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A tiger beetle's pursuit of prey depends on distance

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Abstract

Tiger beetles pursue prey by adjusting their heading according to a time-delayed proportional control law that minimizes the error angle (Haselsteiner *et al* 2014 *J. R. Soc. Interface* **11** 20140216). This control law can be further interpreted in terms of mechanical actuation: to catch prey, tiger beetles exert a sideways force by biasing their tripod gait in proportion to the error angle measured half a stride earlier. The proportional gain was found to be nearly optimal in the sense that it minimizes the time to point directly toward the prey. For a time-delayed linear proportional controller, the optimal gain, k , is inversely proportional to the time delay, τ , and satisfies $k\tau = 1/e$.

Here we present evidence that tiger beetles adjust their control gain during their pursuit of prey. Our analysis shows two critical distances: one corresponding to the beetle's final approach to the prey, and the second, less expected, occurring at a distance around 10 cm for a prey size of 4.5 mm. The beetle initiates its chase using a sub-critical gain and increases the gain to the optimal value once the prey is within this critical distance.

Insects use a variety of methods to detect distance, often involving different visual cues. Here we examine two such methods: one based on motion parallax and the other based on the prey's elevation angle. We show that, in order for the motion parallax method to explain the observed data, the beetle needs to correct for the ratio of the prey's sideways velocity relative to its own. On the other hand, the simpler method based on the elevation angle can detect both the distance and the prey's size. Moreover we find that the transition distance corresponds to the accuracy required to distinguish small prey from large predators.

1. Introduction

Visually guided pursuit behavior [1, 3–10] provides a rich experimental playground to examine connections between behavior and neural computations [11–16]. In spite of the increasingly sophisticated understanding of animal behavior and their neural systems, simple questions, such as how animals measure distance or generally how they extract relevant information from the visual field, do not have clear-cut answers [8, 17–20].

Here we look for clues as to whether tiger beetles use distance information during their pursuit of prey. Tiger beetles are fast diurnal predators capable of chasing prey using closed-loop visual guidance [6]. Because their pursuit takes place in a two-dimensional plane, it provides a convenient system for behavioral analyses. The initial analysis of a tiger beetle's pursuit dynamics elicited by a moving bead showed that the beetle uses a proportional control law in which the angular position

of the prey in the beetle's visual field drives its angular velocity with a delay of half a stride period, about 28 ms [1]. This suggests a physical interpretation of the observed control law: to turn toward its prey, the beetle on average exerts a sideways force proportional to the angular position of the prey measured a half stride earlier. The control gain is close to the critical value, $k = 1/\tau e$, with τ being the time delay. The derivation of the critical value is given in reference [2]. This further suggests that the beetle reorients itself toward the prey in the least amount of time without exciting oscillations.

In this paper we offer clear evidence that tiger beetles adjust their control gain based on distance to the prey. After its initiation, the beetle follows the prey with sub-critical gain. When the prey is within a radius of about 10 cm, the beetle increases its gain to a near-crit-

ical value, and when the prey is within a few strides, the beetle increases its gain again to catch the prey.

2. Previous results

We first summarize the experiments and the control law analysis on which this work is based [1]. Tiger beetles' pursuits of a prey dummy, a high-contrast black sphere of 4.5 mm diameter glued to a nylon monofilament, were digitally filmed at 250 frames per second with 1024×1024 resolution using a high-speed video camera (Phantom v. 5.0, AMETEK, USA). The digital greyscale images were imported into MATLAB (MathWorks, Natick, MA, USA) for analysis. The experiments were performed in a cylindrical arena (33 cm diameter, 18 cm tall). The walls were patterned alternately with black (4 mm) and white (12 mm) vertical stripes to provide contrast for the beetle moving through the arena. Six different beetles were tested and each performed multiple chases. Each beetle was around 13 mm long; they were acclimatized to the arena for 10 min before the prey dummy was introduced by lowering it from above and moving it across the floor by hand. The positions and orientations were extracted using our image analysis algorithm. Figure 1(a) shows the spatial patterns of the beetle and the prey during a typical case in the lab frame. The beetle is represented by a small rod with the head marked by a dot and the prey is depicted by an asterisk. The pattern shows that the beetle orients itself so that the prey is directly in front of it by aligning the body axis (solid line) with the line of sight to the prey (dashed line). The active orientation of the body is described by $\omega_B(t) = K\theta_e(t - \tau)$, where $\omega_B = \dot{\theta}_B$ is the body angular velocity, and θ_e the prey's angular position relative to beetle's body-axis; see figure 1(c) for variable definitions. Figures 1((d)–(e)) show that the correlation coefficient is maximal at $\tau = 28$ ms, and the corresponding gain in the proportional control law is $K = 12.7 \text{ s}^{-1}$. As has been noted previously, given a time delay of 28 ms the gain value is close to the optimal value, $K = 1/\epsilon\tau \approx 13.1 \text{ s}^{-1}$.

3. Current results

3.1. Distance dependence of the proportional gain

The first clue that the proportional gain K depends on the distance can be seen in figure 1(a) when the beetle is close to the prey. After time step 8, the beetle is seen to overshoot in its corrections in the error angle, suggesting an increased gain as the beetle gets closer to the prey. This observation led us to systematically examine distance-dependence of the gain during these pursuit dynamics. Our analysis reveals two transitions in the gain: one at $d \sim 10$ cm in addition to the transition at short distance, $d \sim 2$ cm (figure 1(f)).

To examine the distance dependence of the delay $\tau(d)$ and gain $K(d)$, we apply the same analysis as described for figures 1((d)–(e)) to a series of data subsets, where each subset is binned according to the

distance to the prey. The time delay τ is nearly constant at 28 ± 4 ms over the range of observed distance, from $d = 1$ to $d = 12.5$ cm. We thus keep the time delay fixed at $\tau = 28$ ms throughout the rest of the analysis.

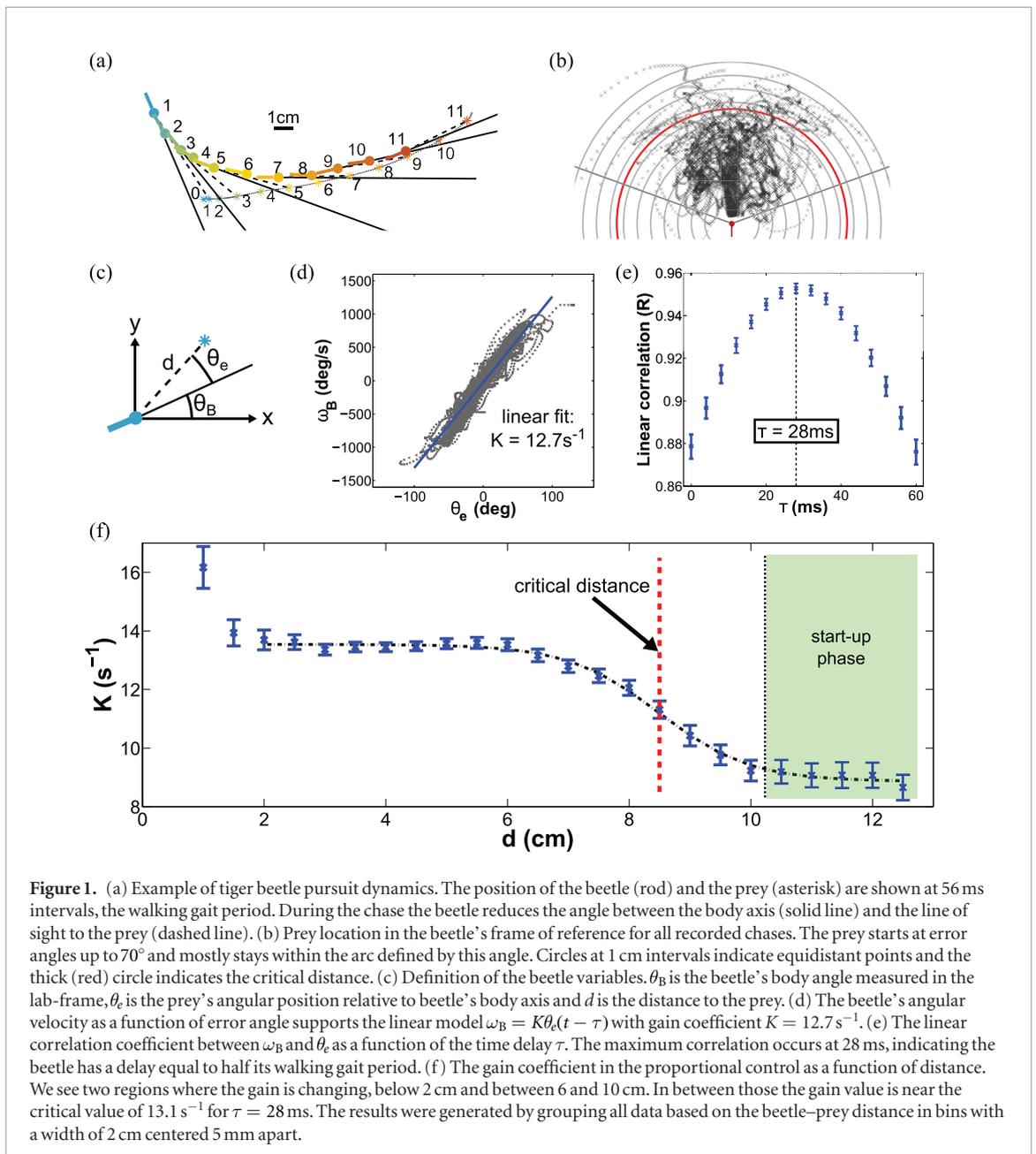
The main result is summarized in figure 1(f), which shows the dependence of the gain on distance. When the tiger beetle is far from the prey, beyond 10 cm, it uses the lower gain of $K = 9.0 \text{ s}^{-1}$. Below 10 cm, the gain increases with decreasing distance and reaches a near-critical value $K = 13.5 \text{ s}^{-1}$ at $d \sim 6$ cm. $K(d)$ can be well fitted by a hyperbolic tangent function between $d = 2$ cm and $d = 12$ cm, with the middle of the transition occurring at the critical distance $d^* = 8.5$ cm. At small distances below 2 cm, when the prey is within reach, the beetle increases its gain sharply to catch the prey.

Our next question is whether the distance is a direct cause of the change in K , as opposed to an indirect cause via other intermediate variables. We plot all the relevant kinematic variables in the system as a function of distance in figures 2((a)–(c)). At $d \geq 10$ cm the beetle increases its velocity, v_B , to initiate the chase. In contrast the beetle's angular velocity, ω_B , initially decreases as v_B increases. However we note that over the range 6–10 cm, where the transition in gain occurs, both of these quantities are nearly constant while $K(d)$ increases. It is therefore unlikely that they are the cause of the observed gain increase. Interestingly, the combination of velocity and angular velocity leads to a nearly constant sideways acceleration, $a_{\perp B} = v_B \omega_B$ (figure 2(c)). This suggests the chases are constrained by the maximal sideways acceleration of the beetle [1].

One can further ask whether the increase in gain might be correlated to the initial start-up phase, where the beetle accelerates. To exclude the initial phase, we selected chases that started with a beetle–prey distance of 6, 8 or 10 cm (± 1 cm) (figure 2(d)). We see that the 10 cm data show the gain transition occurring around the same 8.5 cm. The chases that start at 6 and 8 cm bypassed the lower gain, $K = 9.0 \text{ s}^{-1}$, but started directly with a higher gain. This suggests that the gain increase is not due to a start-up phase.

Finally, another potential candidate for the cause of increase in K is time-to-capture (TTC), a quantity that has been studied in the control of escape behavior [21–26]. If we assume a constant approach velocity, TTC and distance would be proportional to each other. This could have led us to interpret a gain dependence on TTC as a dependence on distance. To differentiate the two scenarios, we grouped our data according to TTC, which was computed as the beetle–prey distance divided by its time-derivative (figure 2(e)). The result shows that the gain does not depend on TTC and, in particular, there is no sharp increase at the small distance, where we would expect TTC would play a role.

All of these observations suggests that the distance to prey is the direct cause of the change of the control gain.



3.2. Methods for distance detection

Insects use a variety of visual cues for distance detection [27]. Many studies have postulated mechanisms for distance detection in a variety of insects [28–33]. Examples include the peering motion used by locusts [34], the long-range distance detection used by honeybees [31], and the head movements used by dragonflies to determine the apparent size of a moving prey [20]. In the case of tiger beetle larvae it was shown that they possess a distance-sensitive visual interneuron [35]. It thus seems plausible that the tiger beetle can determine the distance to the prey using visual cues.

Although it will require further experiments to tease out the means by which tiger beetles detect the distance to their prey, we can at least examine the predictions from different methods and compare with the data we have. For this, we analyze two candidates for distance measurements used by insects: one based on motion parallax [34] and another on the elevation angle of the prey [36].

3.2.1. Motion parallax

Like many other insects, tiger beetle vision is monocular, as the visual fields of their two eyes do not have a large overlap [33, 37]. The beetle can however move its head back and forth to simulate binocular vision to detect distance, a strategy known as motion parallax [28, 30, 34, 38]. The distance d can be measured by the amplitude of the side-to-side motion of the observer, A , and the change in the angular position, α : $d = A/\tan(\alpha/2)$ (figure 3(b)). Recent work further suggests that insects have developed specific movement patterns to facilitate distance measurement through motion parallax [12, 14, 32, 39].

The above simple formula applies to a stationary prey and an observer moving only perpendicular to the line of sight, whereas in a pursuit both are moving freely. This raises two interesting questions: does the beetle measure and make use of the prey's velocity, and does it subtract its own velocity? For our analysis,

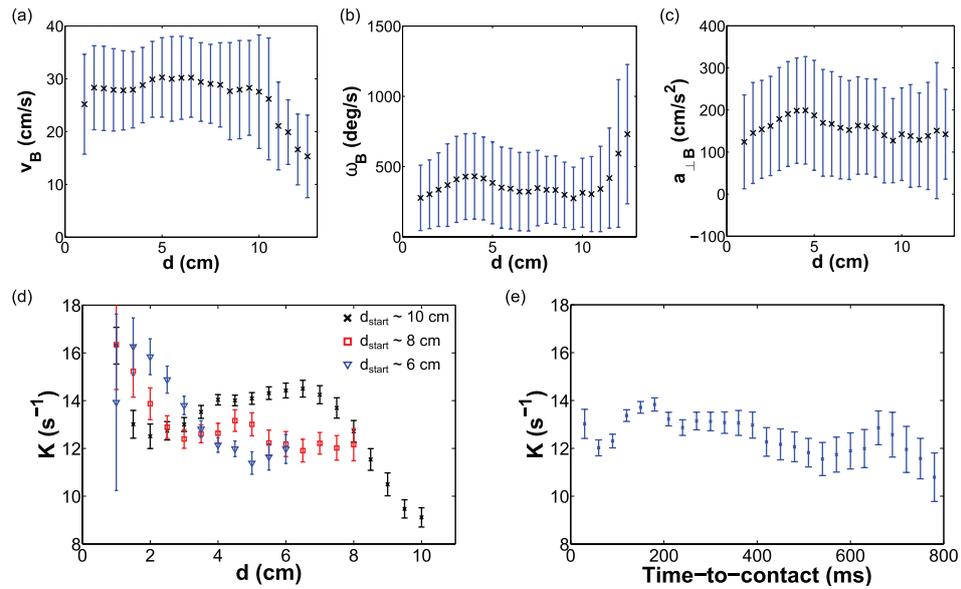


Figure 2. ((a)–(c)) Distance dependence of the absolute value of the beetle’s velocity, angular velocity and sideways acceleration, respectively. Each shows the mean value and standard deviation of all measurements, without removing the stride oscillations, within the same bins as in figure 1(f). The velocity and angular velocity of the beetle show a start-up phase beyond $d \sim 10$ cm; however over the distance between 6 and 10 cm, the gain transition region, both variables are approximately constant. In contrast to this, $a_{\perp B} = v_B \omega_B$ is roughly constant over the full range of distances, suggesting that the beetle is using a constant sideways force to reorient its body [1]. (d) Using only the chases that started at a beetle–prey distance of around 6, 8 or 10 cm, we recreate figure 1(f). We notice that for the 10 cm start distance the double transition is at the same location. For the 6 and 8 cm start distance data there is no double transition. This indicates that the chase start-up phase does not cause the transition in K . (e) The gain coefficient in the proportional control as a function of time-to-contact (TTC). The gain fluctuates around the average value of $K = 12.7 \text{ s}^{-1}$, but there is no sharp transition based on TTC. This implies the beetle does not use TTC to modulate its proportional gain.

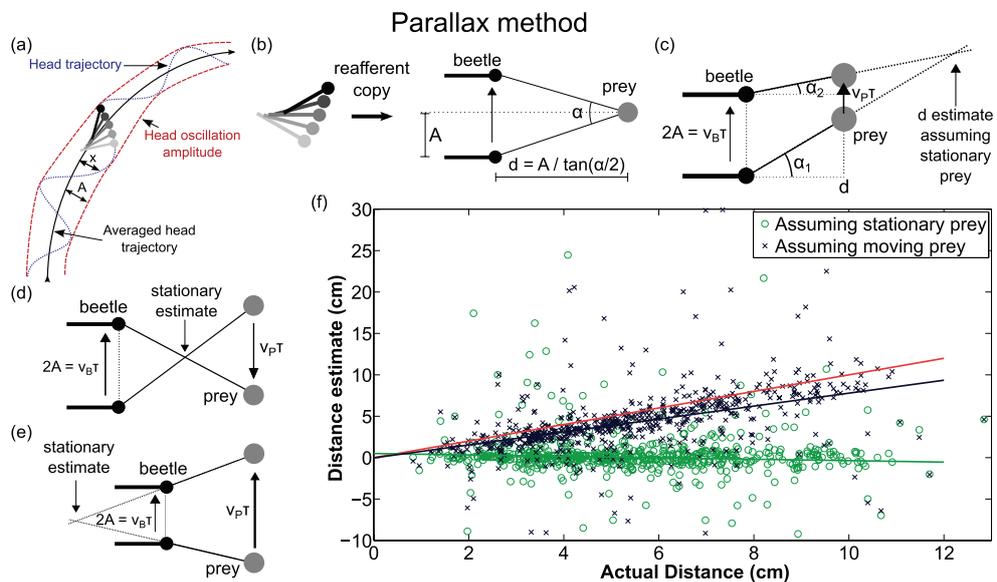
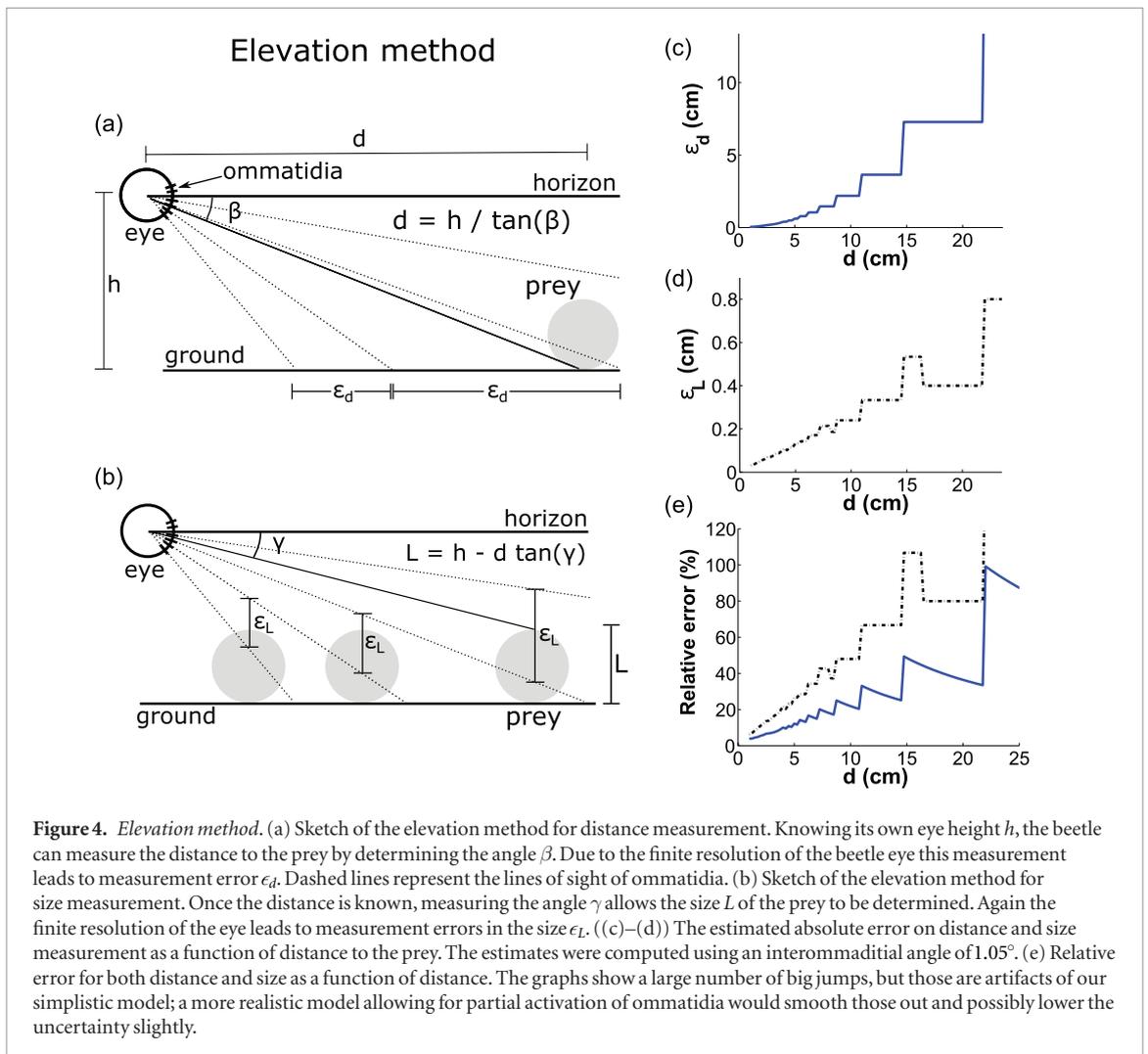


Figure 3. *Motion parallax method.* (a) Sketch of a head trajectory during a chase. Due to the walking gait the head makes a natural sway. The head trajectory can be described as an oscillation on the averaged trajectory. (b) Sketch of the parallax method for a stationary prey. Assuming the beetle can negate the effect of its own motion it would see the prey at different angles during one head oscillation. The angle α can easily be used to compute a distance to the prey. (c) Sketch of the motion parallax method in the case where the prey is moving. The estimated distance, which assumes a stationary prey, needs to be corrected to obtain the actual distance d . (d) Sketch of a case where the estimated distance is very short. (e) Sketch of a case where the estimated distance is negative. (f) Distance computed from measured angles α using the recorded image data. Green circles are used to indicate the distance based on the stationary prey assumption and black crosses for the corrected distance assuming a moving prey. Trend lines, in matching colors, are fits through the data. The red line indicates a perfect measurement.



we will consider two possibilities. In the first case, we assume that the beetle does not make use of the prey's velocity. In the second case, we assume that the beetle can measure the sideways velocity of the prey and take it into account for the distance measurement. Both cases also assume that the beetle can correct for its own body rotation.

To work out the distance detection for a moving prey, we note the geometry (figure 3(c)),

$$v_B T = v_P T + d \tan \alpha_1 - d \tan \alpha_2 \quad (1)$$

where v_B and v_P are beetle and prey velocities, respectively, and T is the time of a half stride. In the case when $\Delta\alpha_{12} = \alpha_1 - \alpha_2$ is small,

$$d \sim \frac{2A}{\Delta\alpha_{12}} \left(1 - \frac{v_P}{v_B} \right) \quad (2)$$

Note that when $v_P = 0$, it reduces to the formula for the stationary prey case, as expected. The correction due to prey movement appears in the form of $\frac{v_P}{v_B}$. If the beetle uses this distance estimate, it needs to estimate the prey's velocity relative to the beetle's.

In figure 3(f), we compare these above two estimates with the data. The formula that takes account of the sideways prey velocity gives a reasonable estimate of the actual distance, while the formula assuming a

stationary prey clearly fails. The latter over-predicts the distance if the prey is slower and moves in the same direction as the beetle (figure 3(c)), while it under-predicts if the prey moves in the opposite direction to the beetle (figure 3(d)). In case where the prey moves faster than the beetle, the formula can even give negative distance (figure 3(e)). These led us to conclude that in order to measure the distance using motion parallax, the beetle must take into account the prey's velocity and, more specifically, it needs to measure the velocity ratio v_P/v_B .

3.2.2. Distance based on elevation angle

Another potential method that tiger beetles can use for distance detection is to measure the elevation angle of the prey (figure 4) [36]. This elevation method exploits the idea that the elevation, or vertical position, of the prey on the visual field is directly related to the distance. This simple method has a few advantages. The visual angle can be readily determined by a compound eye. By measuring the angles both to the bottom (β) and top (γ) of the prey, the beetle can estimate both the distance to the prey (d) as well as its size (L). This distance measurement is less noisy compared to motion parallax, because the prey's sideways stride oscillation does not affect the elevation angle.

In order to find out whether the distance given by this method can be used during the beetle's pursuit, we calculate the accuracy of such measurements. The error in the distance measurement, ϵ_d , is given by the angular resolution of the eye, which is associated with the finite size of the ommatidia. The error increases with the distance. At a distance $d = 8.5$ cm, where the transition occurs, the error is around 20%, or 1.7 cm which, interestingly, coincides with the width of the transition region seen in $K(d)$. A similar calculation also gives the error associated with the estimated size of the prey, ϵ_L . At $d = 15$ cm, $\epsilon_d \sim 80 - 120\%$. This implies that it would not be wise for the beetle to chase a prey, as it would run the risk of chasing objects larger than its own size, including predators.

Our error calculations are based on the geometry shown in figure 4: $d = h/\tan(\beta)$, where h is the beetle's height, and β is the angle downward to the ground where the prey is. If the beetle further measures the angle from its eye to the top of the prey, γ , it can also determine the size of the prey, $L = h - d \tan(\gamma)$ (figure 4(b)). The uncertainty in distance, ϵ_d is due to the angular resolution in β ,

$$\epsilon_d = d_{\max} - d_{\min} = \frac{h}{\tan(\theta_{\min} \cdot \lfloor \frac{\beta}{\theta_{\min}} \rfloor)} - \frac{h}{\tan(\theta_{\min} \cdot \lceil \frac{\beta}{\theta_{\min}} \rceil)}. \quad (3)$$

For angular resolution, we use the value of the minimum vertical interommatidial angle of $\theta_{\min} = 1.05^\circ$, and for the beetle height, we use $h = 8$ mm [36]. The brackets in the first and second terms in equation (3) indicate rounding down and up to the next integer. The uncertainty in size ϵ_L is based on the same idea, but depends on β , through d_{\min} and d_{\max} , and on γ :

$$\epsilon_L = L_{\max} - L_{\min} = d_{\min} \tan(\theta_{\min} \cdot \lfloor \frac{\gamma}{\theta_{\min}} \rfloor) - d_{\max} \tan(\theta_{\min} \cdot \lceil \frac{\gamma}{\theta_{\min}} \rceil) \quad (4)$$

4. Conclusion

In summary, our analysis shows that tiger beetles adjust their gain in the control law during their pursuit of prey. We show that the gain depends on the distance, instead of other variables. The transitions occur at two distances: one near capture, and the other at a distance of about 8.5 cm. We further analyzed two potential methods that a tiger beetle can use for distance detection: motion parallax and elevation angle. We find that, in order for motion parallax to explain the data, the beetle needs to correct for the ratio of the prey's velocity relative to its own. The method based on elevation angle can simultaneously detect the prey's distance and size. The accuracy of distance detection depends on the beetle's visual acuity. Our analysis suggests an explanation for the typical distance at which the beetle

initiates its chase. Beyond this distance, the beetle would run the risk of chasing after a large predator due to the error in determining the size of the moving object. We suspect that the distance dependence in the pursuit of prey may also be present in other insects that use visually guided control laws, and we hope this work will stimulate further investigation in quantifying the role of distance detection in an animal's pursuit dynamics.

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