The role of target elevation in prey selection by tiger beetles (Carabidae: *Cicindela* spp.)

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Summary

The elevation of objects in the visual field has long been recognized as a potential distance cue, but it has been demonstrated to a reasonable extent in only four species: humans, frogs, fiddler crabs and backswimmers. Many tiger beetles hunt in flat, sandy areas, and their eyes show 'flat-world' adaptations, such as an extended visual streak of higher acuity that corresponds to the horizon. They are therefore possible candidates for the use of elevation as a cue for distance. We tested this empirically and with simulation. In a behavioral prey selection paradigm, in which starved beetles were presented moving prey-targets having different size, speed and elevation, the beetles showed a strong preference for large targets when these were low in the visual field and a weaker preference for small targets when these were near the horizon. Striking of targets above the horizon was reduced compared to sub-horizontal targets, and lacked the size–elevation interaction. We simulated these empirical results with a model that converted elevation to distance, and used distance to estimate the absolute size of the targets. Simulated strike probability was then determined by the similarity between this absolute size and an independently confirmed preferred prey size. The results of the simulation model matched the empirical data as well as the best statistical model of the behavioral results. While some aspects of the model, and the beetles' behavior, differ from the strict geometry of the 'elevation hypothesis', our results nevertheless indicate that tiger beetles use elevation to estimate distance to prey, and that it is therefore one of the determinants of prey selection.

Key words: depth perception, insect vision, flat world, predatory behavior.

Introduction

The extraction of depth information from the two-dimensional image of a natural scene on the retinas is a problem for many nervous systems and may be determined only probabilistically (Yang and Purves, 2003). Nevertheless, there are strong selection pressures on animals to extract reliable information. Most animals use distance information to slow down appropriately as they approach a goal. Arboreal animals need to know the distance to the next perch when jumping across gaps. Many visual predators would like to know the distance to potential prey so that they can gauge a strike or at least determine whether the pursuit may be energetically worthwhile. A variety of visual cues may be used to determine or estimate distance to an object in the visual field (Hershenson, 1999). Retinal disparity during static binocular vision, ocular vergence, accommodative state and dynamic peering can directly determine object distance within a certain range, even if the image is composed of random dots (Julesz, 1971). Even insects, with their narrow heads and rigid eyes and lenses, have been demonstrated to determine object distance through stereopsis (Rossel, 1983) and through motion parallax derived from peering (Collett, 1978; Sobel, 1990). Most other cues, such as occlusion, perspective, gradients of motion, size and texture, etc. are indirect and allow only relative distances of objects in the scene to be determined. Nevertheless, there is some evidence that insects or other arthropods can use gradients of motion (Forster, 1979) or size (Collett and Land, 1978) as cues to estimate distance.

Another indirect cue that could lead to precise distance determination, if some geometric constraints of the natural environment are met, is elevation of objects in the visual field (Gibson, 1950; Day, 1972; Sedgwick, 1983). Support for this 'elevation hypothesis' has been clearly demonstrated in humans (McGurk and Jahoda, 1974; Wallach and O'Leary, 1982; Warren and Whang, 1987; Philbeck and Loomis, 1997; Ooi et al., 2001) and frogs (Collett and Udin, 1988). It has also been strongly implied in arthropods, such as fiddler crabs (Hemmi and Zeil, 2003) and backswimmer bugs (Schwind,

1978). These latter two, in particular, would be predicted to use elevation as a distance cue, because the geometries of the natural habitats of both fiddler crabs (intertidal sand/mud flats) and backswimmers (pond water surface) are dominated by a flat substrate, which is required for accurate determination of distance from elevation. Indeed, the visual systems of both animals appear to be well-adapted for converting elevation to distance (Schwind, 1980; Schwind, 1983; Zeil et al., 1986; Zeil et al., 1989; Zeil, 1990; Land and Layne, 1995; Zeil and Al-Mutairi, 1996).

The present study tests whether tiger beetles, *Cicindela* spp., use elevation of potential prey in the visual field as a cue for their distance. Tiger beetles are visual hunters and most species pursue their prey in open, relatively flat habitats, such as sand bars, paths in woodlands, and barren ground scrubland (Pearson, 1988; Kaulbars and Freitag, 1993). Moreover, the beetles' visual optics also exhibit some adaptations to flat-world geometry, such as increased visual acuity around the horizontal equator of the eye (Layne et al., 2003). Thus, visually guided pursuit of prey by the beetles might be expected to make use of elevation as a distance cue.

Here we present evidence that tiger beetles initiate pursuit of a target based on its estimated absolute size, which the beetles compute using elevation as the primary cue for target distance, which is in turn used to convert angular subtense to absolute size. Our evidence is twofold: first, results of behavioral experiments demonstrate that tiger beetles prefer targets of different angular size at different elevations. Second, these empirical data are accurately reproduced by a computer simulation 'beetle' that selects prey based on estimating its absolute size from visual angular size and distance, the latter derived from elevation. Our methodology is unique among tests of the 'elevation hypothesis' in that we present the same stimuli to the beetles at locations above and below the horizon. Previous studies of elevation as a distance cue only presented targets below the horizon, because according to the 'elevation hypothesis' only these locations have a defined distance.

Materials and methods

Prey selection experiments

Arena

Prey selection experiments were conducted in the laboratory in an elevated, stationary, circular arena (15 cm diameter) with a white paper floor and transparent acetate wall, centered in a movable surround (17 cm diameter $\times$ 21 cm high). The surround was the same white paper except for a black, high contrast (m=0.817) square target (2°, 4°, 8°, 12°, 16° and 20° angular subtense as seen by a beetle at the transparent wall of the elevated arena). The lower edge of the target was located at various elevations (−20°, −10°, 0°, +10°, +20°) relative to the height of a beetle's eyes at the transparent wall. The beetle eye-height was estimated to be 8 mm, and the absolute dimensions of the target were adjusted to meet the required angular subtense for each elevation. The surround was rotated around the stationary arena by an adjustable 12 V step motor

at five angular velocities (80, 160, 240, 300 and 480 deg. s^{-1}). The target moved parallel to the arena floor, and always rotated around the arena in a counter-clockwise direction, so it approached the beetle from the right. Because the entire wall was transparent, targets were visible as they approached and receded from the beetles' position, and therefore at times they were viewed at elevations closer to the horizon than those listed above. Beetles nevertheless initiated pursuit of targets when they were almost directly opposite the beetle's position at the wall. A total of 150 stimulus combinations was tested (6 sizes $\times$ 5 elevations $\times$ 5 velocities). In addition to fluorescent room lights, a 100 W incandescent light bulb illuminated the arena from above providing a total illumination of approximately 1.66×10^3 lux at the edge of the arena. The arena was brightly lit with the bulb in such a position that there was little or no contrast texture to indicate the edge. Indeed, the beetles bumped into the wall when trying to attack the targets, as though they did not perceive the 1 cm gap. There is no indication that the beetles used information about substrate contour, *per se*. For approximately half of the trials the arena was viewed remotely on a video monitor; the remaining trials were viewed directly by the experimenter.

Protocol

Beetles were tested from June to October; ~90% of the beetles were *Cicindela hirticollis* (Say) (Carabidae), with the rest being either *C. repanda* (Dejean) or *C. rufiventris* (Dejean). Beetles were fed to satiation then starved for 3 or 4 days prior to their initial test and between subsequent tests, and were tested between 10:00–17:00 h to correspond with their natural period of activity. For each trial (stimulus combination), 11–26 beetles were chosen randomly from a population of 98 individuals, save for those excluded from a particular trial due to the feeding/starvation regimen. Individual beetles were tested only once with each stimulus combination, and no beetle was tested with every combination. At the beginning of a trial the beetle was acclimated to the arena for 5 min, during which time it would invariably move to the edge of the arena and come to rest at a small angle to the transparent wall. It was then presented with a single stimulus of a given size, speed and elevation, whose perceived direction of approach varied slightly due to the uncontrolled difference in angles at which the beetles faced the wall. The beetle was allowed 3 min to strike at the moving target (for slow-moving stimuli) or five passes of the stimulus across the beetle's midline. Trials were scored on a binary system, strike *vs* no response. A strike was scored when the beetle struck with its mouthparts against the transparent arena wall in the direction of the stimulus. In almost all cases of striking, the beetle followed the target around the arena wall, striking repeatedly. The rare (<10%) occasions when the beetle followed, but did not strike, were counted as no responses. Behavior across species did not vary.

Statistical model

To determine which of the stimulus parameters (size, speed and elevation) statistically influenced striking behavior, we

fitted the results of the prey selection experiments with a logistic general linear model (*GLM*; 1992, SAS Institute). All stimulus parameters and interactions between them, plus a dummy variable (see below), were used in an all-subsets regression for variable selection using SAS software. All assumptions of the regressions were met. The resulting variables were used to model striking behavior in Matlab (The Mathworks, Inc., Natick, MA, USA). The final statistical model of strike probability, P, had the form $P=1/(1+e^{-L})$, where $L=\beta_0+\beta_1(\text{size})+\beta_2(\text{speed})+\beta_3(\text{elevation})+\beta_4(\text{size}\cdot z)+\beta_5(\text{elevation}\cdot z)+\beta_6(\text{size}\cdot\text{elevation})+\beta_7(\text{size}\cdot\text{elevation}\cdot z)+\text{error}$; ($N=150$), where z is a factor for discriminating between targets above and below the horizon: $z=0$ if the elevation of the upper edge of the target >0, otherwise $z=1$.

Simulation model

The proportion (p) of beetles striking at prey stimuli was simulated as the product of three stimulus-dependent factors (F) according to the equation:

$$p = F_{\text{size}} \cdot F_{\text{speed}} \cdot F_{\text{elevation}} . \tag{1}$$

These factors were computed under the following assumptions. (1) There is an ideal absolute size (in cm) and speed (in cm s^{-1}) of prey; such targets elicit maximum striking behavior, and striking decreases as prey size and/or speed deviates from the ideal. (2) Tiger beetles use flat-world geometry to infer the absolute quantities from the angular quantities and determine strike tendency by discerning to what degree an experimental stimulus resembles the ideal (see Fig. 1). The simulation requires predetermined input of beetle height above the ground, and absolute ideal prey size and speed. Because no target may exactly match the ideal, and tiger beetles do pursue prey having a range of sizes (Pearson and Mury, 1979), the simulation must also strike at targets that differ from the ideal, and must have some rule for deciding strike tendency for these. We have a good independent estimate of what the ideal prey size should

be, but there are no data available on the relationship between variation in prey size and strike tendency for tiger beetles, i.e. how general is the search image. The simulation therefore uses an optimization algorithm to determine a total of nine coefficients that are associated with strike tendency for non-ideal targets. We are not so interested in finding out *via* optimization what these coefficients really are in the biological system – these should be acquired in formal prey-choice experiments – but rather in whether any such coefficients exist that allow the simulation to closely match the performance of real beetles. In addition to target size and elevation, we vary target speed. The simulation treats target speed as it does target size, and similarly finds coefficients for targets of non-ideal speed.

Below, we first describe how we chose the predetermined absolute values of the ideal absolute prey size and speed. Second, we describe the model's translation of the ideal prey size and speed from absolute values into angular values for comparison with the experimental stimuli. Third, we describe how strike tendency is reduced when the experimental stimulus differs from the ideal. Finally we describe how we arrived at the values that control this reduction in strike tendency toward non-ideal stimuli.

Rationale
Choosing ideal prey absolute size and speed

The model was provided with the beetles' eye-height above the ground, and ideal prey to which it would be most attracted (i.e. the means of the pseudo-normal distributions in Fig. 1). From ground level observations of hunting *C. hirticollis* we estimate eye height to be 8 mm. We imbued the model with the same ideal prey size and speed templates exhibited by real beetles. Pearson and Mury presented tiger beetles of seven species, having mean body lengths ranging from 6–20 mm, with live prey of a range of sizes (Pearson and Mury, 1979). They found that median prey length (*PL*) eaten was related to
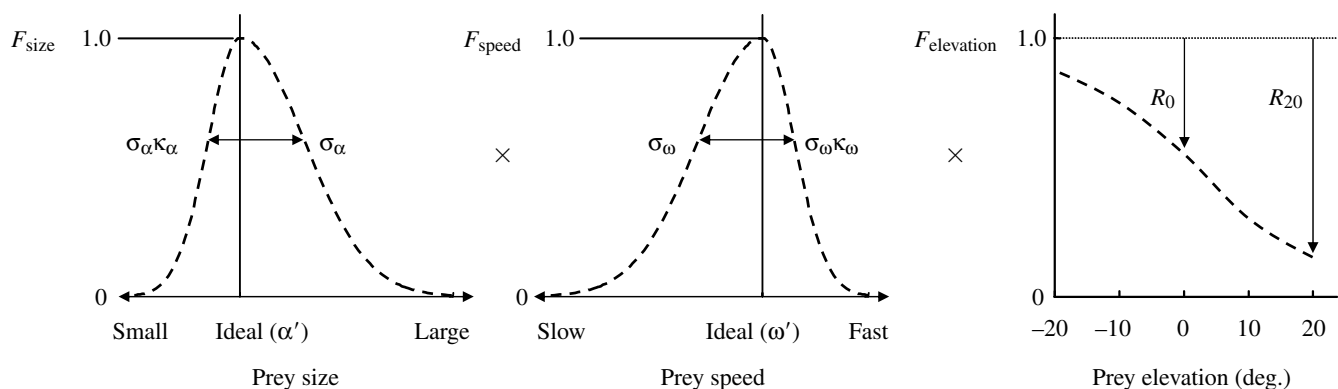
Fig. 1. Scheme of the simulation model. The model's response to the targets is the product of three factors relating the size, speed and elevation of the experimental target to those of an ideal target. For size and speed, the response is unity if the target is ideal, and falls off from unity with increasing deviation from the ideal, following a normal curve with standard deviation σ. The normal curve is symmetrical around the ideal if the constant κ=1, otherwise the response is asymmetrical about the ideal. For elevation, the response factor is 1–*R*, where *R* is an elevation-dependent variable between 0 and 1. These 'prey generalization parameters' σ, κ and *R* are determined by a least-squared means optimization. See text for further details.

beetle mandible length (*ML*) by the relation *PL*=7.69·*ML*–7.91 [r^2=0.92; units are mm; computed from table 1 in Pearson and Mury (Pearson and Mury, 1979)]. While their precise method of measuring of mandible length was difficult ascertain, those authors further showed that mandible length is related to body length (*BL*) as *ML*=0.*202BL*+0.027 (in mm; note: Pearson and Mury estimated this *ML/BL* relationship using 17 species). The mean *BL* (± s.d.) of our *C. hirticollis* was 13.07±0.66 mm. This corresponds to a mean *ML* of 2.67 mm, which in turn corresponds to an ideal *PL* of 12.6 mm. That *C. hirticollis* tend to prefer 12.6 mm prey is corroborated by the behavioral results of the present study. We transformed our experimental target sizes into their perceived absolute values using flat-world geometry and the empirical results showed that targets eliciting the highest strike proportion were 12.3 mm, which is very close to the 12.6 mm prey preferred by similar sized beetles in the Pearson and Mury study. Over all stimulus permutations our beetles tended to prefer slower-moving stimuli. Thus we chose an absolute speed of 3 cm s^{-1}, the slowest absolute speed to which any of our target angular speeds translated (using rearranged Eqn 3). This is a reasonable speed for a prey item, and significantly less than the speeds achieved by hunting beetles (Gilbert, 1997).

How angular dimensions of ideal prey vary with elevation

The elevation hypothesis states that the visual angular size and speed of an ideal prey item vary as a function of stimulus elevation and three constants:

$$\text{Ideal angular size } \alpha' = 2\arctan[(L\sin|E|)/2H] , \qquad (2)$$

$$\text{Ideal angular speed } \omega' = (S\sin|E|)/H , \qquad (3)$$

where *H*=the height of the beetle's eye above the substrate in cm, *L*=ideal prey size in cm, *S*=ideal prey speed in cm s^{-1}, and *E*=elevation in the visual field in degrees.

A problem arises with this formulation when stimulus elevation approaches the horizon (*E*=0°): both α' and ω' reach zero directly at the horizon, which creates the paradoxical situation in which the hypothetical ideal prey has zero size and speed. Furthermore, α' is smaller than the beetle's optical resolution limit in a narrow region above and below the horizon. To avoid this in the simulation, the ideal angular size was given a lower limit equal to the beetle's visual resolution, namely:

$$\alpha' = \begin{vmatrix} \alpha', & \alpha' \geqslant \Delta\phi \\ \\ \Delta\phi, & \text{otherwise} \end{vmatrix} , \qquad (4)$$

where $\Delta\phi$ is the interommatidial angle. Interommatidial angles have been mapped over the entire eye of *C. hirticollis* and aligned with the visual surround (Layne et al., 2003). For this model we used a vertical section through the front of the eye where the highest resolution is directed at the horizon. For similar reasons, ideal angular speed in this small region was computed as a function of the interommatidial angle (now

equal to ideal prey size in this small region) and absolute speed of the ideal prey:

$$\omega' = \frac{2S\tan\left(\dfrac{\Delta\phi}{2}\right)}{L} . \qquad (5)$$

Defining the strike factors F

The 'simulation beetle' assigned a strike proportion of unity to those stimuli that were of ideal angular size α'_E and angular speed ω'_E for their particular elevation (the subscript emphasizes that both α' and ω' vary with elevation). Thus, for stimuli corresponding to ideal prey, F_{size}=F_{speed}=1. Stimuli that differed from these ideals should produce a reduced strike proportion, but how reduced should the response be? The answer has to do with the generality of a tiger beetle's prey search image. We assumed strike proportion to be inversely proportional to the deviation of a stimulus from the ideal. Strike proportion was assumed to fall away from unity following a normal probability distribution centered on the ideal (Fig. 1). We allowed for the possibility that there may be an asymmetry in strike proportion on either side of the ideal. For instance, there may be a larger drop in strike proportion if the stimulus is smaller than the ideal size (rather than larger), or faster than the ideal speed (rather than slower). Thus, the size factor has the form of a lopsided, pseudo-normal distribution:

$$F_{size} = f(\alpha \mid \alpha'_E, \sigma_\alpha\kappa_\alpha) = \frac{1}{\sigma_\alpha\kappa_\alpha\sqrt{2\pi}} e^{\frac{-(\alpha-\alpha'_E)^2}{2(\sigma_\alpha\kappa_\alpha)^2}} , \qquad (6)$$

where α is the experimental stimulus size, α'_E and σ_α are the ideal mean and standard deviation of the normal distribution, respectively, and κ_α is a constant (see Fig. 1). The speed factor is likewise computed as Fspeed=$f(\omega|\omega'_E,\sigma_\omega,\kappa_\omega)$. The constant κ allows for an asymmetry in the effect of stimuli deviating to one side of the ideal or the other; κ_α=1 when $\alpha \geqslant \alpha'_E$ (stimulus is larger than ideal), otherwise $\kappa_\alpha \neq 1$, and κ_ω=1 when $|\omega \leqslant \omega'_E$ (stimulus is slower than ideal), otherwise $\kappa_\omega \neq 1$. This means that the width of the response curve for stimuli larger than ideal will be determined solely by σ_α, and the width of the response curve for stimuli smaller than ideal will be determined by a multiplier on σ_α, namely, κ_α. κ<1 produces a narrower normal distribution, and a greater reduction in striking for stimuli smaller or faster than ideal, while κ>1 produces a smaller reduction in striking for stimuli smaller or faster than ideal.

We have formulated the above ideal size and speed in a way that reflects at the horizon, i.e. they produce identical strike proportions as a function of elevation above the horizon and below. There is a good reason, however, to believe that this is not biologically realistic. For an observer that uses flat-world spatial geometry to produce perceptual visual size constancy, a target seen above the horizon should be interpreted either as an object larger than the observer itself or as airborne object; in either case such targets are likely to be unattractive as potential prey. Our empirical results showed this plainly. We

therefore come to the third factor in the model, $F_{\text{elevation}}$. Based on previous studies on the effect of elevation on prey selection and predator evasion (e.g. Schwind, 1980; Land and Layne, 1995; Gilbert, 1997; Layne et al., 1997; Layne, 1998), we hypothesized that, regardless of angular size and distance, targets at low elevations produce a higher strike proportion than those at high elevations. Thus, the elevation factor is $F_{\text{elevation}}=1-R_{\text{E}}$, where R_{E} is the reduction from unity in strike proportion for a given elevation; $0 \leqslant R_{\text{E}} \leqslant 1$ (see Fig. 1).

Setting generalization and elevation initial states

As discussed, model strike tendency depends on the width of the pseudo-normal distributions that define the reduction in strike proportion for the deviation of a given stimulus size and speed from the ideal, and on R_{E}, which sets the reduction in strike tendency at high elevations (see Fig. 1). The widths of the pseudo-normal distributions are determined by what we will call the prey generalization parameters: $\sigma_\alpha, \kappa_\alpha, \sigma_\omega$ and κ_ω. Unlike the absolute ideals, we have no pre-existing knowledge of what values these parameters should have. Instead, the model arrived at values *via* a simplex optimization algorithm [Matlab's *fminsearch* function; the algorithm is described elsewhere (Lagarias et al., 1998)]. The optimization function was seeded with arbitrary prey generalization parameter values. By adjusting the latter, the simulation algorithm sought to minimize the absolute difference between the model strike proportions and those measured empirically, summed over all 150 combinations of sizes, speeds and elevations tested. That is, it minimizes the term:

$$MD = \Sigma^\alpha \Sigma^\omega \Sigma^E \left| F_{\alpha,\omega E:\,\text{model}} - F_{\alpha,\omega E:\,\text{empirical}} \right|, \qquad (7)$$

where MD is what we call the model deficit.

Due to trapping by local minima, optimization algorithms may produce different results with different initial seed values. Thus, we ran the optimization 500 times, seeded with values drawn from uniform random distributions having the following ranges: σ_α, 10–100 (cm); σ_ω, 100–25 000 (cm s^{-1}); R_{E}, 0–1; κ_α and κ_ω, 0–2. After 500 test runs the model showed a strong tendency towards a minimum MD for a certain optimized parameter combination; the combination that produced the smallest MD was chosen as the best model.

Results

Prey selection by beetles and statistical description

The proportion of beetles attempting to strike targets across all stimulus combinations ranged from 0.13 to 0.75. The tendency to strike was neither uniform nor random across stimulus combinations. There was a tendency for beetles to favor small targets when they were near 0° elevation, and to favor large targets when they were at low elevations. Indeed, in several instances small targets near the horizon produced strike rates identical to those elicited by targets many times larger at the lowest elevations, and the five highest strike rates were observed over three different elevations and three different angular sizes. High elevation was characterized by

Table 1. *Results of logistic General Linear Model*

Term	Parameter	d.f.	Value	P
β0	Constant		0.5924	≪0.001
β1	Size	5	0.0040	0.6133
β2	Speed	4	–0.0012	0.0002
β3	Elevation	4	–0.0509	≪0.001
β4	Size z	5	0.0762	≪0.001
β5	Elevation z	5	0.1161	≪0.001
β6	Size elevation	20	0.0015	0.1358
β7	Size elevation z	20	–0.0046	0.0291

low strike frequency over all sizes and speeds. Of the parameters varied experimentally, striking showed the weakest relationship with stimulus speed.

The General Linear Model (Table 1) demonstrated significant effects on the probability of striking related to stimulus size, speed, elevation, and the interactions between size and z, and elevation and z. In the simulation model, the final optimized prey generalization parameters are σ_α=82.55, σ_ω=15817, R_{-20}=0.06, R_{-10}=0.28, R_0=0.35, $R1_{10}$=0.48, R_{20}=0.64, κ_α=0.31, κ_ω=0.03 (d.f.=7,142). The Least Absolute Deviation (LAD) of the simulation from the empirical data (LAD=MD/N) is 0.0570, meaning for any given stimulus permutation, the model differs from real beetles by just under 6%. This simulation performed nearly as well as the *GLM* (LAD=0.055), a fact borne out in the results of a regression model that tests whether the *GLM* or the simulation was a better predictor of the empirical data. Both had a significant effect ($P<0.001$), with the simulation having a slightly lower coefficient (0.41 compared with 0.62; F=239, d.f.=2, 147).

The values of σ_α, κ_α, σ_ω and κ_ω need explanation. Results from the 500 test runs (data not shown) revealed that σ_α and κ_α can have a wide range of values, as long as their product is about 25, and σ_α is much higher. This means that variation in perceived size of targets that are larger than ideal has little impact on striking, while targets smaller than ideal cause a clear drop-off in striking with decreasing size. Such asymmetric drop-offs are consistent with the beetles' biology as generalist predators that may take prey several times larger than themselves, e.g. caterpillars (C.G., unpublished), but spatial resolution of the visual system and prey handling abilities of the mandibles may ultimately limit responses to tiny objects. A similar relationship emerged for σ_ω and κ_ω, the generalization parameters that control the striking of targets of non-ideal speed. They can have an enormous range of values with little impact on the fit of the model, as long as their product is about 475. Thus, variation in the speed of slower-than ideal targets matters little, while striking clearly decreases as targets move faster than the ideal. Such asymmetric drop-offs are consistent with the beetles' biology as visual predators that also scavenge on stationary objects, but dynamics of the visual system may ultimately reduce the response to fast moving objects.

To illustrate the effect of size and elevation and their interactions with z, we show strike proportion related to size,
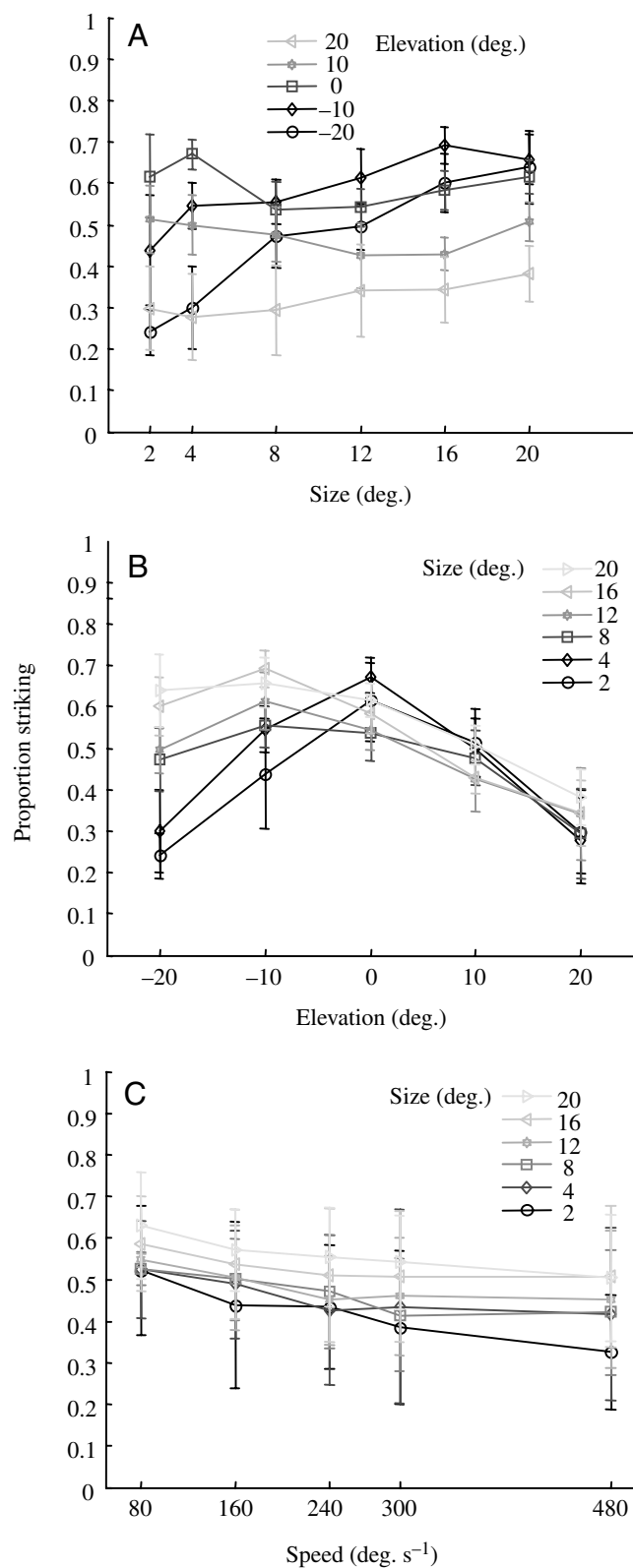
Fig. 2. Proportion of beetles attempting to strike targets. (A) Strike proportion is plotted against size, grouped by elevation, and averaged over the third variable, speed. (B) Strike proportion is plotted against elevation, grouped by size, and averaged over speed. (C) Strike proportion plotted against speed, grouped by size, and averaged over elevation. Values are means ± 1 s.d.

grouped by elevation and also strike proportion related to elevation, grouped by size, both data sets are averaged across all speeds (Fig. 2A,B). The effect of speed is shown grouped by size and averaged over elevation (Fig. 2C); its effect is similar when grouped by elevation. In addition, to clearly see the effect on striking of varying target size, speed and elevation without averaging over any significant variables, we sliced the four dimensional stimulus space of the simulation along the three stimulus axes, in the planes corresponding to the exact stimulus values tested (Fig. 3). The simulation captures major trends that readily yield to mechanistic explanation, although there are also small-scale variations in the response that are more difficult to decipher.

There is a clear increase in overall response to stimuli moving closer to the horizon (0° elevation) or just below, with the response drop-off above 0° being sharper than below. Indeed, elevation·z was the most important single statistical factor in explaining strike tendency (Table 1). This means there is a strong difference in the effect of elevation above and below the horizon. An increase in stimulus elevation from –20° to 0° increased strike probability by 30% on average, while further raising the stimulus from 0° to 20° decreased strike probability by 44%. Elevation alone is a significant factor, because of a trend towards higher strike proportions at low elevations. It had much less explanatory power overall, however, because striking was maximal at middle elevations (–10°, 0°), with minima above and below. The fact that elevation·z explains the most variance shows that elevation, as a generic notion, is the most important factor in determining the beetle's strike probability.

Size taken alone, like elevation, is less important than other factors, and in fact is not significant: a tenfold increase in stimulus size (2° to 20°) increases strike probability by only 30% on average. However, there is a strong difference in the effect of size above and below the horizon. The interaction size·z is clearly seen in Fig. 2A,B and Fig. 3B,C, where below the horizon there is a clear tendency to strike larger targets, but not above. Furthermore, there is an interaction between size and elevation below, but not above, the horizon, as indicated by the interaction size·elevation·z. At –20°, –10° and 0° there is a tendency for the most favorable stimuli to shift from large to small as elevation increases. This is precisely the pattern we would expect if the elevation hypothesis were in effect.

The influence of speed is generally the same for all sizes and elevations, and on both sides of the horizon (Fig. 2C, Fig. 3B). There is an obvious decrease in response with increasing speeds, though the quantitative effect is subtle: increasing speed by a factor of 6 (80 to 480 deg. s^{-1}) decreased strike probability by only 21%. Note again in Fig. 3B the clear shift from striking at large sub-horizontal stimuli to striking at small stimuli near the horizon.

The data slices at the tested stimulus speeds (Fig. 3C) most clearly show the strong interaction between size and elevation in eliciting strikes. Each panel shows the same pattern: there is a high-response band extending from 0° elevation for small sizes, to –10 or –20° elevation for large sizes. Note the lack of
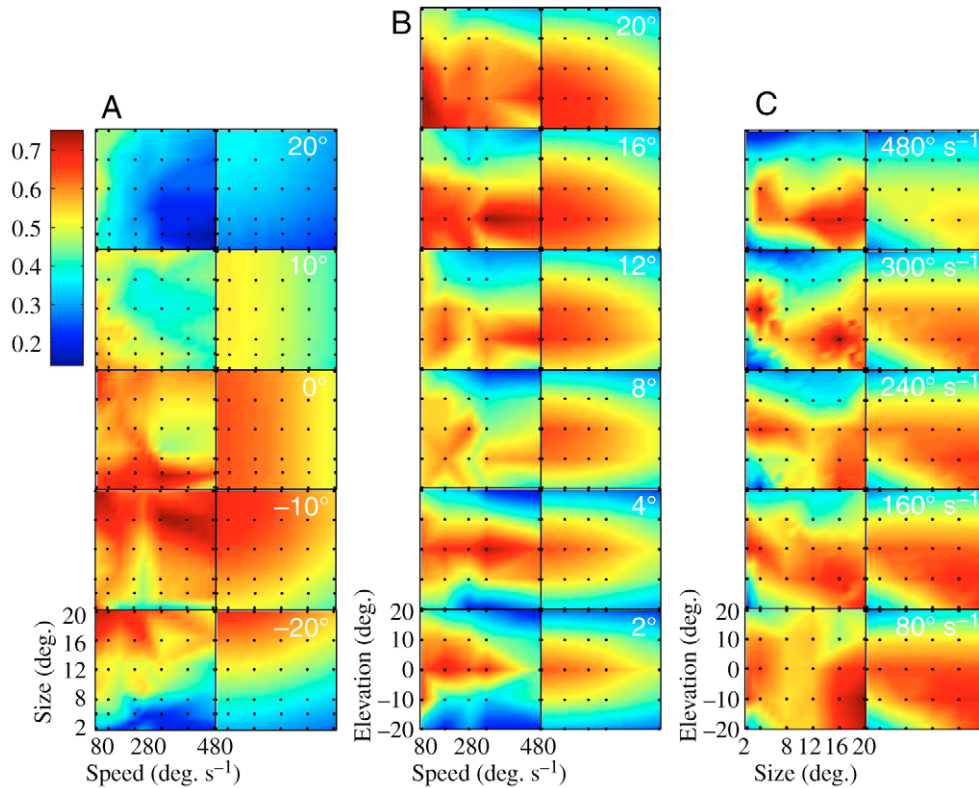
Fig. 3. Panels showing four-dimensional stimulus space sliced at planes corresponding to tested target elevations (A), sizes (B) and speeds (C). Strike proportion for all panels is indicated by the color bar. Loci of tested values are indicated by black dots; values between dots are filled by cubic interpolation. Axis conventions for A–C are in lower left panels. Empirical results are shown in the left column of each pair, and simulation model results in the right column.

any strong between-panel trend, indicating the modest effect of variation in speed over the ranges of values used.

Discussion

Tiger beetles preferred targets of large angular size low in the visual field, and the size of favored targets decreased with increasing elevation. Striking at targets above the horizon was markedly lower, with a slightly greater decrease for large targets than small. There is thus a distinct pattern in the beetles' tendency to strike that is non-uniform and non-random. The pattern can be modeled statistically, but such a statistical description does not speak to the underlying biological/perceptual processes. We posit that the observed pattern strongly supports the 'elevation hypothesis' of distance perception, which states that one may, after some assumptions about the topography of the substrate and whether objects rest on it, use elevation as a proxy for distance which, taken with angular size, allows size constancy, i.e. the correct assessment of absolute size despite differences in apparent angular size. As evidence for this position we offer a simulation of a beetle that prefers to strike prey of a predetermined absolute size and speed, and uses elevation to convert angular visual size to absolute size and speed. The simulation matches the empirical data closely and describes the data as well as the statistical model. The degree to which this result can be considered an affirmation of the use of elevation as a distance cue depends on two things: the extent to which simulation of a process is evidence, and the extent to which the elements of our simulation model reflect those of the real biological system.

Do simulations demonstrate sufficiency?

The degree to which accurate simulation of empirical data may be considered evidence that the components of the model describe those of the physical system is a specific form of a longstanding critique of science in general, namely, the underdetermination inherent in scientific experimentation (Duhem, 1951; Quine, 1951). The argument, simply put, is that any conclusion drawn from the results of an experiment is but one of many logically possible conclusions and therefore all conclusions are, at the very least, weakened. The debate over this issue is ongoing, but many philosophers of science now accept the moderate and pragmatic position that even if there are numerous logically possible reasons for the outcome of an experiment, it does not follow that all options have the same rational merit (cf. Curd and Cover, 1998). Applied to simulation, this means that it falls upon the creator of the model to professionally and responsibly argue its merit (Schmidt, 1987; Laudan, 1990; Law and Kelton, 1991; Kleindorfer, 1993; Kleindorfer et al., 1998; Robinson, 1999), particularly with respect to alternatives. Several simple alternative hypotheses to our model are that there is a direct relationship between striking and either target size, the number of ommatidia subtended by targets, or the number of ommatidia stimulated by the leading edge of the moving targets. These are quickly dismissed by the fact that the most favorable target at different elevations had a different angular size (Fig. 3), while all of these alternative

hypotheses predict that the largest target would be favored. A better alternative is that favored targets stimulate a certain number of ommatidia (e.g. Zeil et al., 1986; Schwind, 1978; Schwind, 1980; Schwind, 1983; Zeil and Al-Mutairi, 1996). This could account for the fact that preferred target size decreases near the horizon, since optical axis density is highest in this area (Layne et al., 2003). In fact, this hypothesis is basically equivalent to the elevation hypothesis, if vertical resolution varies with elevation in the same way that angular size does for objects at different distances on the ground (Zeil et al., 1986). However, this relationship does not hold for vertical resolution in our species. Furthermore, there is no peak in strike proportion for any particular number of subtended ommatidia; targets eliciting the five highest strike proportions subtended from 9 to 161 ommatidia (overall range: 1–210). Similarly, the number of ommatidia stimulated per second by leading edge of targets also shows no peak in strike proportion; targets eliciting the five highest strike proportions stimulated from 276 to 3240 ommatidia per second (overall range: 20–5040).

To what degree does our model test the 'elevation hypothesis'?

Below the horizon the model accurately tests the hypothesis that tiger beetles vary their prey size preferences in a manner consistent with using elevation as a distance cue, and subsequently using this to convert angular to absolute size. This is a reasonable hypothesis, since despite the beetles' small size, their eyes are theoretically capable of providing this information over a useful range. The lower extent of the frontal visual field is at least –65°, so near objects seen in front, including our target stimuli, are visible at close range. As for longer distances, for an 8 mm-tall beetle with a minimum vertical interommatidial angle of 1.05° in the front of the eye (Layne et al., 2003), the farthest intersection of an ommatidial optical axis with the substrate is 8 mm/tan(1.05°)=436 mm. In reality the useful range is probably not this far due to, e.g. inconsistencies in substrate topography, but certainly covers normal prey-striking range. Gilbert found the mean distance at which walking fruit flies elicited tiger beetle attacks was 79.4±9.1 mm (mean ± s.d., N=16), with a range of 47.8–125.8 mm (Gilbert, 1997). This was done in a 300 mm arena, so very large distances were not available. In a less controlled experiment, Swiecimski tested the salience of various prey items in a larger space and found foraging distances of 176.1±67.9 mm (mean ± s.d., N=19) with a range of 65–250 mm (Swiecimski, 1957).

There are, however, two ways in which the elevation hypothesis is not strictly embodied by our model. First, near the horizon the model uses the beetles' minimum visual resolution as the ideal size, rather than the strict mathematical definition of objects at this elevation, which is infinitely small. Our observations show that targets in this area do elicit striking, and the model is designed to accommodate this observation.

Second, and more importantly, the model allows for striking at supra-horizontal stimuli. This represents a major deviation from the elevation hypothesis, especially if it is applied to small predators, because such targets should not have a computable size, and if anything should be considered threats. Experience with tiger beetles in the laboratory, however, shows that after several days they cease to attempt to flee from approaching humans, and will eventually even accept prey offered from above with forceps. None of the beetles in this study attempted escape from the targets. This is very different from their behavior in the field, where their vigilance makes them very difficult to approach, and the best way to do so is, in fact, to crouch low to the ground so as to occlude their dorsal visual hemifield as little as possible. Thus, they quickly become adapted to lab conditions. We do not know whether this changed their responses to the experimental targets.

A key point here is that in the very few tests of the elevation hypothesis, both sub- and supra-horizontal stimuli have never been used, so it is not known how even animals that compute distance from declination below the horizon might react to targets above it. The only other animals having clear visual adaptations for living in a flat world that have been tested with supra-horizontal stimuli, semiterrestrial crabs, apparently make no judgment of distance to objects at high elevations (Zeil et al., 1989; Land and Layne, 1995; Layne et al., 1997; Layne, 1998; Hemmi, 2005a; Hemmi, 2005b), and instead treat such objects categorically as threats. Humans can use declination below the horizon as a distance cue (Ooi et al., 2001). In the human case the perceived increase in distance with increasing elevation below the horizon does not continue above the horizon. In fact, as demonstrated by the well-known moon illusion (Hershenson, 1989), the situation is reversed: the moon appears to grow closer as it rises in the sky. This leads, then, to the inevitable perception that the moon must grow smaller as it rises, since its angular subtense remains constant (Kaufman and Kaufman, 2000). Thus, in humans, as in our model, the perceptual phenomenon does apply above the horizon, as a sort of mirror image of what happens below. Interestingly, the most preferred targets for the five tested elevations from –20° to +20° have sizes of 20°, 16°, 4°, 4° and 12°, i.e. they seem to reverse near the horizon This is a little misleading, because the preference levels are much lower above the horizon, but the pattern is qualitatively similar to what humans perceive.

In the end, the model contains deviations from the strict form of the elevation hypothesis because tiger beetles do not use a strict form. They appear, however, to use it to some degree for estimating distance, likely in combination with other cues, as is certainly the case for humans and frogs.

List of abbreviations

BL	body length
E	elevation
H	beetle eye height above the substrate
L	absolute ideal prey size
ML	beetle mandible length
p	proportion

PL	prey length
S	absolute ideal prey speed
α	experimental stimulus angular size
ω	experimental stimulus angular velocity
α′	ideal stimulus angular size
ω′	ideal stimulus angular velocity
σ	model response standard deviation
κ	constant scaling factor on σ
z	elevation coefficient

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