0.05$). Furthermore, separate matched tests for individual experiments indicated that unprofitable and profitable prey differed in mean waiting times in experiment 3 (no mimicry, means 769.4 and 89.9 ms, respectively, $t_4=4.94$, $P<0.01$), experiment 4 (imperfect mimicry, means 886.2 and 82.8 ms, respectively, $t_4=6.50$, $P=0.003$), and experiment 6 (unprofitable prey tend to survive, means 651.1 and 160.8, respectively, $t_4=4.21$, $P<0.01$).

Closer inspection of the data revealed some interesting patterns (here we have concentrated on evolved waiting times because this parameter had the greatest influence on prey catchability). Analysis of experiment 4 (imperfect mimicry) showed not only that unprofitable prey moved more slowly than their profitable counterparts but also that these unprofitable prey moved significantly more slowly than unprofitable prey in controls with no predation (means 886.2 and 658.6 ms, respectively, $t_{1003}=2.15$, $P<0.05$). No such significant difference arose when we compared the final evolved waiting times of unprofitable prey with no mimicry (mean 769.35 ms, experiment 3) with the same no-predation controls ($t_{1003}=1.05$, $P>0.05$). The possibility that active selection may have contributed to slow movement in unprofitable prey that were imperfectly mimicked (experiment 4) was further supported by investigating the outcomes of selection in each generation. Profitable individuals that survived attack had consistently shorter mean waiting times than conspecifics that did not survive attack (although both declined over time). By contrast, surviving unprofitable prey had consistently longer mean waiting times than those conspecifics that did not survive attack.

When mimicry was perfect but unprofitable prey had a 0.8 probability of surviving attack (experiment 6), unprofitable prey again evolved to move more slowly than profitable prey. However, in this case the final mean waiting times of unprofitable prey were not significantly different from their respective controls (651.0 and 658.6 ms, respectively, $t_{1003}=0.07$, $P>0.05$), indicating that unprofitable prey had differed in movement speeds from profitable prey simply because they were not under intense selection to avoid predation.

Evolution of locomotor mimicry

Finally, we examined what forms evolved in a system with perfect morphological mimicry when the locomotory

behavior of unprofitable prey was fixed and when profitable prey were either unrestrained or restrained from moving quickly (experiments 7–10). Profitable prey did not differ in their final evolved locomotory characteristics when the unprofitable models moved slowly (experiment 7) compared to when unprofitable prey moved quickly (experiment 8). All multivariate tests of the effects of unprofitable prey locomotion on the evolved locomotory characteristics of profitable prey were non-significant ($P>0.05$), while separate ANOVAs were also non-significant (step size $F_{1,8}=0.77$, $P>0.05$; waiting time $F_{1,8}=0.76$, $P>0.05$; angular range $F_{1,8}=0.11$, $P>0.05$); in both cases, profitable prey evolved rapid movement. Indeed, despite the potential advantages of mimicry, profitable prey moved significantly faster than unprofitable prey when unprofitable prey were slow [experiment 7, step size (mean 62.0 vs 25) $t_4=3.79$, $P<0.02$, waiting time (mean 157.69 vs 1,000) $t_4=9.46$, $P<0.001$, angular range (mean 0.60 vs 0.2) $t_4=3.06$, $P<0.05$]. By contrast, when profitable prey were prevented from moving too fast (limiting their ability to escape), they generally evolved to resemble their slow-moving unprofitable models [experiment 9, step size (mean 54.2 vs 25) $t_4=1.91$, $P>0.05$, waiting time (mean 680.1 vs 1,000) $t_4=2.20$, $P>0.05$; angular range (mean 0.53 vs 0.2) $t_4=3.07$, $P>0.05$]. These results are perhaps best visualized by comparing the characteristics of profitable prey items that evolved in experiments 7 and 9 (Figs 4a, b). When profitable prey were unrestrained, they consistently evolved short waiting times and high step sizes because this allowed them to escape predation (Fig. 4a; note the presence of some individuals that may gain advantage through mimicry). By contrast, when profitable prey were restricted in their minimum waiting times, the vast majority of the population evolved closer locomotor mimicry (Fig. 4b).

Discussion

In the artificial world we created, unprofitable species tended to evolve significantly slower movement than profitable prey, a finding consistent with natural observations (Whitman et al. 1985; Marden and Chai 1991; Pinheiro 1996; Hatle et al. 2002). By controlling variables, we have shown that unprofitable prey are likely to evolve slower movement speeds than profitable prey when (1) unprofitable prey are under no, or significantly less, selection to avoid predation compared to profitable prey (as postulated by Chai and Srygley 1990; Srygley and Chai 1990a, 1990b) and when (2) unprofitable prey are under selection to avoid being mistaken for profitable prey (as postulated by Guilford 1986; Srygley and Chai 1990b).

Condition 1 arose when both prey types were morphologically distinguishable (experiment 3), but it also arose when the prey species were morphologically identical and unprofitable prey frequently survived attacks (experiment 6). These latter results serve to emphasize the fact that just because a pair of profitable and unprofitable prey species is morphologically identical, there should not

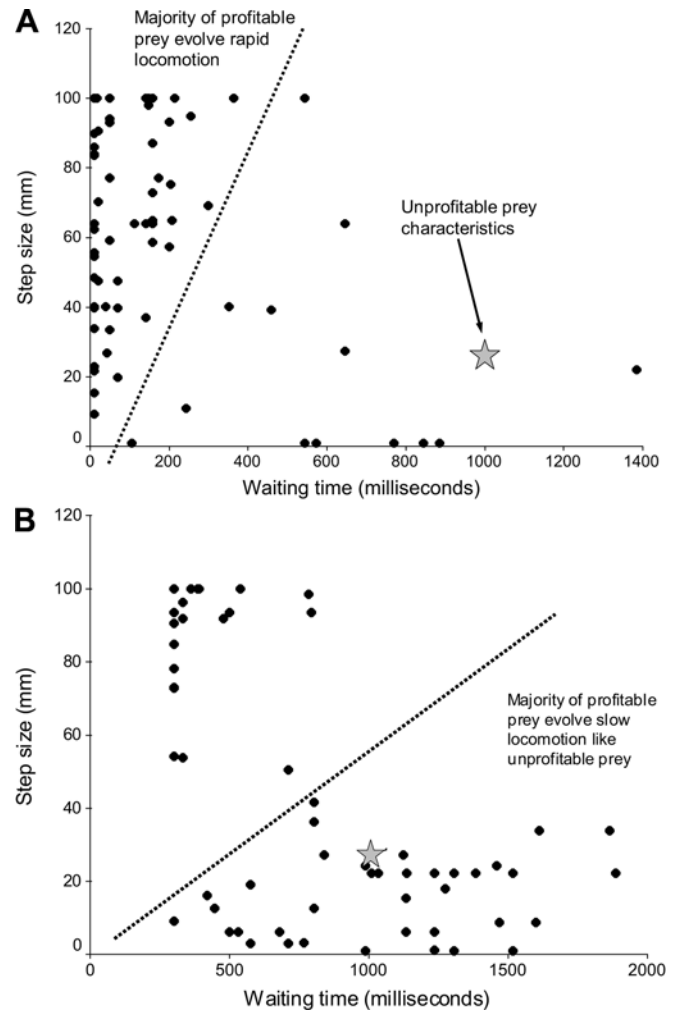


Fig. 4 Combinations of step size and waiting times of profitable prey items that evolved in the final generation of **A** experiment 7 (unprofitable prey slow, profitable prey unrestrained) and **B** experiment 9 (unprofitable prey slow, profitable prey with restricted minimum waiting time). In each case data from all 5 replicates are shown. Morphologically identical profitable prey evolved to mimic unprofitable prey in behavior only when they could not evade predation by flying fast (experiment 9)

necessarily be selection on profitable prey to move like unprofitable prey. Indeed as experiments 7–10 confirmed, only when profitable prey have no reliable means of avoiding predation via movement will there be selection to resemble the locomotory characteristics of unprofitable prey. Srygley (1994) made a similar observation when he analyzed morphological characters associated with butterfly flight and suggested that Batesian mimics (such as the butterfly *Consul fabius*) may retain certain features that contribute to their speed and maneuverability. Put simply, if mimics can avoid predation by flying quickly, then there may be little or no selective advantage in precisely adopting the flight characteristics of slow-flying models. Mimicry can only generate as good a survivorship (=1) as an effective escape, but never higher survivorship. Interestingly, the dronefly *Eristalis tenax* resembles the honeybee *Apis mellifera* not only in morphology but also

generally in its flight behavior, yet here again the mimic appears to retain certain characteristics that enable it to evade predators (Golding et al. 2001).

Condition 2 arose when unprofitable and profitable prey resembled one another closely but not perfectly (experiment 4). Under these conditions, unprofitable prey experienced active selection to slow down so that they could be more readily identified as the unprofitable species. Clearly, members of profitable prey species would not gain any selective advantage by similarly adopting more sluggish behavior, since slow movement would ensure that they were more readily identified and attacked. These observations are entirely consistent with the perceptive comments of Chai (1996) who noted (p. 63), “the low frequency of cheaters is probably due to the fact that unpalatable butterflies with their associated morphological and behavioral adaptations facilitate detection and capture” (this may be no mere coincidence—see Sherratt and Beatty 2003).

Further experiments (Sherratt, Rashed, and Beatty, unpublished) have found that the locomotory parameters of profitable and unprofitable prey will evolve in response to the metabolic costs imposed (introduced by reselecting a potential parent in the inheritance algorithm with a particular probability, dependent on the step size, waiting time, and angular range). However, even with high costs, profitable prey still evolved more rapid movement than unprofitable prey. In effect, a compromise was achieved in which profitable prey evolved to reduce their metabolic costs without making themselves too easy to catch. The parameter that responded most clearly to the imposition of metabolic costs was angular range. This result is readily understood because while angular direction was metabolically expensive, it had little effect on prey catchability.

In a general sense, our work supports the view that escape and unpalatability are alternative ways of avoiding attack (Pinheiro 1996). Thus, when unprofitable (unpalatable) prey were readily recognized, there was no selection on these individuals to evolve the rapid movement that necessarily evolved in profitable prey. However, important complications arise when a degree of mimicry occurs. When unprofitable and profitable prey were distinguishable through some subtle differences in morphology or survivorship, unprofitable prey typically evolved slower movement, often as a signaling trait. By contrast, our results predict that when the mimetic burden is high and when unprofitable and profitable species are completely indistinguishable (experiment 5), then even unprofitable prey should evolve fast movement that renders them difficult to catch by predators.

In summary, the outcomes from our artificial simulations appear to match what researchers have observed in nature and generally support their earlier interpretations. Our approach differs considerably from a typical simulation model in that we have used living predators, albeit humans, rather than simplified mathematical algorithms to represent psychological and mechanistic processes such as learning and prey capture. We hope that this type of computer experiment, using humans as predators, may

prove to be a valuable tool for assisting in the evaluation of hypotheses relating to the evolution of defensive traits, particularly those traits which are otherwise difficult to manipulate experimentally.

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