Balancing Biomechanical Constraints: Optimal Escape Speeds When There Is a Trade-off between Speed and Maneuverability

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Synopsis The ability for prey to escape a pursuing predator is dependent both on the prey’s speed away from the threat and on their ability to rapidly change directions, or maneuverability. Given that the biomechanical trade-off between speed and maneuverability limits the simultaneous maximization of both performance traits, animals should not select their fastest possible speeds when running away from a pursuing predator but rather a speed that maximizes the probability of successful escape. We explored how variation in the relationship between speed and maneuverability—affects the optimal choice of speed for escaping predators. We used tablet-based games that simulated interactions between predators and prey (human subjects acting as predators attempting to capture “prey” moving across a screen). By defining a specific relationship between speed and maneuverability, we could test the survival of each of the possible behavioral choices available to this phenotype, i.e., the best combination of speed and maneuverability for prey fitness, based on their ability to escape. We found that the shape of the trade-off function affected the prey’s optimal speed for success in escaping, the prey’s maximum performance in escaping, and the breadth of speeds over which the prey’s performance was high. The optimal speed for escape varied only when the trade-off between speed and maneuverability was non-linear. Phenotypes possessing trade-off functions for which maneuverability was only compromised at high speeds exhibited lower optimal speeds. Phenotypes that exhibited greater increases in maneuverability for any decrease in speed were more likely to have broader ranges of performance, meaning that individuals could attain their maximum performance across a broader range of speeds. We also found that there was a differential response of the subject’s learning to these different components of locomotion. With increased experience through repeated trials, subjects were able to successfully catch faster and faster dots. However, no improvement was observed in the subject’s ability to capture more maneuverable prey. Our work highlights the costs of high-speed movement on other traits, including maneuverability, which make the use of an animal’s fastest speeds unlikely, even when attempting to escape predators. By investigating the shape of the trade-off functions between speed and maneuverability and the way the environment and morphology mediates this trade-off, we can begin to understand why animals choose to move at the speeds they do when they are running away from predators or attempting to capture prey.

Introduction

Predation is one of the most powerful ecological factors affecting the functioning of ecosystems (Lima and Dill 1990). Both the direct and indirect actions of predators can shape populations, communities, and ecosystems (Lima and Dill 1990; Schmitz 1998; Pavey et al. 2008; Wesner et al. 2012; Miller et al. 2014). Because the threat of predation is so important, animals must constantly decide how best to use their time to balance the need to acquire energy and nutrients for growth, maintenance, and reproduction against the dangers of being eaten...
(Brown and Kotler 2007). Greater time spent foraging to gain resources makes it more likely that an individual will encounter a predator (Brown and Kotler 2007). Understanding how animals optimize their foraging decisions to balance these trade-offs between resources and predation has been a focus within foraging ecology for decades (Ydenberg et al. 2007). Although biomechanical trade-offs also have the potential to shape the behavior of prey, we know little about how animals balance these competing functional demands (Wilson et al. 2014). For example, the ability for an animal to escape a pursuing predator will rely not only upon its speed of movement but also upon its ability to make sharp, rapid turns away from the predator (Howland 1974; Hedenstrom and Rosen 2001; Wilson et al. 2013). However, the faster an animal moves forward the poorer its ability to turn becomes (Alexander 1982). Speed compromises turning ability because animals require larger coefficients of friction when turning at higher speeds or at sharper angles (Alexander 1982). Northern quolls (Dasyurus hallucatus), for example, must decrease their speed to about 35% of their maximum in order to successfully navigate a 135° turn, with speeds higher than 50% of their maximum markedly increasing their probability of crashing at this angle (Wynn et al. 2015).

Given the biomechanical trade-off between speed and maneuverability, and the importance of both traits for escaping predators, how fast should an animal run away from a pursuing predator? Selection of the optimum combination of speed and maneuverability should be based on the strategy that results in the highest probability of survival. Howland (1974) modeled the influence both of forward speed and of turning radius on whether prey can escape a predator using sharp, rapid turns in a turning game. Based on this model, he suggested that a prey should escape when its normalized speed (prey speed/predator speed) is greater than the square root of its normalized turning radius (prey’s turning radius/predator’s turning radius). One complication for exploring the importance of both speed and maneuverability for escape behavior and exploring the optimal locomotor behavior of prey is that it is more difficult to quantify an individual’s maneuverability than its straight-line speed. Encouraging individuals to run and maneuver around obstacles at different speeds is problematic—and it is not surprising that most studies of performance only quantify speed using straight runways (Miles 2004; Irschick and Meyers 2007; Irschick et al. 2008; Clemente et al. 2009).

Recently, Clemente and Wilson (2015) used a custom, tablet-based game that simulated encounters between predator and prey as an alternative approach for exploring the relative roles of speed and maneuverability for success in escaping predators. Human subjects were asked to “capture” simulated on-screen prey (dots on screen) by touching them as they moved across the tablet’s display; prey varied in size, speed, and maneuverability. Clemente and Wilson (2015) manipulated the prey’s maneuverability by altering the angle that prey changed directions while keeping the number of turns constant. The maneuverability of their simulated prey was based on the evasive tactics of fruit flies, which explore their habitat using a series of straight flights interspersed with rapid turns in random directions (Tammero and Dickinson 2002). These routine erratic turns during flight were found to be more successful in avoiding predators than were active evasive maneuvers (Combes et al. 2012). So is it better to be fast or to perform erratic turns in order to escape predation? Clemente and Wilson (2015) found that success in escaping was determined both by speed and by maneuverability—slow prey could still escape predation when highly maneuverable, while prey that were poorly maneuverable could only escape when traveling rapidly. Importantly, because small changes in speed translated into successful escape in a different way than did changes in maneuverability, the shape of the trade-off between speed and maneuverability—or how an individual’s ability to turn is affected by its speed—is likely to have complex effects on the success of escape. Yet would the same optimum behavior be found in a wide variety of environments?

An animal’s environmental substrate is likely to affect the way increases in speed affect its maneuverability and the optimal combination of both parameters for successful escape. For example, surfaces with high friction should allow much greater turning angles at high speeds than would surfaces with low friction (Fig. 1) (Alexander 1982). Anyone who has tried to change directions while running along a slippery surface has experienced the dangers of a low-friction surface for maneuvering. High straight-line speeds may offer a much greater probability of successfully escaping a predator on low-friction surfaces (e.g., ice) than does using a maneuver that would only be possible at very low speeds. In contrast, it may be possible to also use highly maneuverable turns at a greater range of speeds on high-friction surfaces, broadening the potential fitness-landscape. In other words, the
optimum choice of speed for escape may be dependent on the environmental conditions that affect the shape of the speed-maneuverability trade-off.

In this study, we explored how variation in the relationship between speed and maneuverability—or the shape of the trade-off—affects the optimal choice of speed for escaping a predator. We built upon the work of Clemente and Wilson (2015) by using the custom, tablet-based game that simulated encounters between predator and prey. By defining a specific relationship between speed and maneuverability (shape in trade-off), we could then test the survival of each of the possible behavioral choices available to this phenotype. Thereby, for each specific trade-off between speed and maneuverability we could determine the best combination for escaping a predator. We used five independent experiments to test how variation in the shape of the trade-off between speed and maneuverability affects the relationship between a prey's speed and its probability of escape. The logic behind our analyses is that we sought to identify the speed of the prey (which coincides with a specific maneuverability depending on the trade-off) that resulted in the highest probability of successful escape. As each experiment compared different trade-offs between speed and maneuverability, we wanted to (i) compare the optimum speed for successful escape among these trade-off functions, (ii) detect the range of speeds of potential prey that were associated with relatively high success in escaping (performance breadth), and (iii) identify the peak escape-performance that occurred at their optimal speed.

**Methods**

**Programming the tablet**

Our experiment was based on a simulated prey item (dot) moving across the visual field of a predator (human subject) and assessing the prey's ability to avoid capture. Each trial—or encounter with a predator—involved a single dot (representing the prey item) moving from left to right across the screen of a 10-inch Android Tablet (Google Nexus 10—2560 x 1600 pixels, Running Android Ver 4.2). The speed and maneuverability of the dot was varied, based on a pre-populated list that was dependent on the function of a trade-off between each parameter of performance (Fig. 2—input). The ability of the prey to escape was then assessed across the range of combinations of speed and maneuverability that were associated with each trade-off. Five functions that described the trade-off between speed and maneuverability were tested in each experiment. Each function describing a trade-off was represented by 20 individual prey that differed in speed and maneuverability.

For each experiment, an individual human subject was exposed twice to the 100 different combinations of the speed and maneuverability of prey. That is, each of the 100 phenotypes were taken from the five trade-off functions, each represented by 20 individual prey. The order of trials within each experiment was randomly allocated using a random-sequence generator. In total, 152 subjects, half of which were males and half of which were females, were recruited from the University of Queensland and surrounding suburbs. Each subject then attempted to catch the prey item by tapping on the moving dot. Subjects were given feedback on their success after each trial, as either a hit (error < radius) or a miss (error > radius). Subjects were not required to
try to capture every prey dot, yet there was no penalty for attempting to do so.

The program was written using the open-source programming language Processing (Processing.org) and then transferred to the tablet using the Android-system development kit (developer.android.com). The code used during trials was similar to that used by Clemente and Wilson (2015). In summary, the code repeats a draw loop that moves an ellipse a given distance for each loop. The draw loop functions at 60 Hz. At the beginning of each trial, speed and maneuverability of the dot are read from the pre-populated list for each experiment. Speed was measured in pixels per loop and determines the distance moved from left to right per loop. Maneuverability defines a potential arc of movement from 0 degrees (i.e., only able to move left to right across the screen) to 180 degrees (able to move at any angle from the horizontal of left to right). The direction is modified every 5th loop by randomly selecting an angle that deviates from horizontal, within the given arc. Thus, for each loop, the dot will move a set distance in the direction defined by the angle from the horizontal.

Each prey continues across the screen until either the screen is touched or the dot reaches the limit of the screen’s width on the right-hand side of the tablet. At the conclusion of each single event a line of text is written that contains the trial number, the distance and range moved, the position of the dot when the screen is touched, and the center of the point where the screen is touched. The error is the straight-line distance between the center of the dot and the center area of touch.

Comparison of prey’s escape-performance between trade-off functions

We used five independent experiments to test how variation in the shape of a trade-off between speed and maneuverability affects the relationship between the speed of the prey and its probability of escape. In Experiment 1, we examined how speed affected the probability of escape for prey that possessed five different linear trade-offs between speed and maneuverability ($N=28$ subjects). The point of intersection of all five trade-off models occurred at the prey’s top speed in which their maneuverability was lowest. Across all five trade-offs, speed varied from 0.1 to 60 pixels per loop. This upper limit of speed was chosen because preliminary experiments found this to be the approximate limit of most subjects’ ability to catch moving dots across the screen. Each of the five trade-off functions differed in how maneuverability increased with decreases in speed. The shallowest trade-off was for the function in which only small increases in maneuverability resulted from larger decreases in speed. This shallowest trade-off was designed to replicate a situation in which an animal is running along a slippery substrate that constrains the animal’s ability to change directions at higher speeds. Subsequent models had steeper trade-offs between speed and maneuverability, which are representative of running and changing directions on increasingly higher-friction substrates. Experiment 2 was identical to Experiment 1 except that the maximum absolute speed was lower, and the range varied between 0.1 and 40 pixels per loop ($N=30$ subjects). We expected that this lower range in maximum speed would result in a lower probability of escape for the prey that used only straight movements. This accurately describes many predator–prey interactions in nature in which it is the predator, rather than the prey, that possesses the greater maximum speed.

In Experiments 3 and 4, we again explored how speed of movement by the prey affected the probability of escape when the magnitude of the trade-off between speed and maneuverability varied. However, in this case the points of intersection between all the trade-off functions occurred at mid-speeds. This meant that any increases in maneuverability at lower speeds were associated with equivalent decreases in maneuverability at higher speeds. It was the slope of this function that represented the magnitude of the trade-off. Thus, we compared five different trade-off functions that differed in magnitude, with the steepest trade-offs possessing the highest maneuverabilities at low
speeds and the lowest maneuverabilities at high speeds. The lowest trade-off showed no change in maneuverability with a change in speed. In Experiment 3 the top speed was 60 pixels per loop and in Experiment 4 the top speed was 40 pixels per loop (N=30 subjects in each case).

Finally, in Experiment 5 we explored how speed of the prey affected the probability of escape when the shape of the trade-off between speed and maneuverability varied in non-linear ways. The ability of some animals to change direction may not be greatly affected until they are close to their top speed. Alternatively, an animal’s ability to maneuver may be compromised at low speeds. In Experiment 5 the top speed was 40 pixels per loop (N=30 subjects).

Varying predators’ ability
The above examples varied only the attributes of the prey species, but it is also of interest to determine the effect of variation in a predator’s performance as it affects the prey’s optimal speed for escape. To do this we allowed four subjects to complete Experiment 1 10 times in a row with the expectation that predators will become better at catching dots with more experience. We then analyzed the effect of increased skill of the predator on different types of trade-off.

Statistical analysis
The logic behind our analyses is that we sought to identify the prey’s speed that resulted in the highest probability of successful escape. For each trade-off between speed and maneuverability, we wanted to (i) compare the optimum speed to use for escape among these trade-off functions, (ii) identify the range of potential speeds of the prey that were associated with high success in escape, and (iii) ascertain the peak performance in escape that occurred at the prey’s best speed. Using performance curves to evaluate function–value traits has a rich history in thermal biology (Huey and Stevenson 1979; Huey and Kingsolver 1989; 1993; Angilletta et al. 2002, 2010; Angilletta 2009) and we used the methodologies for describing thermal performance curves to compare the parameters of success for each trade-off function between speed and maneuverability. To quantitatively compare the effects of the different trade-off functions within each experimental group on the prey’s performance in escape, we used the error distance (the distance between the center of the dot and the center of touch) as a continuous variable to produce a performance curve for each trade-off model with increasing speeds. The greater this distance, the greater is the error by the predator, and the farther is the prey from the predator’s strike. This distance was logarithmically transformed to normalize it. Based on analyses of thermal performance curves, we then extracted three variables to compare among the phenotypes with different trade-off functions (Fig. 3). The maximum error of the score (MaxErr) was the greatest mean distance between the prey’s position and the central point of the predator’s strike for each phenotype. The prey’s speed at the maximum error was taken as a phenotype’s optimal speed of escape (SpEsc). The range of prey’s speeds over which a phenotype had an error distance that was 80% of their maximum error was taken as their breadth of performance (BrScr).

Data were analyzed in the statistical computing language R (R Development Core Team 2014). We used the glm.R function from the base package in R to perform the binomial generalized linear model fit, to confirm that both speed and maneuverability had a significant effect on the probability of the dot being hit. For each of the three variables that were extracted from the performance curves, we used a one-way within-subjects ANOVA using the aov.R function from the base package in R. Tukey post-hoc tests were performed using the TukeyHSD.R function also from the base package. To determine the effect of learning we used the error distance in a three way-factorial design implemented using the aov.R function in R, including speed, maneuverability, and trial number. Similarly for performance-curve variables, we used a two-way within-subjects ANOVA using the aov.R function.

Results
Both speed and maneuverability independently affected the probability of escape (Experiment 1: Speed z=-32, P<0.001; Maneuverability z=-11, P<0.001). The relationship between a prey’s speed and its success in escaping was described by a logistic function (Fig. 4a) while there was a positive linear relationship between maneuverability and escape (Fig. 4b).

For Experiment 1, the peak performance and the optimal speed of escape did not significantly vary among the phenotypes that differed in trade-offs between speed and maneuverability (MaxErr $F=0.84$, $P=0.499$; SpEsc $F=1.8$, $P=0.133$). However, the range of speeds over which escape performance was 80% of maximum significantly
Fig. 3 The input (left) and results (right) for five different experiments modeling trade-offs between speed and maneuverability. For each experiment five different model trade-offs were tested, representing low friction surfaces (lighter shades) to higher friction surfaces (darker shades). (This figure is available in black and white in print and in color at Integrative and Comparative Biology online.)
varied among phenotypes with different trade-offs (BrScr $F=7.1$, $P<0.001$; Fig. 5). A Tukey post-hoc test suggested that phenotypes with the shallowest trade-offs (phenotypes 1 and 2) were significantly different from phenotype 5. In Experiment 2, peak escape performance and the optimal speed of escape also did not significantly vary among the phenotypes (MaxErr $F=0.35$, $P=0.854$; SpEsc $F=0.34$, $P=0.849$). However, the breadth of speeds over which escape performance was 80% of maximum significantly varied among the phenotypes (BrScr $F=4.7$, $P=0.001$; Fig. 5), with a significant difference between the two most extreme phenotypes (phenotypes 1 and 5) (Tukey post-hoc test).

For Experiment 3, peak performance significantly varied among the phenotypes (MaxErr $F=4.59$, $P=0.002$; Fig 5), with a Tukey’s post-hoc test revealing phenotype 1 (no trade-off) as having the highest peak performance and phenotypes 4 and 5 (steepest trade-offs) the lowest. However, the optimal speed of escape did not vary significantly among the phenotypes that differed in trade-off functions (SpEsc $F=0.67$, $P=0.611$), with the mean optimal speed across all phenotypes at approximately 90% of maximum speed. As for previous experiments, the range of speeds over which performance was 80% of maximum significantly differed among the phenotypes (BrScr $F=4.2$, $P=0.003$; Fig. 5). Phenotypes with the steepest trade-offs (phenotypes 4 and 5) had the broadest range in performance (Tukey post-hoc test). For Experiment 4, the peak performance and the optimal speed of escape did not vary significantly among the phenotypes that differed in trade-off functions (MaxErr $F=0.88$, $P=0.479$; SpEsc $F=1.5$, $P=0.198$), but breadth did vary significantly (BrScr $F=2.62$, $P=0.039$; Fig. 5) and was broadest for those phenotypes with the steeper trade-offs (phenotypes 3 and 5).

For Experiment 5, the peak performance and the optimal speed of escape significantly varied among phenotypes that differed in trade-off functions (MaxErr $F=7.1$, $P<0.001$; SpEsc $F=4.3$, $P=0.003$), but the breadth of the curve did not change among phenotypes (BrScr $F=1.0$, $P=0.384$). The peak performance was greatest for those phenotypes in which increases in the speed of the prey decreased maneuverability only at the higher speeds (phenotypes 4 and 5). Optimal speeds of escape were also lowest for those phenotypes in which increases in the prey’s speed decreased maneuverability only at the higher speeds, which was approximately 70% of peak speed (Tukey’s post-hoc test).

Effect of learning on prey’s survival
When our human subjects conducted more trials their ability to capture the simulated “prey” moving across the tablet’s screen improved. Success in capturing prey increased and the mean error distance decreased as participants performed more trials (Fig. 6). However, the effect of learning on success in capturing prey was dependent on the prey’s speed but not on its maneuverability, suggesting that any improvement in the subjects increased their ability to capture fast, but not maneuverable, prey (Table 1).

We also compared how improvement in the subject’s ability affected parameters that described a prey’s performance among the different phenotypes with varied trade-off functions (Fig. 7). Maximum performance by the prey was affected by its phenotype and trial number. Further, the ability of the subject to improve depended upon the prey’s phenotype, with steeper trade-offs associated with a lower learning response (Table 2). However, optimal escape speed was not affected by the prey’s phenotype or by the trial number (Table 2).

![Fig. 4](https://academic.oup.com/icb/article-abstract/55/6/1142/2363860) Effects of speed and maneuverability showing the effect of speed for all points in Experiment 1, model 1 where maneuverability is nearly constant (a) and the effect of maneuverability, when speed is held constant at 21 pixels/loop (b). The line in each panel represents the curve predicted from the logistic regression model for each performance measure with the probability of being hit. (This figure is available in black and white in print and in color at Integrative and Comparative Biology online.)
Finally, the range of speeds over which performance was 80% of maximum was significantly affected by the prey’s phenotype (as shown above in Experiment 1) but not by its trial number (Table 2). These results indicate that only the maximum performance of the prey was affected by learning, and the magnitude of this change was dependent upon the prey’s phenotype.

**Discussion**

Animals rarely use their fastest running speeds in nature, even when they are fleeing from predators (Irschick and Losos 1998; Wynn et al. 2015). The biomechanical trade-off between speed and maneuverability—both of which are important for escaping predators, make the use of top speeds when running away from predators unlikely. In this
In this study, we explored the influence of different trade-off functions between speed and maneuverability on the way an animal’s selected speed affects its success in escaping predators. We used tablet-based games that simulated the interactions between predators and prey—human subjects acted as predators by attempting to capture “prey” (dots) moving across the screen. Our metric of success in escaping was the distance between the prey (position of the dot on the screen) and the human “subjects” point of contact on the tablet’s screen. The assumption was that the greater the distance between the subject’s contact with the screen and the prey’s position, the lower would be the probability of capture. Although results varied among experiments, we found the shape of the trade-off function between speed and maneuverability affected the prey’s optimal speed for success in escaping, and the breadth of speeds over which the prey’s performance was high relative to its maximum performance.

We found that the optimal speed for escape only varied when the trade-off between speed and maneuverability was non-linear. Phenotypes possessing trade-off functions in which maneuverability was only compromised at high speeds exhibited lower optimal speeds of escape. Because speeds at 80% of a phenotype’s maximum also exhibited relatively high maneuverabilities, then these speeds offered the highest probabilities of successful escape. In contrast, phenotypes possessing trade-offs in which substantial increases in maneuverability were only possible at very low speeds possessed higher optimal speeds for success in escaping. Thus, our results, based on our simulated predator–prey games, show that optimal speeds of escape can be dependent on the nature of the trade-off between speed and maneuverability.

Testing this idea using real-world predator–prey interactions is an important next step and could be undertaken by examining the speeds and trajectories of animals running on different substrates. First, one could quantify the effect of substrate friction (e.g., compacted substrate versus slippery rock) on the straight-line running speed and turning ability of an animal. Next, one could observe the actual selected running speeds of the study animal when escaping along the different substrates, thereby testing how they modify their locomotor behavior in response to the kind of substrate. Intuitively, we know that humans do this when running or driving along different substrates (e.g., dry bitumen versus ice), so we should also expect animals to be capable of selecting the most appropriate locomotor behavior for specific circumstances.

Phenotypes that exhibited greater increases in maneuverability for any decrease in speed were more likely to have broader ranges of performance,
meaning that individuals could attain at least 80% of their maximum performance across a broader range of escape speeds. Greater potential speeds with similar successes in escape offer prey a broader range of strategies, making the tactics of prey more difficult to predict. In other words, the advantage of this strategy would be increased behavioral flexibility, allowing an organism to be able to negotiate a range of

![Graph showing the interaction between learning (trial) with different trade-off models based on three characteristics of the performance curve: (a) the maximum error over a range of speeds—MaxErr, (b) the speed at the maximum error—SpEsc, and (c) the breadth score of the performance curve when the error is greater than 80% of maximal error—BrScr.](https://academic.oup.com/icb/article-abstract/55/6/1142/2363860)
environments without a drastic reduction in fitness. Erratic and unpredictable movements can reduce the likelihood of predation (Humphries and Driver 1967; Driver and Humphries 1988; Combes et al. 2012). In addition, a wider range of strategies can allow prey to potentially tail their escape behavior to specific predators and thereby exploit the predator’s weaknesses. Some predators may be very successful at capturing rapid, straight-running prey but struggle when attempting to capture prey that use more maneuverable strategies. Several examples exist in which prey species tailor their escape strategy to the identity and the perceived threat of a predator (Bonenfant and Kramer 1996; Cooper 1997, 2011; Blumstein and Daniel 2005; Cooper and Frederick 2007). If prey species can select among multiple strategies with similar successes, then they should select the strategy that is going to be more difficult for the specific predator.

Flexible tailored strategies have also been observed in response to specific environmental conditions in leaf-cutter ants, *Atta sexdens* (Angilletta et al. 2008). Leaf-cutter ants used straighter, more-predictable trajectories at higher temperatures (when ants are faster) and curved, less-predictable trajectories at lower temperatures (when ants are slower). In a similar way, specialization of *Anolis* lizards to different diameters of perches can have consequences for their behavioral flexibility. *Anolis* with short limbs tend to occupy habitats with narrow perches, while longer-limbed species occupy broad, flat surfaces (Williams 1983). The long-limbed species are faster than shorter-limbed species on broad, flat surfaces, but their speeds dramatically decline on the narrow perches, along with an increase in the number of slippages (Losos and Sinervo 1989). In contrast, the shorter-limbed species experience little decline in speed on narrow perches (Irschick and Losos 1998, 1999; Spezzano and Jayne 2004), and have the flexibility to choose escape paths on narrow and broad surfaces with little decrease in the capacity for performance.

Another potential advantage for a maneuverable strategy is that it could be more difficult for a predator to learn to adapt to unpredictable turns than to the more predictable, but faster, straight-line movement. We tested this idea by examining the ability for our human subjects to learn to capture high-speed prey and highly maneuverable prey. We found there was a differential response to learning these different locomotor components. With increased experience through repeated trials, subjects were able to successfully catch faster and faster dots. However, no improvement was observed in the subject’s ability to capture more maneuverable prey. This reflects previous results using this table-game; human subjects waited for longer periods before attempting to catch faster prey, but the time it took to capture the dot was insensitive to changes in the prey’s maneuverability (Clemente and Wilson 2015). Together, these data suggest that when predators have the potential to improve with experience, there may be a survival advantage for those prey favoring maneuverability at the expense of speed, which decreases the optimum speed for successful escape.

Previous studies exploring the underlying determinants of success in escaping predators have primarily focused on the role of maximum running speeds. There is certainly an intuitive appeal to the idea that individuals with the fastest straight-line running are those that are most likely to escape predation. Indeed, some studies reveal that faster individuals are more likely to escape predators than are slower individuals, but many studies also show a limited influence of the maximum speed of prey on the probability of escape. For example, faster juveniles and adults of the lizard *Urosaurus ornatus* were more likely to survive until the next sampling period than were slower individuals (Miles 2004; Irschick and Meyers 2007); yet sprint speed did not affect survival for hatchlings of the lizard *Sceloporus occidentalis* (Bennett and Huey 1990). However, both speed and maneuverability are likely to determine the probability of escape from a pursuing predator,
and because these two traits are negatively associated we should also expect that the highest probability of escape would result from a compromised strategy between the relative importance of speed and maneuverability. We found that the shape of the trade-off function between speed and maneuverability affects the optimal speed for escape and the flexibility of the behavioral options available to the prey. Our work highlights the need to recognize that the costs for high-speed movement on other traits, including maneuverability, make the use of an animal’s fastest speed unlikely, even when attempting to escape predators.

By investigating the shape of the trade-off functions between speed and maneuverability and the way the environment mediates this trade-off, we can begin to understand the choices of speed by animals running away from predators or attempting to capture prey. We also hope that tablet-based games inspire further studies investigating the evolution of predator-avoidance tactics. The current program has the potential to directly compare the strength of selection on different performance variables, by including multiple generations of dots that are subjected to predation events. Selection of traits over successive generations may highlight competing strategies associated with phenotypic trade-offs and behaviors, and lead to a better understanding of this process, in a way that is almost impossible when studying natural populations.

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